Theo. Gill

DEVONIAN FISHES

OF IOWA

BY CHARLES R. EASTMAN

From Iowa Geological Survey, Vol. XVIII
ANNUAL REPORT, 1907, pp. 29-386

DES MOINES
PUBLISHED FOR IOWA GEOLOGICAL SURVEY
1908

Theo. Gill
Jan '09.

IOWA

GEOLOGICAL SURVEY

VOLUME XVIII

ANNUAL REPORT, 1907

WITH

ACCOMPANYING PAPERS

SAMUEL CALVIN, Ph. D., State Geologist
JAMES H. LEES, Assistant State Geologist

DES MOINES
Published for Iowa Geological Survey
1908

DES MOINES:
EMORY H. ENGLISH, State Printer
E. D. CHASSELL, State Binder
1908

GEOLOGICAL BOARD

His Excellency, A. B. Cummins.....Governor of Iowa
Hon. B. F. Carroll.....Auditor of State
Dr. Geo. E. MacLean.....President State University of Iowa
Dr. A. B. Storms.....President Iowa State College
Dr. Samuel Calvin.....President Iowa Academy of Sciences

GEOLOGICAL CORPS

Samuel Calvin	State Geologist
James H. Lees	Assistant State Geologist
Neilie E. Newman	Secretary
Charles R. Eastman	Special Assistant
S. W. Beyer	Special Assistant
W. H. Norton	Special Assistant
T. H. Macbride	Special Assistant
B. Shimek	Special Assistant
M. F. Arey	Special Assistant
I. A. Williams	Special Assistant
S. W. Stookey	Special Assistant
Henry Hinds	Special Assistant

CONTENTS

LIST OF ILLUSTRATIONS

DEVONIAN FISHES OF IOWA

BY

Charles R. Eastman, Harvard University

"Aus der Natur, nach welcher Seite hin
man schaue, entspringt Unendliches."
—*Goethe.*

DEVONIAN FISHES OF IOWA

BY

CHARLES R. EASTMAN

CONSPECTUS

"Die Natur ist das einzige Buch, das auf allen Blättern gewissen Inhalt bietet."—*Goethe.*

DEVONIAN FISHES OF IOWA

I.

Aim and general outlook of palaeontological inquiry, and relations of palaeichthyology to biology

"Die Weisheit ist nur in der Wahrheit."—*Goethe.*

SCIENCE is knowledge. It is knowledge coordinated, arranged and systematized. To ascertain and communicate knowledge is the primary object of science. Its mission is the quest after Truth, the discovery of the facts of actuality, of the invariable laws operating in the universe; and finally the dissemination of this knowledge among men. The work of a true man of science, in the words of a great astronomer of our day, is "a perpetual striving after a better and closer knowledge of the planet on which his lot is cast, and of the universe in the vastness of which that planet is lost." Imperfect, painfully imperfect as may be our present knowledge, its gradual extension quickens our life into a higher consciousness. Progressive understanding has also these advantages: it draws us out of and above our instincts and purely personal interests; it enables the intellect to project itself in a certain measure beyond our humanity, and to consider it from the exterior; it stirs within us that spiritual discernment which led Francis Bacon to exclaim: "Truth, which only doth judge itself, teacheth that the enquiry of truth is the sovereign good of human nature." And likewise Boileau: "*Rien n'est beau que le vrai, le vrai seul est aimable.*"

What is true of science in general is true of any one of its subordinate members in particular. Palæontology is sometimes considered as an independent branch of inquiry, but this is to misconceive its relations to kindred sciences. For that reason it may be profitable, before passing to our special subject of fossil

fishes, to survey the larger aspects of palæontology and to set forth something of its general aim and scope. And first it is to be noted that the study of extinct animal organisms, that is, palæozoology, is merely an extension of zoological science, just as the study of fossil plants is an extension of botanical science. The former of these is, in fact, merely the rehabilitated zoology of the past, as the latter is merely the rehabilitated botany. The true aim of palæontology is to restore to us visions of vanished life-periods; to unfold to our view the ceaseless procession of animate forms that, slowly transforming, very gradually progressing, sometimes retrograding, keeps up its steady file through the ages from twilight antiquity down to our own day. Figuratively speaking, this science realizes the dream of the ancient poets who described certain gifted mortals as having been privileged to descend into the interior of the earth, and, after their return to the upper air, amazing their fellows with tales of the wonders thus revealed. Only, in the present case, the wonders are not imaginary but real, and we are permitted to behold through the windows which palæontology opens up for us amid stratifications and ruins, not only a manifold of shifting phenomena, but anon the glint and shimmer of the wheels, as it were, of the controlling mechanism. Science shows us these manifestations, philosphy teaches us to think of them in terms of cause and effect, and to sift out from them certain ultimate conceptions.

If the mind of the astronomer wearies in the effort to contemplate an infinity of space, so the palæontologist is overwhelmed by the sweep of the universe through endless time. In his domain a sense of the time-element is ever-present and all-pervading. He acquires the habit of contemplating all things *sub specie aeternitatis.* He is concerned with fixing the order and character of events throughout all past time in all places. By virtue of the time-element entering into it, palæontology becomes at bottom an historical science, and the underlying attitude of the inquirer is, therefore, on a parity with that of the historian of human events. It is well not to lose sight of this fact.

Nor, on the other hand, must it be supposed that the province of palæontology is limited to the investigation merely of dead organisms, any more than historical inquiry terminates in a dead knowledge of what happens to have happened during the course of human experience. Every student realizes that the profit of studying history lies in *understanding* what has happened, in perceiving the principles and causes that have determined the progress of society, in discerning the action of those forces, motives, vicissitudes and transformations that, in so far as they affect the fate of nations or individuals, we can call by the name of Destiny. In human history as in all other phenomena of life and motion, it is not so much the events or manifestations that interest us, as their interpretation. We are not satisfied short of knowing the why, the whence and wherefore. To register the actual fact, whether in history or in science, is the indispensable first step, but only the first; its necessary complement is to perceive the *relations* between one fact and other facts, to search for causal sequences, in a word to conceive of things in terms of cause and effect.

Let us illustrate our meaning a little further. What is there in a dead shell that interests the naturalist primarily? Is it the relation between the mollusk and its covering, or is it not rather the relation of the animal *plus* shell to another animal together with its shell, and so on until each has been assigned its position in the series of shell-bearing animals? And what matters it whether the animal has but recently become inanimate, or has lain entombed in the rocks throughout geologic cycles? The palæontologist is concerned with life, life in past periods it is true, but it is a purely secondary consideration that he has to deal with defunct materials. He takes his materials as he finds them, and though they be merely dry bones or considerably worse residue of mortuary corruption, eloquent of death and decay,* they are to him merely as so many inscriptions he has

*The old-school idea of these things is poetically expressed by Chateaubriand: "C'est dans le cœur de l'homme que sont les grâces de la nature. Quant à celui qui étudie les animaux, qu'est-ce autre chose, s'il est incrédule que d'étudier des cadavres? A quoi ses recherches le mènent-elles? quel peut être son but? Ah! c'est pour lui qu'on a formé ces cabinets, écoles où la Mort, la faux à la main, est le demonstrateur; cimetières au milieu desquels on a placé les horloges pour compter des minutes à des squelettes, pour marquer des heures a l'éternité!"

to decipher, or as the blocks with which he has to construct his temple of truth. Industriously to seek out his building stones, assemble them, and fit them deftly together, that is his proper function. Just as in the physical sciences the chief work to be done is observation and experiment, since from these alone conclusions can be drawn; so also in the natural history of the past the first duty of the worker is careful investigation before he may offer a presentation of results. It is incumbent upon him equally with the historical student to "expend all diligence in discovering and investigating all possible material, and after this has been done, to examine it with rigorous critical acumen." Enormous and bewildering as may be the task of assembling the material, the collection of facts is but preliminary to research of really useful character; facts must be reduced to orderly system, results must be combined, many phenomena included under one law, and many subordinate laws under one more comprehensive, before we can gain approximate understanding, or before judgment can be passed on knowledge. The method of both physical and natural science, as has been said, is to draw conclusions from known and recorded phenomena; and the ultimate object of each is to widen knowledge and deepen our understanding. Especially is the mind of the naturalist alert to grasp general principles involved amid the multiplicity and complexity of phenomena; by training he acquires a vivid sense of relations; it is instinctive with him for the part to suggest the whole; his intellect leaps from the specific instance to an apprehension of the general law; and finally his generalizations attain significance through the clarifying agency of "reorganizing ideas".

By reorganizing ideas we mean those great and illuminating conceptions that enter the world of thought at propitious moments and are sometimes epoch-making for the progress of science. "Emancipating conceptions" they are called by some, *idées directrices* is the corresponding French term. "That which usually forms a grand conception," says Montesquieu, in portraying their influence, "is a thought so expressed as to reveal a number of other thoughts, and suddenly disclosing what we could not anticipate without patient study." If we may be

pardoned the digression, let us reflect for a moment on the far-reaching consequences of the Copernican conception of the world, one of the profoundest of all reorganizing ideas. Place alongside of it Newton's theory of gravitation, which gave for all time a definite and demonstrated system of the universe, and to these two add Darwin's theory of descent—that is, of organic evolution—we shall then have the leading factors which have immeasurably extended the material world in modern times, and vastly enlarged our horizon. Through their medium our ideas of space, durations and existence have acquired new validity, present a surprisingly larger manifold, and disclose to cognition unfathomable riches. If it be true, as Pascal says, that "all our dignity consists in thought," how greatly have the boundaries of our mental vision been widened and illumined, thanks to these three revolutionary ideas.

To illustrate: We all know, for instance, that the ancient conception of the world was strictly limited. For the ancient and mediæval man our earth stood at the middle of the world, and the vault of heaven, supposed to be not distantly removed, formed the outermost limit of creation. The Homers and Dantes of their time have pictured to us what a comfort and support this limited world-conception yielded to human imagination. But so soon as Copernicus had shown that the simplest way to conceive the world was to think of the earth as an unsupported ball revolving about the sun, both being lost in limitless space, our planet could no longer occupy the center of the universe, and the satisfying framework which had supported the old cosmography was shattered in pieces. Religion itself received a violent shock as the thought gained ground that the human race was by no means the goal and acme of the universe. The established faith revolted at the idea of ultimate extinction of man and all his works, and repudiated whatever reasoning gave countenance to the prediction.

Before the era of modern science had begun, leaders of public opinion were satisfied on the basis of traditional or preconceived ideas to explain what man is, whence he came, whither he is bound, what he may become, and what he should be. Armed with new truths, and enriched by a vast supply of demonstrated

facts, how different is the picture which the human mind draws of nature under the influence of eighteenth-century philosophy! How greatly has the point of view shifted, and how shrunken and inadequate is the older world-conception! The change is strikingly shown towards the middle of the century, when we find a naturalist of great ability like Buffon proclaiming, in his *Théorie de la Terre* (1749), the vast antiquity of life, the slow formation of stratified deposits and exceedingly gradual transformation of the earth's surface. We owe to this author a truly grand picture of cosmic history. His writings describe for us, as a later compatriot has said, "in approximate features the entire history of our globe, from the moment it formed a mass of glowing lava down to the time when our species, after so many lost or surviving species, was able to inhabit it." As opposed to the traditional view that in man's destiny lies the central and most significant fact of the universe, that this is in verity the

"Far-off, divine event,
Towards which the whole creation moves,"

we find a man of Buffon's genius rebuking such self-conceit. To his way of thinking, "a mite that would consider itself as the center of all things would be grotesque, and therefore it is essential that an insect almost infinitely small should not show conceit almost infinitely great."

The same thought is amplified in interesting fashion by the philosopher-historian Taine, whose attitude is identical with that of the palæontologist. He bids us consider the spectacle of nature as if we were removed in imagination to another planet. This is the outlook that presents itself:

"Amidst this vast and overwhelming space and in these boundless solar archipelagoes, how small is our own sphere, and the earth, what a grain of sand! What multitudes of worlds beyond our own, and, if life exists in them, what combinations are possible other than those of which we are the result! What is life, what is organic substance in this monstrous universe but an indifferent mass, a passing accident, the corruption of a few epidermic particles? And if this be life, what is that humanity which is so small a fragment of it? Such is man in nature, an atom, an ephemeral particle; let this not be lost sight of in our theories concerning his origin, his importance, and his destiny. . . How slow has been the evolution of the globe itself! What

myriads of ages between the first cooling of its mass and the beginnings of life! Of what consequence is the turmoil of our ant-hill alongside the geological tragedy in which we have borne no part, the strife between fire and water, the thickening of the earth's crust, the formation of the universal sea, the construction and separation of continents! Previous to our historical record what a long history of animal and vegetable existence, what a succession of flora and fauna! What generations of marine organisms in forming sedimentary strata, what generations of plants in forming coal deposits! And at length comes man, the latest of all, shooting up as the terminal bud at the top of a lofty antique tree, growing there a few seasons, but destined to perish, like the tree, after a few seasons, when the increasing and foretold congelation allowing the tree to live shall force the tree to die. He is not alone on the branch: beneath him, around him, on a level with him, other buds shoot forth, born of the same sap; but he must not forget if he would comprehend his own being, that, along with himself, other lives exist in his vicinity, graduated up to him and issuing from the same trunk. If he is unique he is not isolated, being an animal among other animals. . . . Thus surrounded, brought forth and borne along by nature, is it to be supposed that in nature he is an empire within an empire? He is there as part of a whole, by virtue of being a physical body, a chemical composition, an animated organism, a sociable animal, among other bodies, other compositions, other social animals, all analogous to him; and by virtue of these classifications he is, like them, subject to laws. . . . In all this man continues nature; hence, if he would comprehend himself, he must observe him in her, after her, and like her, with the same independence, the same precautions, and in the same spirit."

An immediate application of the view just stated is that it constantly brings before us the eternal in the midst of the present. Turning now to our own times, by far the most trenchant of reorganizing or emancipating ideas that has modified the world of thought is the theory of organic evolution, first fully set forth by Darwin in 1858, although foreshadowed, suggested, and even explicitly proposed by various clear-sighted thinkers before a new era was opened up in natural science by the *Origin of Species*. Noteworthy is the fact that practically the same theory of the descent of species, though without the causo-mechanical explanation of their origin by means of natural selection (the essential idea to which the term Darwinism is prop-

erly applied), had been proposed by Lamarck in France a score of years earlier, only to be ignominiously rejected. All educated readers are familiar with the example of Darwin's persistent, long-continued striving for the truth, how at first it was dimly perceived and at length fully revealed to him after making the most wonderful collection of illuminating and explaining facts which had ever been assembled in biology by any single investigator, and how with utmost intellectual candor he tested it, as we are told, "by applying to it successively fact after fact, group after group, and category after category of facts, until he convinced himself of the theory's consonance with all this vast array of observed biological actuality." * Thanks in part to his masterly presentation of the theory, it gained almost immediately a wide acceptance, and is now held to be as thoroughly demonstrated a part of natural science as is Newton's law of gravitation in physics, or the heliocentric system in cosmography.

Palæontology in particular received a profound stimulus under the influence of evolutionary ideas, and its whole aspect, method and outlook were revolutionized in consequence. It is now universally admitted that "the facts revealed by the study of palæontology are explicable wholly satisfactorily by the theory of descent and in no single instance do they contradict it." Consider for a moment what this means. Naturalists are acquainted nowadays with about 400,000 species of living animals and half as many species of existing plants. A computation based on the number of new species being found and described from year to year, and the extent of biologically unexplored areas of the earth's surface, shows that the total number of species constituting the modern fauna must number at least several millions. For the insects alone, entomologists hold that a total of two million species is not an excessive estimate. And these all belong to but a single geological epoch, the present. But in the case of extinct species, "those hosts of strange denizens of our changing earth in the ages gone," it is evident that the variety of forms preserved for us in the rocks is but an insignificant fraction of

* See the interesting recent work by Professor V. L. Kellogg, "Darwinism Today", and his joint production with President Jordan, "Evolution and Animal Life", 1907.

the grand total that has existed since life began.* How now shall science answer the question as to the origin of these myriads of forms? Evolution answers it in this way: the language in which it is here stated is that of Professor Kellogg (*ibid.* p. 10):

"Now all these millions of kinds of animals and plants can have had an origin in some one of but three ways; they have come into existence spontaneously, they have been specially created by some supernatural power, or they have descended one from the other in many-branching series by gradual transformation. There is absolutely no scientific evidence for either of the first two ways; there is much scientific evidence for the last way. There is left for the scientific man, then, solely the last; that is, the method of descent. The theory of descent (with which phrase organic evolution may be practically held as a synonym) is, then, simply the declaration that the various living as well as the now extinct species of organisms are descended from one another and from common ancestors. It is the explanation of the origin of species accepted in the science of biology."

It is needless to pursue the subject further. Sufficient has been said to convey some notion of the extraordinary impetus given to science and all forms of speculative thought through the medium of a few grand illuminating conceptions, pre-eminent among which is the theory of evolution. Bear in mind that rarely are great truths hit upon offhand, as the result of hazard, by a fortunate guess, or by intuition. Enlightenment, the reward

*The marvelous properties of radium furnish unexpected aid to the palæontologist by way of granting him a much greater time-estimate than physicists have been willing to allow. Professor Lankester, in his presidential address before the British Association at the York meeting (1906), states the matter in this wise:

"Even a small quantity of radium diffused through the earth will suffice to keep up its temperature against loss by radiation! If the sun consists of a fraction of one per cent. of radium, this will account for and make good the heat that is annually lost by it.

"This is a tremendous fact, upsetting all the calculations of physicists as to the duration in past and future of the sun's heat and the temperature of the earth's surface. The geologists and biologists have long contended that some thousand million years must have passed during which the earth's surface has presented approximately the same conditions of temperature as at present, in order to allow time for the evolution of living things and the formation of the aqueous deposits of the earth's crust. The physicists, notably Professor Tait and Lord Kelvin, refused to allow more than ten million years (which they subsequently increased to a hundred million)—basing this estimate on the rate of cooling of a sphere of the size and composition of the earth. They have assumed that its material is self-cooling. But, as Huxley pointed out, mathematics will not give a true result when applied to erroneous data. It has now, within these last five years, become evident that the earth's material is *not* self-cooling, but on the contrary self-heating. And away go the restrictions imposed by physicists on geological time. They are now willing to give us not merely a thousand million years, but as many more as we want."

only of unremitting toil, may be won by those who have been willing to suffer, endure, and devote lifetimes to the discovery of a small number of new truths. *Ars longa, vita brevis.* It is characteristic of science to be content with slight advances that may be slow as the precession of the equinoxes, if only they be sure; and the utmost that even the most patient and ingenious worker can achieve is to contribute but one little stone or two towards the building of that stately edifice in which Truth may dwell. Yet that little is enough. For Truth, no less than Wisdom, as saith the Preacher, "exalteth her sons, and taketh hold of them that seek her. He that loveth her loveth life; and they that seek her early shall be filled with gladness. . . . For at first she will walk with him in crooked ways, and will bring fear and dread upon him, and torment him with her discipline, until she may trust his soul, and try him by her judgments: then she will return the straight way unto him, and will gladden him, and will reveal to him her secrets. If he go astray she will forsake him, and give him over to his fall."

In palæontology, though our knowledge has indeed grown apace, it is still uncertain and confused in places, and in others there are distressing voids. The present state of this special branch of science may be likened, even as archæology has been likened, to a mosaic of colored tesseræ, which, though broken here and there, yet shows broad patterns and many curious details. Scattered in the surrounding débris and sometimes buried by this are the little cubes waiting to be found and fitted into their proper places. For the parts of the mosaic now complete, we have to thank the explorers of the past, for the filling in of the lacunæ, the explorers of the future. And we may be assured that future laborers, with broader knowledge, better training and greater means of investigation must eclipse all that the ablest workers of our generation can accomplish. Content as every earnest naturalist is to serve so pure and unapproachable a mistress as Truth, let each join in the hope that those who come after us, more favored than ourselves, may be permitted to hold some converse with the Sphinx!

Finally, before passing from these general reflections to our special province, two thoughts may be singled out from the rest because they bear closely upon the real concerns of humanity,

and refuse to be cast down amid the realm of vague and transitory ideas. They possess real and immediate values, and profoundly affect the attitude of modern science, as will be seen from one or two typical illustrations. The first of these comprises a sense of the immeasurable, and indeed inconceivable length of time that life-processes have been at work on our planet, the chain of forms persisting in unbroken succession and ever-varying transformation since its earliest manifestations down to the exuberance and complexity of the world of today. And the second bids us contemplate not only the vast antiquity of life, but, which is still more impressive, the almost infinitely slow, gradual, often imperceptible advance in the scale of development, yet nevertheless indicating a constant tendency toward perfection. Here if anywhere stands revealed to us, not the operation of blind forces amid the eternal flux of things, but a supreme intelligence manifesting itself through forever unchancing universal laws.

Many examples might be chosen to show how these thoughts are reflected by scientific workers of our day: we will, however, single out but the two following in closing. The first is from Poincaré, in his essay on *The Value of Science;* the second is from Suess, founder of the "new geology," and is contained in the final passage of *The Face of the Earth.*

Says the former: "All that is not thought is pure nothingness; since we can think only thought and all the words we use to speak of things can express only thoughts, to say there is something other than thought, is therefore an affirmation which can have no meaning. And yet—strange contradiction for those who believe in time—geologic history shows us that life is only a short episode between two eternities of death, and that, even in this episode, conscious thought has lasted and will last only a moment. Thought is only a gleam in the midst of a long night. But it is this gleam which is everything." *

*The salient thought here recalls one of Pascal's Pensées, to which we have already once referred: "All our dignity consists in thought. It is from thought that we should take our point of departure, and not from space or duration, which we cannot fill. Let us endeavour then to think well; this is the principle of morality." The central idea contains also a perhaps unconscious reflection from pagan sources. Compare, for instance, the following rendering from a fragment of Æschylus: "Pauvre espèce humaine, qu'éphémère est ta sagesse, rien de solide, l'ombre d'une fumée."

In these words Suess concludes his treatise: "There is no means of comparison by which we can illustrate directly the great length of cosmic periods, and we do not even possess a unit with which such periods might be measured. We hold the organic remains of the past in our hand and consider their physical structure, but we know not what interval of time separates their epoch from our own; they are like those celestial bodies without parallax, which inform us of their physical constitution by their spectrum, but furnish no clue to their distance. As Rama looks out upon the Ocean, its limits mingling and uniting with heaven on the horizon, and as he ponders whether a path might not be built into the Immensity, so we look over the Ocean of time, but nowhere do we see signs of a shore."

Remains one more word only and we have done. For those to whom the prospect seems cold and dreary that modern materialistic science discloses to our view, and for those who are not content with the mere objective values of science, there may be brought before the mind this inspiring message of Darwin. Readers who are not over-familiar with his works may be surprised to be told that this passage forms the conclusion of the *Origin of Species:*

"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. . . . [The more important of these laws are then enumerated.] Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is a grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

[NOTE—The reader who desires information on the more particular relations of palæichthyology to biology—since we have preferred to dwell in the above on the larger aspects of palæontology—will do well to consult two addresses by Smith Woodward: the first printed in the Proceedings of the Geologists' Association for 1906, entitled "The Study of Fossil Fishes;" and the second in the Reports of the International Congress of Arts and Sciences at St. Louis, vol. IV, 1906, under the title of "The Relations of Palæontology to Biology."]

II.

Stratigraphy of the Devonian fish-bearing beds of Iowa.

The assemblage of sediments representing the Devonian system in Iowa forms a belt averaging fifty miles in width, stretching along the Cedar river from the Minnesota line to Muscatine county, and extending thence eastward into Illinois. The larger part of these rocks consists of limestones and shales whose bedding, in general conformable, gives indication of continuous deposition, whose faunal content is on the whole fairly characteristic of the Middle Devonian, and yet none of whose parts can be definitely correlated with formational units referred to the same system in New York. The reason for this non-homogeneity in the faunal characteristics of the two areas, namely the eastern or "Ohian" as it has been termed (known also as the "Appalachian"), and the western interior or "Dakotan", lies in the fact that these were distinct geographical provinces throughout the Devonian. They remained, in fact, completely separated from each other until towards the close of the Middle Devonian, and thereafter communication was maintained between them by means of a comparatively narrow passageway extending through Illinois and Wisconsin. These conditions are well portrayed in the palæogeographic maps given in Plates XIV-XVI, hitherto unpublished, and for whose use we are indebted to Professor Schuchert.

A tripartite division of the Iowan Middle Devonian rocks into the Wapsipinicon, Cedar Valley, and Lime Creek stages was first proposed by Professor Calvin in 1878. It was pointed out also by the same author that, owing to migration of species, the faunas of the summital (Lime Creek) and basal shales (Independence beds of the Wapsipinicon stage) are substantially identical, and that the fauna of the Cedar Valley limestone corre-

sponds more or less closely with that of the Hamilton in the more eastern ("Ohian") region.* To the Upper Devonian were referred two units—the Sweetland Creek shales, and the State Quarry limestone—which rest unconformably upon the Cedar Valley limestone, and occur as outliers in the east central part of the State. The former of these is developed chiefly in Muscatine county, and the latter in Johnson county northward of Iowa City. A scheme of classification adopted in earlier volumes of the Survey Reports is reproduced immediately hereinafter for the purpose of showing the succession of Middle Devonian sediments as they have been commonly interpreted until within the past year or two. Conformably, however, to Professor Calvin's most recent interpretation of the Lime Creek shales, based upon a study of their faunal relations, they are now assigned a somewhat higher stratigraphic position. This change is indicated in the second synoptical table presented herewith, which is reproduced from Professor Calvin's "Notes on the Geological Section of Iowa" (*Journ. Geol.*, 1906, vol. 14, p. 572). In connection with the latter it is necessary to bear in mind the following statement of the author by way of explaining the succession: "The three units referred to the Upper Devonian—the Sweetland Creek shales, Lime Creek shales, and State Quarry limestone—do not lie one above the other, but each is developed locally and lies uncomformably on the Cedar Valley limestones."

*Calvin, S. On the fauna found at Lime Creek, Iowa, and its relation to other geological faunas. Amer. Journ. Sci. (1883), **25**, pp. 432-436.—*Idem*, Devonian System (in Geology of Buchanan county). Rept. Iowa Geol. Surv. (1898), vol. **VII**, p. 221.

SYNOPTICAL TABLE OF THE DEVONIAN FORMATIONS OF IOWA*

SERIES	STAGE	SUBSTAGE
Upper Devonian		State Quarry limestone and Sweetland Creek beds
Middle Devonian	Lime Creek	Owen beds Hackberry beds
	Cedar Valley	Not yet subdivided
	Wapsipinicon	Upper Davenport limestone Fayette breccia or Lower Davenport beds Independence shale Otis limestone
Lower Devonian		Not represented

*Compiled from earlier Survey Reports (vols. VII–IX).

REVISED TABULATION OF THE DEVONIAN SEDIMENTS OF IOWA,

ACCORDING TO S. CALVIN

SERIES NAME	FORMATION NAME	THICKNESS (Feet)	CHARACTER OF ROCKS
Upper Devonian	State Quarry	40	*Limestone, mostly brachiopod coquina
	Lime Creek	120	*Mostly shales
	Sweetland Creek	20	*Shale (*All three units locally developed features, each lying unconformably on the Middle Devonian)
Middle Devonian	Cedar Valley	100	Limestones, shaly limestones, some dolomites in the northern counties
	Wapsipinicon	60–75	Limestones, shales, shaly limestones

Distribution of Fish-remains in the Devonian System of Iowa.—Detached teeth and other fragmentary fish-remains occur somewhat sparsely in different horizons of the Middle Devonian of this State, but are present in such remarkable abundance in the Upper Devonian outliers as to constitute, locally at least, veritable fish-beds. Although numerically rich, the fauna is singularly undiversified in character, consisting almost exclusively of Chimaeroids (Ptyctodonts, including theoretically associated fin-spines), Arthrodires and Lung-fishes. Probably it is not an exaggerated estimate that reckons Chimaeroids as constituting, according to numerical abundance, perhaps ninety per cent of the Devonian vertebrate fauna of the State, and Lung-fishes more than half of the remainder. Everywhere is a notable dearth of Selachians, and there appears to be but one certainly recognized Crossopterygian genus. Chimaeroids (introduced by Rhynchodus), Dipterines and Arthrodires all make their first appearance in the Cedar Valley limestone, and continue throughout the system in this State, Illinois and Wisconsin. On the other hand, the peculiar dental plates of the Synthetodont type are limited, so far as known, to the State Quarry and Sweetland Creek divisions of the Iowa Upper Devonian. The successive fish-bearing stages of the Middle and Upper Devonian may be briefly enumerated as follows:

Wapsipinicon stage.—The vertebrate fossils from this horizon are limited to dental plates of *Ptyctodus calceolus* and fragments of Arthrodiran armor. In Linn county they occur in the so-called Fayette breccia, which corresponds to the brecciated non-fossiliferous Lower Davenport beds in Scott county. From the Upper Davenport beds in the latter county ("Phragmoceras beds" of Barris), have been found, according to Professor W. H. Norton,* "teeth and plates of several species of fish, of which only *Ptyctodus calceolus* N. and W. has been identified." Barris† describes the dermal plates occurring in the Davenport beds as "measuring nearly an inch in thickness, and several inches in length and breadth. As in other localities, their entire surface is covered with small stellate tubercles." These meagre indications probably refer to Dinichthys, certainly not to Macropetalichthys, as the author is inclined to suppose.

*Ann. Rept. Iowa Geol. Surv. (1899), vol. **IX**, p. 451.
†Proc. Davenport Acad. Sci. (1897), vol. **VII**, p. 19.

Cedar Valley stage.—The vertical succession of faunas in the Cedar Valley limestone of Scott and Muscatine counties, and in the vicinity of Rock Island, Illinois, has been carefully investigated and tabulated by J. A. Udden.* Two species of Dipterus occurring in this formation mark the earliest known advent of this genus in the Palæozoic rocks of America. One of these was obtained from the basal ledges of the formation in Scott county, the other, *D. calvini,* from near its summit in Muscatine county. Excellently preserved dental plates of Ptyctodus and Rhynchodus, spines of Heteracanthus, cranial and abdominal plates of Dinichthys, and various more or less fragmentary remains of Onychodus have been obtained from exposures of Cedar Valley limestone in Bremer, Cerro Gordo and Johnson counties. Especially from the vicinity of Waverly and Waterloo a large and interesting collection was brought together by Orestes H. St. John prior to the organization of the preceding State Survey, and is now deposited in the Harvard Museum. Some further material has been gathered by Professors Savage and Norton, and a list of determined species is published by the latter in Vol. XVI., (p. 356) of the present series of Reports.

UPPER DEVONIAN.

Lime Creek substage.—The shales representing this member are exposed only in Cerro Gordo and Franklin counties, and although they carry a complex invertebrate fauna, fish-remains are in general very sparse. As shown in the first instance by Professor Calvin in 1878, and also at subsequent times by the same author, the faunal relations of these beds are more intimate with those of the Independence shales than with any other formation in Iowa.† In seeking to explain this state of affairs Calvin reaches the following interesting conclusion: "During the time represented by the shales and limestones which lie between the Independence and the Lime Creek shales the peculiar fauna of the lower shale horizon, adapted to life on a muddy sea-bottom, persisted in some congenial localities at present unknown, suffering in the meantime only a slight amount of modification, and again appeared, reinforced by a number of other species, when the sea-bottom offered conditions favorable to its success."‡ The only satisfactorily determined fossil fishes from this member of the Upper Devonian are *Ptyctodus calceolus, Dinichthys*

*Journ. Cincinnati Soc. Nat. Hist. (1897), **19**, pp. 93-95, Amer. Nat. (1898), **32**. p. 557. Ann. Rept. Iowa Geol. Surv. (1899), **IX**, p. 302, pl. 6.

† Bull. U. S. Geol. and Geog. Surv. (1878), **4**, pp. 725-730.

‡ Ann. Rept. Iowa Geol. Surv. (1897), **VII**, p. 169.

pustulosus, and fragments of heavy, coarsely tuberculated plates indistinguishable from those of Aspidichthys. A considerable quantity of this class of remains was brought together some years ago by Mr. Clement L. Webster, of Charles City, Iowa.

State Quarry substage.—A small outlier of Upper Devonian rocks near North Liberty, Johnson county, several miles north of Iowa City, which has received the name of State Quarry limestone, is remarkable for carrying a vast quantity of fish teeth, a fact first discovered and made known by Professor Calvin * about a dozen years ago. The remains occur in a single cherty layer not over eighteen inches thick, but so great is their profusion as to justify the appellation given to it by its discoverer as a "fish-tooth conglomerate". The homotaxial relations and peculiar faunal characters of these beds have been set forth with considerable fulness by Professor Calvin in his report on the Geology of Johnson county, to which is appended a special notice of the fish-remains by the present writer. Detailed descriptions of the known species are also given in a subsequent part of this Report.

Sweetland Creek substage.—The beds that have been designated by this name consist of argillaceous shales that are frequently found overlying the Cedar Valley limestone in Scott county, and are not only uncomformable with the latter, but contain a markedly different fauna. A description of the local sections and lists of fossil species that have been found are given by Professor J. A. Udden in Vol. IX (1899) of the present series of Reports. Tritors of *Ptyctodus calceolus* and dental plates of the Synthetodus type are the only known vertebrate forms in the assemblage.

*Proc. Iowa Acad. Sci. (1896), **4**, pp. 16-21. Ann. Rept. Iowa Geol. Surv. (1897), **VII**, pp. 74, 108.

III.

Evolutionary History of Fishes and Scheme of Their Systematic Arrangement.

The geological succession of the class of Fishes is very satisfactorily known from the middle of the Silurian onward, and the essential features of the past history of this chain of life are now comparatively well ascertained. Facts have been brought to light, and broad generalizations established upon them, through study of this history, which have an important bearing upon many of the fundamental problems of biology, illustrating as they do not only general principles of organic evolution, but enabling us to construct a natural system of classification reflecting the development, and expressive of the true relationships of Pisces. As might be expected, the evolutionary history of Fishes is consistent at all points with those principles of organic development that are the final outcome of investigation carried on in other departments of palæontology; and indeed, it is within the very group we are now considering that some of the fundamental laws of organic progress have been discovered.

It will suffice for our present purpose to summarize briefly the main facts concerning the geological succession observed among Fishes, and thereafter to explain the general basis of classification that is now currently adopted. And in the first place we must note that concerning the immediate origin of the group of Fishes and fish-like vertebrates, palæontology reveals no certain clue. Nor is it likely from the nature of things that authentic documents will ever be discovered, there being abundant reason to suppose that the primitive forerunners of the vertebrate phylum were soft-bodied creatures, and incapable of preservation in the rocks.

As to the once popular theory which still finds adherents in some quarters, namely, that the earliest fish-like vertebrates are derived from the Arthropod stem, sharing features in common

with Merostomes (Eurypterids etc.) and Arachnids (Scorpions etc.), it is important to recall that the groups mentioned had already attained a high degree of specialization in the early Palæozoic, and had diverged widely along certain directions from the primal trilobitic type of organism. Applying here the universal rule that the progenitors of a new type are to be sought not among the more highly modified, but among the more generalized members of an old race, we are forced to exclude Merostomes and Arachnids as possible ancestors of backboned animals by virtue of the fact that they are already too highly specialized. However plausibly the trilobitic organization may be regarded as ancestral to the higher Crustacea, and even Insects, it does not even remotely suggest affinities with chordates; and in case the gap between the two phyla cannot be bridged over at this point, we must perforce deny that there is any connecting link between them. The latter proposition is now commonly accepted, and such resemblances as are shared by Merostomes and early fish-like vertebrates are explained as due to mimicry, or to adaptation of creatures of different grades to a similar environment. On the other hand, there are no theoretical objections to looking upon the worm-like Enteropneusta, by some actually placed among the Protochordates,* as possible ancestors of the vertebrate stem. And it may be suggested that the Cambrian probably affords a sufficient time-interval for the elaboration necessary to overcome differences of grade.

*The terms Chordata and Protochordata are thus distinguished by President D. S. Jordan, in his *Guide to the Study of Fishes*, vol. I, p. 460.

"*Chordata.*—The chordate animals are those which at some stage of life possess a notochord or primitive dorsal cartilage which divides the interior of the body into two cavities. The dorsal cavity contains the great nerve centers or spinal cord; the ventral cavity contains the heart and alimentary canal. In all other animals which possess a body cavity, there is no division by a notochord, and the ganglia of the nervous system, if existing, are placed on the ventral side or in a ring about the mouth.

Protochordata.—Modern researches have shown that besides the ordinary backboned animals certain other creatures easily to be mistaken for mollusks or worms, but being chordate in structure, must be regarded as offshoots from the vertebrate branch. These are degenerate allies, as is shown by the fact that their vertebrate traits are shown in their early or larval development and scarcely at all in their adult condition.

Enteropneusta.—Most simple, most worm-like, and perhaps most primitive of all the [Proto-]Chordates is the group of worm-shaped forms, forming the class of *Enteropneusta*. . . . With the [lower] Chordates, and not with the worms, this class, *Enteropneusta*, must be placed if its characters have been rightly interpreted. It is possibly a descendant of the primitive creatures which marked the transition from the archaic worms, or possibly archaic Echinoderms, to the archaic Chordate type."

Whatever form of vertebrate life may have existed during the Cambrian, and it is reasonable to postulate its existence during that period, no traces of it have been preserved, owing doubtless to the total absence of hard parts. Detached scales, plates and other fragmentary remains of fish-like organisms are known from a few localities of Ordovicic (or Lower Silurian) age in this country, but their very inferior state of preservation prevents any reliable conclusions in regard to them. Not until the middle (Niagara in this country) and upper (Ludlow * and Downtown in Great Britain, "Passage Beds" in northern France) divisions of the Silurian do we find at all satisfactorily preserved hard parts of primitive vertebrates, differing in marked degree structurally from ordinary fishes in that they have incompletely formed jaws, no paired fins, and are without calcified endoskeletal parts. Hence, under the name of Ostracophores (or Ostracoderms) bestowed by Cope in allusion to their shell-like external covering, they are very properly awarded an inferior position in the scale of piscine evolution. Their lack of a lower jaw articulating with the cranium, a character which they share in common with existing lampreys, suggested to Cope the propriety of including both Ostracophores and Marsipobranchs in a separate class, named by him Agnatha, in contradistinction from Pisces proper. The validity of this distinction appears to be beyond question, and there are other characters ratifying it besides the important ones we have mentioned. Throughout this discussion, therefore, Ostracophores will be considered as primitive vertebrates belonging to a lower grade than Fishes proper, and included on that account in a different class, Agnatha, among Protochordates. Their advent slightly preceded that of ordinary Fishes in point of chronological sequence, although both classes probably had a common origin in times anterior to the Ordovician. The earliest recognizable indications of Fishes proper appear sparsely (Diplacanth Acanthodians) toward the close of the Silurian.

*Woodward, A. S., Notes on the Geology and Fossils of the Ludlow District. Proc. Geol. Assoc., 1904, vol. **18**, pp. 429-442.—Hinde, G. J., The Bone-bed in the Upper Ludlow Formation. *Ibid.*, pp. 443-446.--Leriche, M., Contribution a l'étude des poissons fossiles du Nord de la France et des régions voisines. Mém. Soc. Géol. de la France, 1906, vol. **5**, Mém. 1, pp. 13-39.

Like Eurypterids and certain other contemporary invertebrates accompanying them in the same fauna, the earliest recognizable fish-like vertebrates, that is to say, Silurian Ostracophores, appear to have been mere mud-grovellers inhabiting the bottom of shallow seas. Imperfectly equipped for locomotion, and making little progress throughout their subsequent history in the direction of improved swimming-organs, their evolutionary advance took place along lines immediately conditioned by their sedentary mode of existence. Thus, their growth-energy seems to have been expended chiefly in the elaboration of a protective exoskeleton, constituted in the more primitive forms of dermal granules or tubercles scattered throughout the tough but flexible integument, but becoming fused and segregated by successive stages into hard, sometimes even heavy plates, arranged according to a definite pattern. The culmination of their progress fell short, however, of the development of calcified endoskeletal structures, of paired limbs homologous with those of all higher vertebrates, and of completely formed jaws articulating with the cranium and functioning in the normal manner. These lowly fish-like organisms are, therefore, chiefly interesting in that they inform us regarding the manner in which a hard skeleton was first acquired among vertebrates, and illustrate successive stages of its elaboration.

Fortunately very satisfactory records of this evolutionary history are now available, a number of well preserved examples of primitive Ostracophores having recently become known from the Upper Silurian of Scotland,* and Lower Devonian (Hunsrück slates) of Rhenish Prussia.† Our knowledge of the skeletal modifications displayed by the lower types of Ostracophores is due chiefly to the researches of Dr. Ramsey H. Traquair, dean of Scottish palæichthyology, and to the brilliant generalizations based upon them that we owe to Dr. A. Smith Woodward, than whom is no higher authority or more experienced student of fossil fishes. Valuable enlightenment has also been

*Traquair, R. H., Report on Fossil Fishes collected by the Geological Survey of Scotland, etc. Trans. Royal Soc. Edinburgh, 1899, **39**, pp. 827-864.—Supplemental Report, *Ibid.*, 1905, **40**, pp. 879-888.

†Traquair, R. H., The Lower Devonian Fishes of Gemünden. Trans. Roy. Soc. Edinburgh, 1903, **40**, pp. 723-739.—Supplement, *Ibid.*, 1905, **41**, pp. 469-475. Also short papers in Geol. Mag. for 1900 and 1902.

derived from the recent studies of Dr. Otto Jaekel, in Germany, and Professor William Patten, of Dartmouth College, in this country.

Without entering at this point into the basis of classification, it may be remarked in passing that the different families of Ostracophores are commonly arranged in four ordinal divisions, of which the Heterostraci are regarded as the most primitive. This order comprises the curious group of Pteraspidians, the structure of whose hard shield is unique among vertebrates, and also the remarkable forms included within the families of Coelolepidæ and Psammosteidæ. Especially noteworthy among Coelolepids are the genera Thelodus (Fig. 1) and Lanarkia (Fig. 2), known

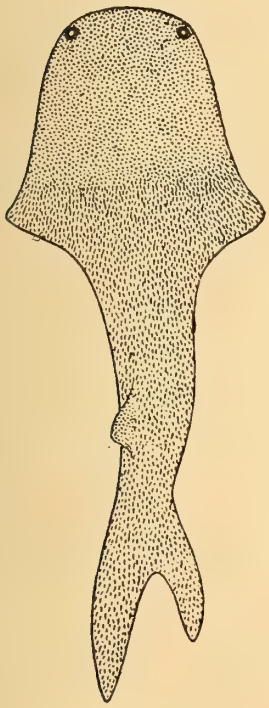


FIG. 1.

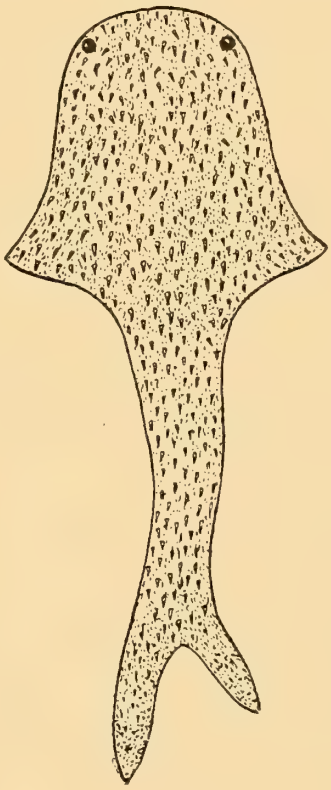


FIG. 2

Fig. 1. *Thelodus scoticus* Traq. Silurian (Ludlow beds) of Logan Water. Diagrammatic restoration showing dorsal fin and position of the eyes. The tail is flexed so as to show the caudal fin in profile, x ¾ (after Traquair).

Fig. 2. *Lanarkia spinosa* Traq. Silurian (Downtonian), of Scotland. Diagrammatic restoration similar to that of Fig. 1. Dorsal fin not yet observed, x ¾ (after Traquair).

FIG. 3.

Fig. 3. *Ateleaspis tesselata* Traq. Silurian (Downtonian) of Scotland. Diagrammatic restored outline showing tail in profile, x ½ (after Traquair).

by complete skeletons in which the dermal covering consists merely of small shagreen tubercles, sometimes beautifully ornamented, or of minute hollow spines. Another interesting form of great systematic importance is Ateleaspis (Fig. 3), which is regarded by Dr. Traquair as annectant between Heterostraci and the next higher order, Osteostraci. Under the last-named are included such well known forms as Cephalaspis (Fig. 4, page 58), Trematastpis, Thyestes, etc. Only in the case of the most specialized order, Antiarchi, comprising the single family Asterolepidæ, are we unable to trace the lines of descent, owing to non-acquaintance with intermediate forms linking this group with any of the preceding. The suggestion that Asterolepids may have

been independently derived from some invertebrate progenitor cannot possibly be entertained in the light of the following facts; (1) their dermal plates are composed of true bone;* (2) the head-shield and body armor have a well developed sensory canal system; and (3), in Pterichthys, at least, there is a tail covered with scales, a membranous dorsal fin, and a genuinely piscine heterocercal caudal fin.

Enlightenment as to the initial stages by which Ostracophores acquired a hard skeleton is furnished by primitive Coelolepid genera, vast quantities of whose granular skin-tubercles occur in the Upper Ludlow bone-bed, and whose complete skeletons have become known during recent years from the Upper Silurian rocks of the south of Scotland. If, now, we are prepared to accept Smith Woodward's contention that the order in which the different kinds of hard parts were evolved may be reasonably inferred from the order in which they successively predominate, then it becomes an easy matter to understand how these modifications arose. The manner in which these phenomena were progressively introduced is thus interpreted by the same author in the following passage.†

"From numerous well-preserved specimens it is clear that the hard skeletal parts of the Ostracoderms were confined exclusively to the skin; and in most of the earliest representatives of the group these hardenings are merely scattered granules or tubercles of limy matter which form a flexible external armour. It is true that each tubercle is beautifully fashioned, with a definite internal structure round a papilla of the skin, like a tubercle from the shagreen of a modern shark; but the armour is essentially a scattered deposit or segregation of superfluous mineral matter in the normally soft tissue, suggesting that the Ostracoderms toward the end of their race had experienced precisely the same affliction as that now experienced by some of the highest mammals in the latter part of their individual life, namely, a kind of "gout". Myriads of the isolated skin-tubercles of *Thelodus* occur in the Upper Ludlow bone-bed, while numerous nearly complete specimens both of this fish (Fig. 1) and *Lanarkia* (Fig. 2) have been found in the contemporaneous

*The bone structure of Pteraspis is well described and illustrated by microphotographic sections in a paper by F. Drevermann, entitled "Ueber *Pteraspis dunensis*," etc. Zeitschr. deutsch. geol. Ges. 1904, **56**, pp. 275-289.

†Woodward, A. S., The Study of Fossil Fishes. Proc. Geol. Assoc. 1906, **19**, p. 267.

and somewhat later rocks in Lanarkshire. There is, indeed, no doubt that the granular armour was the "fashionable" fish-skeleton of Upper Silurian time.

It soon became usual, however, for the skin-tubercles to fuse together into groups, and in the earliest Devonian faunas the most common Ostracoderms are those like *Cephalaspis* and *Pteraspis*. The first of these (shown in Fig. 4) is especially instructive as showing how the tubercles became plates, and how the shape of these plates depended on the nature of the underlying parts of the body. In the head-armour of *Cephalaspis* a few regularly spaced tubercles grew larger than the others, and each of these became a center of attraction with which the immediately surrounding tubercles coalesced, by the thickening of their base, to form polygonal plates. Where the underlying soft parts were not in constant motion these polygonal plates fused again into a continuous shield; while in the roof of parts, such as the presumed gill-chambers, where flexibility was needed, the plates remained as a loose mosaic, which is often lost in the fossils. . . .

FIG. 4.

Fig. 4. *Cephalaspis murchisoni* Egert. Lower Old Red Sandstone; Herefordshire. Headshield seen from above, tail twisted to show dorsal fin and heterocercal tail mainly in side-view, x ½ (after Smith Woodward).

The latest "fashion" among the Ostracoderms of the Devonian period consisted in an armour of symmetrically arranged overlapping plates on the top of the head and round the body, with a pair of flippers similarly armoured and appended to the latter. Here the the primitive skin-tubercles seem to have fused, not into polygonal plates, but along the lines of the slime-canals which traverse the skin of many of the Ostracoderms, though unfortunately none of the early stages in the process have hitherto been discovered. So far as known, this arrangement of armour suddenly appears in *Pterichthys* (Fig. 8, page 75) in the middle of the Devonian period, and it persists without essential change until the extinction of *Bothriolepis* just before the dawn of Carboniferous times."

Ostracophores, though forming the dominant feature of Silurian fish life, and making, as we have seen, considerable progress in the development of an external skeleton, were yet accompanied in the Upper Silurian by creatures which surpassed them in grade; and these vertebrates, by reason of having completed their jaws and acquired a pair of lateral fin folds, are entitled to rank as true fishes. These oldest remains of typical fishes evidently belong very near to that primordial stock from which is descended the great group of Elasmobranchs, a group represented at the present day by sharks and skates, and whose early offshoots are commonly held to be ancestral to all higher types of ordinary fishes. No connection can be traced between the earliest known Elasmobranchs and Ostracophores, yet it is interesting to note that dermal armor originates among them in precisely the same fashion as already noted among primitive Coelolepids. That is to say, these very old Elasmobranchs, which are called Acanthodians after the name of the first described genus, resemble the oldest fossilized Ostracophores in having the body completely covered by small, hard skin-granules. Not only did the armor begin among Acanthodians in the same way as in the most primitive fossil chordates, but there was also occasional fusion of the skin-granules into plates where rigidity was possible or necessary. This tendency is sometimes carried even to disadvantageous extremes, as in the case of the unduly stiffened and cumbersomely armed paired fins. Evolutionary progress in the direction of improved swimming-organs is very clearly indicated by Acanthodian fin-structures, the general trend of development being succinctly stated by Smith Woodward in the following language:

"These very old Acanthodians are known because they are completely covered by small, hard skin-granules like those of the oldest fossilized Ostracoderms. . . . A few of the granules fused together at the front edge of the median fins above and below the body, thus forming cut-waters or "spines"; and as a double series of exactly similar "spines" occurs along the lower border of the abdomen where the two pairs of fins are found in later fishes, it is reasonable to infer that these are likewise the stiffened front edges of fins. In other words, paired fins were not originally restricted to two pairs, but formed a double series

along the entire length of the abdomen. Therefore, if the separate median fins were produced by the subdivision of a primitively continuous median membrane along the back and the lower side of the tail, the paired fins arose similarly by the subdivision of continuous membranes which extended as a symmetrical pair along the outside walls of the body-cavity.

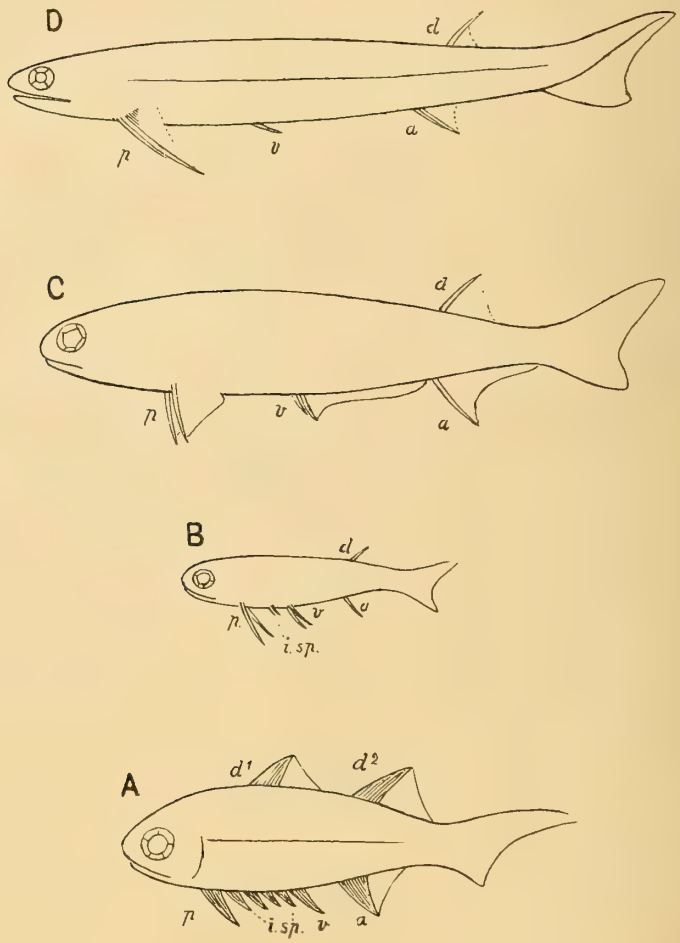


FIG. 5.

Fig. 5. OUTLINES OF ACANTHODIAN FISHES, illustrating their gradual elongation in shape and loss of intermediate spines during successive periods. A, *Climatius scutiger* Egert. Lower Old Red Sandstone; Scotland. B, *Mesacanthus mitchelli* (Egert.); *ibid.* C, *Acanthodes sulcatus* Ag. Lower Carboniferous; Edinburgh. D, *Acanthodes gracilis* Roemer. Lower Permian; Bohemia. *a*, anal fin; *d*, dorsal fin; *i. sp.*, "intermediate spines"; *p*, pair of pectoral fins; *v*, pair of pelvic fins. (From Smith Woodward, partly after Traquair and Fritsch.)

Even in the fashionable Acanthodians of the Silurian and Lower Devonian periods (*Climatius,* Fig. 5*A*), the foremost and hindmost pairs of spines were somewhat larger than the others; and in all later members of the group the "intermediate spines" dwindled to insignificance (*Mesacanthus,* Fig. 5*B*), or disappeared (*Acanthodes,* Fig. 5*C,* 5*D*), so that only the two normal pairs of fins remained. The fixation and stiffening of these fins, however, were so completely unsuited for further elaboration while they depended solely on skin-structures, that the Acanthodian fishes gradually declined towards insignificance and extinction. They lost their graceful fusiform proportions; some unwieldy and overgrown species became round-bodied grovellers in the mud of Carboniferous seas and estuaries (*Gyracanthus*) while the latest members of the race, which did not increase much in size, became almost eel-shaped before they died out in the Permian period (*Acanthodes,* Fig. 5*D*). All races which do not progress tend to become represented by eel-shaped species in their latter days, and the Acanthodians formed no exception to the rule. . . .

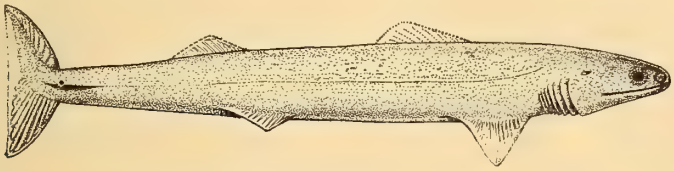


FIG. 6.

Fig. 6. *Cladoselache fyleri* Newberry. Cleveland shale (Upper Devonian); Cleveland, Ohio. Right side-view, about one-tenth natural size. A primitive shark illustrating the simplest kind of paddle-fins, which are supported by nearly parallel bars of internal cartilage (after Bashford Dean).

There must, however, have been some primitive allies of the Acanthodians with their pairs of fins reduced to the normal two, in which the stiffening was attained by internal rods of cartilage instead of mere skin-structures; for a long-bodied (and thus senile) survivor of this allied tribe occurs in the Upper Devonian of Ohio (*Cladoselache,* Fig. 6). Here the fin-flaps are strengthened inside by a row of simple parallel bars of cartilage, which exhibit a tendency to be squeezed together. The early fishes which had reached this stage were prepared for further advance. Those which failed to make any progress in their skin-skeleton experienced very slight changes in their whole anatomy, and gradually passed into the modern sharks and skates. Those in which the skin-skeleton always remained extensive, and soon took the form of symmetrically arranged bony plates and scales, rapidly became developed into the higher fishes which swarm today."

At the same time that early Elasmobranchs were strengthening and otherwise improving their paired fins, similar modifications were in progress among two other groups of typical fishes which suddenly became dominant during the Devonian. One of these groups is that commonly known as Dipnoans (Dipnoi, or more properly, Dipneusti), the name of "double-breathers" referring to their power of respiration by both gills and lungs. The second competing rival in the line of advance is the group of Crossopterygii, or "fringe-finned ganoids". Both are possibly descended from primitive Elasmobranchs, and both are conspicuous for their conversion of paired fins into paddles suitable for crawling in the mud, or for ordinary swimming in water. A curious feature of evolutionary progress is that to which Smith Woodward has called attention in another recent article,* namely, no sooner had fishes acquired the paddle-shaped paired fins than "they suddenly became the special feature of the Devonian period in all parts of the globe that have hitherto been geologically examined, and they attained their maximum development, being more numerous and more diverse in form than at any subsequent time."

The paddle-shaped type of fin became prevalent among the highest fishes at about the very epoch (Middle and Upper Devonian) when terrestrial four-legged vertebrates were just beginning to make their appearance. The coincidence is noteworthy, and favors the current opinion that Labyrinthodont amphibians (Stegocephalia) are descended from primitive Crossopterygii. There are still some controverted points in regard to this theory, whose consequences are far-reaching, hence it will be instructive to compare the views of the English author we have already quoted both on this matter and on the development of effective fins in higher fishes. His diction is given in slightly condensed form in the following paragraph.

"During the Middle and Upper Devonian there was a general tendency for the most advanced fishes to become crawlers rather than swimmers; and there cannot be much doubt that the known Crossopterygii are the unsuccessful survivors of the race which

*Woodward, A. S., The Relations of Palæontology to Biology. Ann. Mag. Nat. Hist. 1906, ser. 7, **18**, p. 315. Extract from an address delivered before the International Congress of Arts and Science, St. Louis.

originally produced the earliest crawling lung-breathers or Labyrinthodonts. No intermediate forms have hitherto been discovered, while the links are still wanting between the simple paddle of the fish and the five-toed or four-toed limb of the Labyrinthodont; but the Devonian and some later Crossopterygii are the only fishes which agree with the Labyrinthodonts in (1) the arrangement of their external head-bones; (2) the complexity of their tooth-structure; (3) the possession of vomerine tusks; (4) the frequent presence of a pineal foramen in the skull; and (5) the common occurrence of sclerotic plates around the eye. These resemblances can scarcely be accidental, especially considering the period at which they occur; and it is one of the problems of palæontology to determine the exact relationships between the paddle-finned fishes and the lung-breathers by the discovery of perhaps Lower Devonian links."

Passing now to the next higher grade of fishes, the Chondrostei, or Sturgeon tribe, which flourished especially during the Carboniferous and Permian, we note this peculiarity of their fin-structure: the internal cartilages formed only an effective basal support for an expanse of membrane, which was stiffened by flexible skin-fibres. The latter eventually formed fin-rays, and articulated with the basal pieces when the cartilage was replaced by bone. Thus arose the best form of appendage both for balancing the body and for progression in water. The typical Palæozoic Chondrosteans having this type of fin were rapacious fishes, and a few of them survived with little change until Upper Jurassic times. Some of them degenerated into eel-shaped creatures during the early Mesozoic, while others grew to unwieldy proportions and eventually passed into the modern sturgeons. The median fins became absolutely complete in the Protospondyli, after the upper lobe of the tail had shortened so that the caudal fin formed a flexible fan-shaped expansion at the blunt end of the body, while each separate ray in the other median fins was provided with its own definite support. The Protospondyli characterized the Triassic and Jurassic periods, and exhibited endless variety; but their sole survivors at the present day are the long-bodied Lepidosteus (garpike) and Amia (bowfin) of American fresh waters.

Associated with almost the earliest Protospondyli, there were a few precocious fishes which evidently completed their vertebral column at once. This race, including such genera as Pholidophorus and Leptolepis, seems to have temporarily exhausted itself in the effort, for it always occupied a secondary place in the fish faunas until the beginning of the Cretaceous period, when it rapidly multiplied, became dominant, and replaced the Protospondyli. Thus arose the modern fishes, of the same grade as the herring and salmon, characterized not only by a complete vertebral column, but also by a simplified lower jaw, which consists only of two pieces on each side. The Isospondyli, as they are termed, being thus provided with a completely bony internal skeleton as well as completed fins, admitted of many more variations than any of their forerunners.

Among fishes, as among other animals, spines characterize only the latest representatives of the class. The Acanthopterygii ("spine-finned") are thus the highest and latest fishes of all, though they sometimes eventually descend from their high estate by degeneration. They exhibit all the peculiar changes in the skull, upper jaw, and pelvic fins noticed as first appearing in a variable manner in the Cretaceous Isospondyli. The spiny-finned fishes began by Berycoids and possibly Scombroids in the Chalk, closely resembling, but not identical with, genera living at the present day. By the Eocene period, however, nearly all the modern groups of Acanthopterygii had become completely separated and developed, and their sudden appearance is as mysterious as that of early Eocene mammals.

In reviewing the history of this chain of development that has now been traced, we are struck with the fact that fundamental advances in the grade of fish life have always been sudden and have begun with excessive vigor at the end of a long period of stagnation, while each advance has been marked by the fixed and definite acquisition of some new character—an "expression point", as Cope termed it,—which seems to have rendered possible, or at least has been an essential accompaniment of, a fresh outburst of developmental energy. As we have seen, the successive "expression points" among fishes were the acquisition of (1) paddle-like paired fins; (2) shortened fin-bases but per-

sistent heterocercal tail; (3) completed balancing fins and homocercal tail; and (4) a completed internal skeleton.

Finally, to recapitulate the brief summary given by Woodward in more general terms, "fossils prove that the earliest known fish-like organisms strengthened their external armour so long as they remained comparatively sedentary; that next the most progressive members of the class began to acquire better powers of locomotion, and concentrated all their growth-energy on the elaboration of fins; that, after the perfection of these organs, the internal bony skeleton was completed at the sacrifice of outer plates, because rapid movement necessitated a flexible body and rendered external armour less useful; that, finally, in the highest types the vertebrae and some of the fin-rays were reduced to a fixed and practically invariable number for each family or genus, while there was a remarkable development of spines. As survivors of most of these stages still exist, the changes in the soft parts which accompanied the successive advances in the skeleton can be inferred. Hence Palæontology furnishes a sure basis for a natural classification in complete accord with the development of the group." *

General Classificatory Scheme.—It is now in order to consider the more salient features of classification adopted for arranging the different groups of fishes in a natural system, one that is founded on broad general distinctions, and aims to be expressive of genetic relations. The fundamental principle which serves as the basis of classification is that which takes cognizance of two distinct types or plans of cranial structure among fishes, plans that have been manifest at least ever since Lower Devonian times, and between which no definitely intermediate conditions are to be observed. Huxley has appropriately named one of these types of cranial structure "autostylic", and the other "hyostylic".† In the former, as illustrated by Chimaeroids and modern Lung-fishes, the upper segment of the mandibular arch is directly fused with the chondrocranium, while the corresponding segment of the hyoid arch is atrophied or absent. But in the

* Woodward, A. S., The Relations of Palæontology to Biology. Ann. Mag. Nat. Hist. 1906, ser. 7, **18**, p. 314.

† Huxley, T. H., On *Ceratodus forsteri*, etc. Proc. Zool. Soc. 1876, p. 40.

hyostylic condition, on the other hand, as exemplified by Elasmobranchs, bony-scaled fishes ("Ganoids") and modern osseous fishes ("Teleosts"), the same elements are loosely articulated with the primordial cranium, and the upper segment of the hyoid arch forms a movable suspensorium (hyomandibular). The autostylic condition was carried to a still higher phase of development by terrestrial amphibians, and through them transmitted to all higher vertebrates; whereas the hyostylic condition culminates in the extreme specialization characteristic of the more modern types of fishes—those expressions of vertebrate life which are most completely adapted to an aquatic habitat. It may be remarked parenthetically that only a few sharks, such as the existing Notidanus, and perhaps the Permian Pleuracanthus (Fig. 15, page 93), display an arrangement by which both the mandibular and hyoid arches have their own separate and independent connections with the cranium, and the skull in that condition is said to be "amphistylic".*

The nature of the attachment of the lower jaw to the cranium being regarded as of prime importance for distinguishing major divisions, the next most valuable criterion for systematic purposes is provided by the structure of the exoskeleton. This happens to be constructed in such wise that two groups, both of the autostylic and of the hyostylic fishes can be readily distinguished. Thus, the placoid dermal calcifications, or "shagreen" covering the head and body of Chimaeroids are fundamentally distinct from the bony headshield and regularly disposed imbricating squamation of Dipnoans. The same distinction applies with equal force in separating Elasmobranchs from Teleostomes, this latter title being Owen's comprehensive designation for both "Ganoids" and "Teleosts". Among Teleostomes, the rhombic was probably the more primitive form of scales, this type being characteristic of the geologically older scaly fishes. Structurally the scales of Dipnoans are not unlike those of Teleostomes, though there are minor differences in detail. The resemblance in scale-structure between such widely distinct groups is without special significance, however, other than as an example of evolutionary convergence.

* Huxley, T. H., Proc. Zool. Soc. 1876, p. 41 *et seq.*

On the basis of the foregoing distinction it follows that Pisces proper are divisible into four subclasses, all of which were in existence as early as the beginning of the Devonian, and have followed distinct courses of development ever since. The ancestors of these subclasses are indeed unknown, but would probably fall under the designation of primitive Elasmobranchs.* For determining the ordinal position of any fish within its appropriate subclass, the most satisfactory recourse is afforded by the degree of specialization of the paired fins. It is now a well established principle in palæontology that both the median and the paired fins of fishes originated in the first instance from continuous dermal folds, and during the course of their elaboration passed through definite phases, the most important of which are summarized by Smith Woodward in the following propositions:

1. Fishes originally possesed (*a*) a continuous median dermal fold, and (*b*) a pair of continuous lateral folds, each supported by a regular series of parallel endoskeletal rods diverging from the axial skeleton.

2. These continuous folds (the median fold in most cases and the lateral folds always) soon became subdivided, with a concomitant reduction in the size and number of their supports.

3. Gradual and constant specialization has been marked by the shortening-up of the endoskeletal supports of the resulting fins, and by the concomitant strengthening of the dermal rays.

4. In the course of this evolution the endoskeletal fin-supports have eventually lost all direct connection and correlation with the axial skeleton, those of the dorsal and anal median fins becoming correlated instead with the dermal rays, each supporting one of these rays.

The order in which these stages in the evolution of paired fins are successively passed through by the four leading divisions or subclasses of fishes is apparent from the following table, which we have reproduced after Smith Woodward:

* See on this point President Jordan's remarks on C. T. Regan's taxonomic conclusions as presented in his paper on the "Phylogeny of Teleostomi". *Guide to the Study of Fishes*, vol. 1, p. 623.

SCHEME OF SUBCLASSES AND ORDERS OF THE CLASS PISCES

Stages in Evolution of Paired Fins	*Hyostylic Fishes*		*Autostylic Fishes*	
	ELASMOBRANCHII	TELEOSTOMI	HOLOCEPHALI	DIPNOI
1. Supports as parallel rods	PLEUROPTERYGII (early Palæozoic)	[Unknown]	[Unknown]	[Unknown]
2. Archipterygium of Gegenbaur (elongate or abbreviate)	ICHTHYOTOMI (late Palæozoic)	CROSSOPTERYGII (Palæozoic and Mesozoic)	[Unknown]	SIRENOIDEI (Palæozoic to Recent)
3. Pectorals di- or tribasal; pelvics abbreviate	SELACHII (late Palæozoic to Recent)	CROSSOPTERYGII (Recent)	CHIMAEROIDEI (early Mesozoic to Recent)	[Unknown]
4. Basal cartilages small or rudimentary	ACANTHODII (Palæozoic)	ACANTHOPTERYGII (Palæozoic to Recent)	[Unknown]	ARTHRODIRA (early Palæozoic)

We will conclude our remarks on the subject of classification by presenting the following outline scheme, which shows the arrangement of the higher divisions of fishes and fish-like vertebrates that seems to accord best with the present state of our knowledge, and is sanctioned by competent authorities.

Class AGNATHA

SUBCLASSES	ORDERS	FAMILIES
1. CYCLOSTOMI	1. Hyperotreta or Myxinoidea	[Unknown as fossils]
	2. Hyperoartia or Petromyzontes	[Unknown as fossils]
2. OSTRACOPHORI	1. Heterostraci	Coelolepidae Psammosteidae Pteraspidae
	2. Anaspida	Birkeniidae Euphaneropidae
	3. Osteostraci	Ateleaspidae Cephalaspidae
	4. Antiarchi	Asterolepidae

Class PISCES

SUBCLASSES	ORDERS	SUBORDERS
1. ELASMOBRANCHII	1. Pleuropterygii	
	2. Ichthyotomi	
	3. Acanthodii	
	4. Selachii.....	Asterospondyli Tectospondyli
2. HOLOCEPHALI	1. Chimaeroidei	
3. DIPNEUSTI	1. Ctenodipterini	
	2. Sirenodei	
	3. Arthrodira	
4. TELEOSTOMI	1. Crossopterygii	1. Haplistia 2. Rhipidistia 3. Actinistia 4. Cladistia
	2. Actinopterygii	1. Chondrostei 2. Protospondyli 3. Aetheospondyli 4. Isospondyli. &c. &c.

IV.

Systematic Account of Devonian Fishes, with Special Reference to those of Iowa and Adjoining States.

"Wenn ich ein zerstreutes Gerippe finde, so kann ich es zusammenlesen und aufstellen; denn hier spricht die ewige Vernunft durch ein Analogen zu mir, und wenn es ein Riesenfaulthiere wäre."—*Goethe.*

Class **AGNATHA.**

Cyclostomes, or as they are sometimes called, the Marsipobranchs, in allusion to their pouch-like branchial sacs, include the most primitive of all existing vertebrates. They are divided into two orders, the first comprising the Hag-fishes or Myxinoids, and the second the Lampreys. These orders are very distinct from each other, though sharing important characters in common which separate them widely from ordinary fishes. For instance. they differ collectively from Pisces proper in the total absence of limbs, together with pectoral and pelvic arches for their support, and, more strikingly still, in the lack of a lower jaw. Most students are of the opinion that the absence of these structures in Cyclostomes is a primitive character, although it has been thought by some that jaws and limbs were primordially present, and have since become lost through degeneration. As stated by President D. S. Jordan, "there is no clear evidence that the [sub-]class of Cyclostomes, as now known to us, has any great antiquity, and its members may be degenerate offshoots from types of greater complexity of structure."

In regard to the occurrence of supposed extinct Cyclostomes, such as the much debated Palæospondylus, whose relations are still considered doubtful, the same distinguished author speaks as follows:

"No species belonging to the class of Cyclostomes has been found fossil. We may reason theoretically that the earliest fish-like forms were acraniate or lancelet-like, and that lamprey-like forms would follow these, but this view cannot be substantiated from the fossils. Lancelets have no hard parts whatever, and could probably leave no trace in any sedimentary deposit. The lampreys stand between lancelets and sharks. Their teeth and fins might at least occasionally be preserved in the rocks, but no structures certainly known to be such have yet been recognized. It is, however, reasonably certain that the modern lamprey and hagfish are descendants, doubtless degraded and otherwise modified, from species which filled the gap between the earliest chordate animals and the jaw-bearing sharks." *

Among the earliest and most primitive forms of fish-life with which Palæontology acquaints us, there appears in the Middle and Upper Silurian, and continues thenceforth throughout the Devonian, a curious group of Craniates whose organization stands in sharp relief to that of fishes proper, whose more precise relations are still considered doubtful, and whose origin is involved in complete obscurity. This group is commonly known under Cope's title of Ostracophores, or Ostracoderms. Appearing suddenly and unheralded, and passing away at the close of the Devonian without leaving descendants, we can only speculate in regard to the ancestry of these creatures; yet the inference seems warranted that they took their rise from Protochordates at about the same time as primitive Elasmobranchs, and diverged in a different direction. Their adaptive energy was expended chiefly in the development and elaboration of a hard external skeleton, and their progressive modifications stopped short of acquiring completely formed jaws, of arches for the support of paired limbs, and of the ordinary type of fish fins. Indeed, appendages of any kind do not occur except within the limits of a single family,† the Asterolepidae, where jointed

* Jordan, D. S., Guide to the Study of Fishes, 1905, vol. 1, p. 487.

† On the alleged occurrence of several pairs of appendages in the Cephalaspidae and Trematapidae, see the following papers by Professor Patten in the American Naturalist for 1902 and 1903: On the Structure and Classification of the Trematapidae. **36**, pp. 379-393.—On the Appendages of the Trematapidae. **37**, pp. 223-242 (with critique, p. 573).—On the Structure of the Pteraspidae and Cephalaspidae. **37**, pp. 827-859.

oar-like swimming-organs are attached to the pectoral region, but are of very different nature and structure from the fins of gnathostomous fishes. Membranous median fins are developed, however, the form of body is fish-like, there is a genuinely piscine heterocercal tail, scales or scutes usually cover the abdominal region, a well-defined sensory canal system is present in the higher forms, and when the headshield is continuous it is often pierced by branchial apertures. On account of these latter characters we are warranted in postulating community of descent between Ostracophores and the progenitors of ordinary fishes.

Of the four orders of Ostracophores now commonly recognized, all have American representatives. The simplest forms (Anaspida and Heterostraci) occur in the Upper Silurian and Devonian, and are without paired appendages. Bone cells are probably present in the calcifications of the Anaspida, but wholly lacking in the Heterostraci. The third order, Osteostraci, is confined for the most part to the Upper Silurian and Lower Devonian, though occasionally found in the Upper Devonian. Bone cells are present, but there is no trace of dermal sense organs either upon or within the shield. The fourth order, Antiarchi, with a complex system of dermal plates and a remarkable pair of appendages, is essentially Devonian, and as abundant in the uppermost as in the lowest strata. The subclass becomes extinct at the close of the Devonian, without taking part in the evolution of the fishes of later periods.

Order **HETEROSTRACI.**

These primitive Ostracophores are represented in the Palæozoic rocks of North America by two genera, Cyathaspis and Palæaspis, occurring in the Silurian, and by a variety of Thelodus-like scales (Pl. I, Figs, 7, 8, 15; Pl. II, Figs. 13, 14) from the Lower and Middle Devonian. No indications of such forms, however, have yet been found in States adjoining the Mississippi Valley. The only American species of Cyathaspis that has been recorded, *C. acadica* (Matthew), is founded upon indifferently preserved material from strata of supposed Niagara age in New Brunswick, and is the oldest trace of vertebrate life yet discovered in Canada. Palæaspis likewise appears to

be known in this country by a solitary species occurring in the middle portion of the Salina beds in Perry county, Pennsylvania, the horizon being approximately equivalent to the English Ludlow, or to the interval between that and the Wenlock. The great antiquity of this interesting form entitles it to a brief notice in this connection.

Palœaspis americana Claypole.

1884. *Palœaspis americana* E. W. Claypole, Am. Nat. **18,** p. 1224.
1884. *Palœaspis bitruncata* E. W. Claypole, *Ibid.*, p. 1224.
1885. *Palœaspis americana* E. W. Claypole, Quar. Journ. Geol. Soc. **41,** p. 62, woodcut fig. 7.
1885. *Palœaspis bitruncata* E. W. Claypole, *Ibid.*, p. 62, woodcut fig. 8.
1885. *Palœaspis bitruncata* and *elliptica* E. W. Claypole, Proc. Amer. Assoc. Adv. Sci., 33d Meeting, p. 426.
1885. *Palœaspis elliptica* E. W. Claypole, Rept. Brit. Assoc. Adv. Sci., 54th Meeting, p. 733.
1892. *Palœaspis americana* E. W. Claypole, Quar. Journ. Geol. Soc. **48,** p. 561, fig. 8.
1893. *Palœaspis americana* E. W. Claypole, Amer. Nat. **27,** p. 375.
1895. *Palœaspis americana* B. Dean, Fishes, Living and Fossil, p. 71.
1898. *Palœaspis americana* A. S. Woodward, Outlines of Vertebrate Pal., p. 6.
1906. *Palœaspis americana* M. Leriche, Mém. Soc. Géol. du Nord de la France, **5,** p. 24.
1907. *Palœaspis americana* C. R. Eastman, Mem. N. Y. State Museum **10,** p. 29.

This species, whose synonymy is indicated above, differs from the British *P. sericea* only in minor particulars, and both approximate very closely to the type of Cyathaspis. In fact, one of the latest students of these forms, M. Leriche, has proposed to unite them in a single genus.* Pteraspis itself, of which the type is *P. rostrata* (Fig. 7), is strictly European, and common

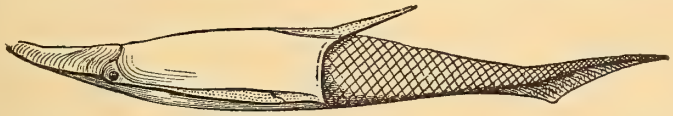


FIG. 7.

Fig. 7. *Pteraspis rostrata* Agassiz. Lower Old Red Sandstone; Great Britain. Left lateral aspect of partially restored individual, x ⅔. The tail is not certainly known to be heterocercal.

to both marine and estuarine, or possibly even fluviatile (Old Red Sandstone) deposits.

*Leriche, Maurice, Contribution a l'étude des poissons fossiles du Nord de la France et des régions voisines. Mém. Soc. Géol. du Nord de la France, 1906, **5,** p. 25.

Orders **ANASPIDA** and **OSTEOSTRACI.**

Neither of these orders is represented in the fossiliferous rocks of the United States. A single species described as *Euphanerops longaevus* by Smith Woodward is known from the Upper Devonian of Scaumenać Bay, Province of Quebec, Canada, and the Osteostraci are represented by four species of Cephalaspis (text-fig. 4, page 58), two from the Lower, and two from the Upper Devonian of British North America. Notwithstanding their rarity in rocks of the western hemisphere, these forms enjoyed a cosmopolitan distribution during the Devonian, as is shown by the recent discovery of Thyestes in Australia.*

It has been claimed by Professor Patten that the genus Cephalaspis is provided with "a fringe of jointed and movable appendages (25 to 30 pairs) along the ventral margin of the trunk," the structures commonly known as marginal scales being interpreted by him as swimming-organs, or as he calls them, "fringing processes". These fulcra-like scales were even regarded by this author at one time as probable "antecedents of the lateral fold of vertebrates"; but in the light of Dr. Gaskell's re-examination of their structure, and the unanimity of opinion in the minds of all other students that paired appendages do not occur, we may continue to believe that the term marginal scales is not a misnomer for the structures in question.†

Order **ANTIARCHI.**

The Antiarchi of the Devonian possess a much more complex system of dermal plates than other groups of Ostracophores, and are provided with a pair of singularly jointed armored appendages, usually movable, evidently serving as organs of progression, and totally unlike the limbs of other vertebrates.‡ The head- and body-shields are always movably articulated, and both are traversed by well defined sensory canals. The bone structure is dense, though with vascular cancellae in the middle layer of

* *Cf.* F. Chapman, in Proc. R. Soc. Vict., 1906, n. s., **18**, pp. 93-100.

† *Cf.* W. H. Gaskell, in Journ. Anat. and Physiol., 1903, **37**, p. 198. Also Dr. O. Jaekel in Zeitschr. deutsch. geol. Ges. 1903, **55**, p. 84, and articles by the present writer in Amer. Nat. and Science for 1903 and 1904.

‡ For references to different views of the nature of these organs, see an article on Asterolepid appendages in Amer. Journ. Sci., 1904, ser. 5, **18**, pp. 141-144.

the more thickened plates. The external ornament always consists of tubercles and coarse rugae. At least one membranous dorsal fin is present, and in Bothriolepis two have been detected by Patten. The tail, either naked or scaly, is furnished in Pterichthys at least with a large membranous caudal fin of genuinely heterocercal form.

The forms belonging to this order are included within a single family, the Asterolepidae, sometimes, but incorrectly called the "Pterichthyidae". The typical genus, Pterichthys (text-figs. 8-11), is not known to occur in this country; but the Upper Devonian Bothriolepis, which differs from Pterichthys principally in its longer appendages, scaleless tail, and minor details of the body armor, is found both in the eastern part of North America and in Colorado, four species having been described from this continent in all. Asterolepis itself appears to be represented by portions of the body armor occurring in the Chapman sandstone of Aroostook county, Maine, the accompanying invertebrates indicating a lowermost Devonian horizon. This species, which has been described under the name of *A. clarkei,* is noteworthy

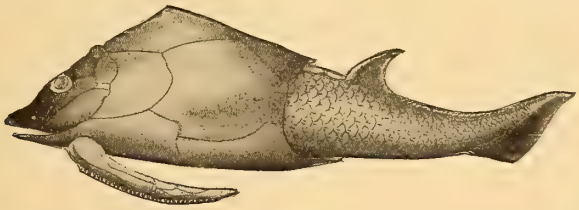


FIG. 8.

Fig. 8. *Pterichthys testudinaris* Agassiz. Lower Old Red Sandstone; Scotland. Left lateral aspect, restored by Dr. R. H. Traquair, x ½.

for continuing the history of Asterolepids back to a more remote period than has previously been known for this group. The so-called *Astraspis desiderata* of Walcott, from the Ordovician (Trenton) of Canyon City, Colorado, by some conjecturally referred to the Asterolepidæ, is of entirely problematical nature.

Family **ASTEROLEPIDAE.**

Head and body covered with dermal plates which are externally sculptured and tuberculate, the dorsal and ventral shields of the trunk firmly united by the lateral plates. Orbits very closely approximate, separated by a loose interorbital median

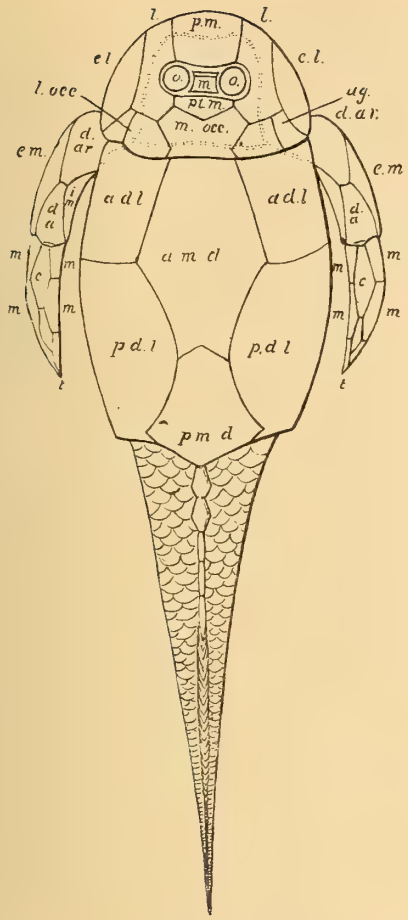
plate. Position of the nasal organs not definitely known. One pair of paddle-like swimming appendages, completely encased in osseous plates, and articulated by a complex joint with the anterior ventro-lateral plates of the trunk. Sensory canal system well developed. Tail either naked or scaly; one or two dorsal fins, and a completely heterocercal tail in at least the typical genus.

To form an adequate conception of the creatures indicated by numerous detached fragments of Asterolepid armor from the Upper Devonian of the eastern United States and Colorado, it is necessary to pay strict attention to recent work that has been done in investigating Scottish and Canadian species. The principal advance that has been made during late years is owing to the researches of Dr. R. H. Traquair, of Edinburgh, Professor William Patten, of Dartmouth, and Professor Otto Jaekel, of Greifswald, Germany, whose results are scattered through a very considerable number of papers. Without doubt the most notable contribution, and at the same time one of the most authoritative, is Dr. Traquair's *Monograph on the Asterolepidae,* still in course of publication by the Palæontographical Society of Great Britain. As students who have not access to special libraries can hardly be supposed to be familiar with the parts* of this work already published, we shall probably do well to present here a revised account of the Asterolepid organization, which has been very slightly condensed from the Scottish author's descriptions. This account follows immediately.

Structure of Asterolepids, as illustrated by Pterichthys.—Before entering into a description of individual forms, it is first of all necessary to understand the general structure of an Asterolepid, and to know the names by which the various parts found in the fossil state may be distinguished. For this purpose it is well to take Pterichthys (Figs. 9-11), as being the genus best known in its entirety, if not in every manner of detail.

The body armor consists of osseous plates closely fitted together, closed above, below and at the sides, but open in front for the head, and behind for the tail. The head is covered almost entirely by a dorsal shield, formed also of plates united by su-

*Part ii. No. 1, 1894; No. 2. 1904; No. 3, 1906.



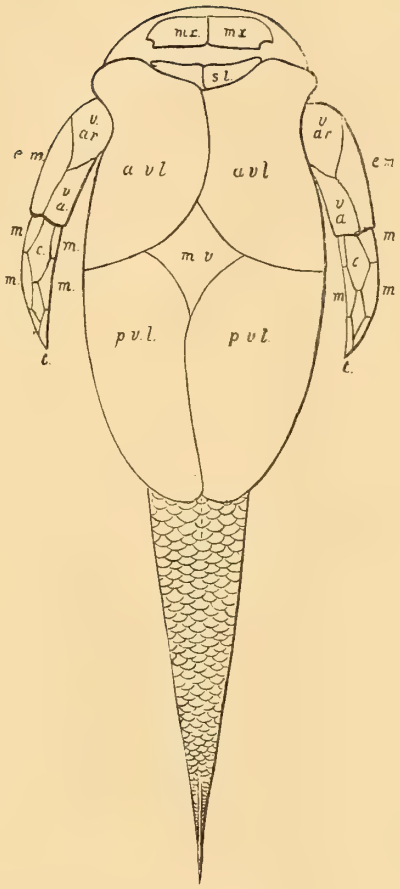


FIG. 9. FIG. 10.

Fig. 9. *Pterichthys milleri* Agassiz. Lower Old Red Sandstone; Scotland. Restored outline of dorsal aspect, x ¾ (after Traquair).

Fig. 10. The same from the ventral aspect. Lettering for both figures, and for Fig. 11: *m. occ.*, median occipital; *l. occ.*, lateral occipital; *ag.*, angular; *pt. m.*, post-median; *p. m.*, pre-median; *l.*, lateral; *e. l.*, extra-lateral; *m.*, median; *o.*, ocular; *mx.*, maxilla; *s. l.*, semilunar; *a. m. d.*, anterior median dorsal; *p. m. d.*, posterior median dorsal; *a. d. l.*, anterior dorso-lateral; *p. d. l.*, posterior dorso-lateral; *a. v. l.*, anterior ventro-lateral; *p. v. l.*, posterior ventro-lateral; *m. v.*, median ventral; *d. ar.*, dorsal articular; *v. ar.*, ventral articular; *e. m.*, external marginal; *i. m.*, internal marginal; *d. a.*, dorsal anconeal; *v. a.*, ventral anconeal; *c.c.*, centrals of lower limb; *m. m. m. m.*, marginals of lower limb; *t.*, terminal of lower limb.

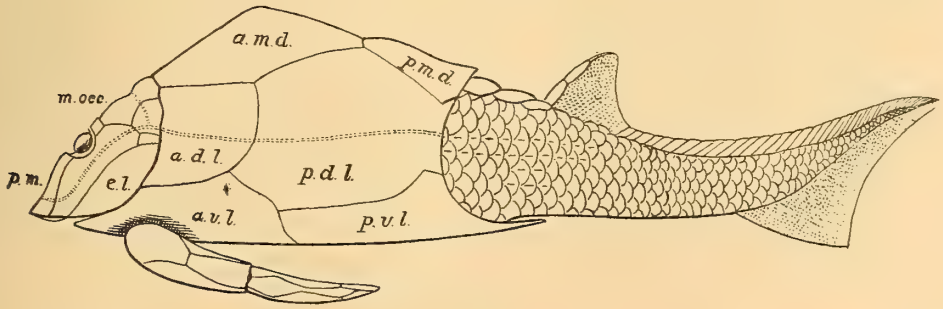


FIG. 11.

Fig. 11. *Pterichthys milleri* Agassiz Restored outline of lateral aspect, x ¾ (after Traquair).

ture. The two pectoral limbs consist also of plates similarly united, and are internally hollow so far as their remains in the stone are concerned.

The headshield (text-fig. 9) is semielliptical in shape, rounded in front and truncated behind, where it joins the system of body plates. In the center it shows a transverse aperture, the median opening or orbit, slightly contracted in the middle and expanded at each of its rounded sides. This opening is in perfect specimens filled up by at least three other plates, which, being loose, are usually lost. Of these, one is in the center, quadrate in shape, but with concave outer margins, and may be called the median or pineal plate (*m*), as it shows on the internal aspect a shallow rounded pit, pointed out by Dr. Smith Woodward as probably the impression of the pineal body. This is, by its outer concave margins, in contact on each side with a rounded convex ocular plate (*o*), indicating certainly the position of the eye, but whether or not due to an ossification in the sclerotic is doubtful. [In Bothriolepis the orbits have two sclerotic plates each, according to Professor Patten.] The nuchal region is occupied by a large plate, the median occipital (*m. occ.*), shaped something like the conventional royal "crown", but without the pinnacle in the center. In front of this and immediately behind the median opening is a smaller plate, the postmedian (*pt. m.*); while between the anterior margin of that opening and the front of the cranial shield is one of larger size and somewhat quadrate shape, the premedian (*p. m.*). Two large pieces, the lateral plates (*l*), one on each side, bound the opening laterally, and also extend to the front of the shield. Behind these, and forming part of the hinder margin of the buckler external to the median occipital, are two other paired plates, the lateral occipital (*l. occ.*) and the angular (*ag*).

The upper and lateral aspect of the cranial shield is now completed by a plate on each side, which is only loosely articulated in Asterolepis and Pterichthys, though formerly sutured in Bothriolepis. This is the extra-lateral (*e. l.*) or opercular plate, as it has also been called by some writers.

On the lower aspect of the head and close behind the anterior margin of the shield are two transversely oblong plates (*mx*),

right and left, the position of which was first determined by Whiteaves in Bothriolepis,* an observation corroborated by Smith Woodward.† These plates must have been situated in front of the mouth, and may therefore be referred to at least conventionally, as "maxillae." There can be no doubt that they were similarly placed in Pterichthys ("mental plates"), and in Asterolepis they were designated *maxillae inferiores* by Pander. Close to the postero-external angle of each of these plates there is a rounded notch, considered by Smith Woodward in Bothriolepis as possibly indicating a nasal opening.‡

The body-carapace is box-like, very nearly flat below and vaulted above. It is composed of thirteen plates, of which three are median and ten paired, and these are united with one another by overlapping sutures, a marginal band along the internal surface of the overlapping plate being excavated to fit on to a correspondingly excavated band along the margin of the outer surface of the plate overlapped.

On the upper surface we see the anterior and posterior median dorsal plates (*a. m. d.* and *p. m. d.*) succeeding each other in the middle line and on each side; passing down also on the lateral wall are the anterior and posterior dorso-laterals (*a. d. l.* and *p. d. l.*). On the under surface, and also taking part in the formation of the lateral wall, are two pairs of plates, the anterior and posterior ventro-lateral (*a. v. l.* and *p. v. l.*), of which the anterior requires special attention, as to it the pectoral limb is articulated. Near the anterior extremity of this plate, on the outer aspect and close above the angle which separates the lateral from the ventral surface, is a shallow excavation, from the bottom of which rises a peculiar process resembling a thick-walled cup or helmet, whose hollowed-out "mouth" points outwards, and also somewhat backwards and downwards, the cup itself being fixed by a stout ridge which traverses the containing hollow from behind forwards and also slightly downwards. This may be called the brachial process ("helmet-process" of Pan-

*Trans. Roy. Soc. Canada, 1887, **4**, section iv, pp. 103, 104.

†Geol. Mag. 1892, decade 3, **9**, p. 484.

‡This notch is somewhat differently placed in Bothriolepis, being fair on the outer margin of the plate instead of at its postero-external angle. The plates here called maxillae are interpreted by Professor Patten as mandibles.

der), as it is grasped by the two articular plates of the upper arm, and thus forms the brachial joint. Immediately behind this brachial process is a small oval aperture, the brachial foramen, perforating the brachial fossa from the interior, and which no doubt served to convey to the arm the blood-vessels and nerves required for its supply.

The ventral surface of the carapace is completed by the median ventral plate (*m. v.*, Fig 10), in the center, and in front by two very small semilunar plates (*s. l.*), each of which occupies a space cut out from the inner half of the anterior margin of the anterior ventro-lateral, and is in contact in the middle line with its fellow of the opposite side. In Bothriolepis these last-mentioned plates seem to be represented by a single median one.

Each of the hollow arms or brachia is divided by a transverse elbow-joint into two segments, proximal and distal. The proximal segment or "upper arm" is trigonal in transverse section, getting more flattened towards the elbow, and shows three surfaces, a dorsal slightly convex, a ventral flat, and a somewhat concave internal one, the latter fitting on to the side of the carapace when the arm is flexed. The proximal extremity of the arm is formed by two articular plates (*d. ar.* and *v. ar.*), dorsal and ventral, whose rounded and hollowed proximal expansions grasp between them the brachial cup-like process of the anterior ventro-lateral plate of the body. These plates are consequently not in apposition at the joint, but are separated by an interval or slit, which contains and moves on the ridge attaching the brachial cup to the bottom of its fossa, and this interval is closed internally by the internal articular plate, and externally by the upper narrow extremity of the external marginal.* The internal articular plate (*i. ar.*) placed right on the inner surface of the arm below the joint, is not seen in these figures; its free upper margin is concave, forming a rounded notch, over which the nerves and nutrient vessels of the arm must have passed. The external marginal (*e. m.*) forms the whole of the outer border of the upper arm, and has nearly opposite to it the smaller internal marginal (*i. m.*), while dorsally and ven-

*In Bothriolepis, however, the slit is completed externally by the two articular plates coming together above the external marginal.

trally this part of the limb is completed by the dorsal and ventral anconeal pieces (*d. a.* and *v. a.*).

The distal portion of the limb, or "lower arm", is more flattened, and shows a dorsal and ventral surface, two sharp margins, external and internal, and a sharp apex or point. The ventral surface, and presumably the dorsal as well, is composed of two central pieces (*c*), and six marginals (*m*), three of which are external and three internal. It is the distal marginal on the inner side which forms the acute point or apex of the appendage, as first noticed by Jaekel.*

The elbow-joint is somewhat complicated. Each upper marginal of the lower arm is furnished above with an articular process, which is received within the lower extremities of the internal and external marginal plates respectively of the upper part of the limb. Then, on the other hand, each anconeal plate, dorsal and ventral, of the upper arm has a small, flat articular process below, which fits into a slit on the outer surface of the upper extremity of the corresponding upper central of the lower arm. It is hard to say how much movement could have been here allowed, but from the form of the joint it seems probable it was limited to a slight flexion and extension, and possibly only in the horizontal plane, as in the case of the shoulder.

The tail (in Pterichthys) is covered with small, rounded, slightly imbricating osseous scales, which are arranged in longitudinal rows, and also in transverse bands. On the dorsal aspect behind the carapace there is a small median fin. Along the dorsal margin the scales are in the form of a few narrow longitudinal median plates; behind it they are elongated and imbricating, like the fulcra or V-scales along the body prolongation of the tail of a Palæoniscid fish. The dorsal fin is triangular, acuminate, and covered with small scales, no distinct "rays" being seen; and along its anterior margin some prominent elongated scales are placed, producing an appearance which has been mistaken for a spine. The hinder extremity of the fish is formed by a completely heterocercal caudal fin, the body axis curving upwards as a pointed and slightly arched prolongation, and

*Jaekel, O., Ueber die Organisation und systematische Stellung der Asterolepiden. Zeitschr. deutsch. geol. Ges., Mai-Protokoll, 1903, **55**, pp. 41-60.

giving origin below to a fin-expanse which is triangular in form, or slightly excavated behind, but not bilobate.

On the body and head there was a well marked lateral sensory canal system, indicated by grooves on the external surfaces of certain of the osseous plates, which grooves have often been mistaken for sutures, especially those on the cranial shield. On each side the lateral groove passes from behind forwards over the posterior and anterior dorso-lateral plates, and thence on to the external occipital, where it at once bifurcates, a transverse branch passing across the median occipital to join its fellow of the opposite side. The main groove then runs forward on the lateral cranial plate, and arriving in front of the median opening it bends inwards to join the opposite groove on the premedian plate; a slightly different arrangement, however, is seen in Bothriolepis, as we shall see when that genus comes to be specially considered.

Genus **ASTEROLEPIS** Eichwald.

Median dorsal plate overlapping both the anterior and posterior dorso-lateral plates. Arms shorter than the system of body plates; articular plates of the upper arm scarcely meeting externally over the external marginal; forearm consisting of two centrals, two pairs of marginals and a terminal, the latter forming the pointed extremity of the limb. Postmedian plate of the head large and broad, excluding the median occipital from the margin of the orbit; premedian plate notched in front; extralateral plate loosely articulated with the rest of the cranial shield. Superficial ornament consisting of raised tubercles with stellate bases, which may be sometimes confluent. Lateral line system on the head connected by two commissural canals, a posterior one crossing the hinder part of the median occipital, and an anterior one crossing the premedian plate in front of the orbit. Tail unknown.

The characters of this genus do not differ materially from those of Pterichthys, so far as known, except as regards the mode of articulation of the anterior median dorsal plate, and in the number and arrangement of the plates of the pectoral appendage. No specimens of Asterolepis have yet been discovered, however, which show the tail. Like Bothriolepis, this

genus has until recently been supposed to be confined to the Upper Devonian, but indications of a proemial species, which has received the name of *A. clarkei* in honor of the New York State Geologist, are now known to occur in the lowermost Devonian (Chapman sandstone) of Aroostook county, Maine. In the opinion of Dr. J. M. Clarke, the accompanying invertebrate forms indicate an assemblage having a strong element of affiliation with the Coblenzian (Lower Devonian) of the Rhine district, and certain identities with the Helderberg and Oriskany of New York State.

Genus **BOTHRIOLEPIS** Eichwald.

Premedian plate of headshield not notched in front; postmedian small, not excluding the median occipital from the posterior border of the orbit; extralateral, if present, small and narrow. Posterior commissural canal of headshield formed by a V-shaped groove, the apex of which is situated on the median occipital, and the anterior termini in about the center of the lateral plates. Anterior dorsomedian plate overlapping the antero-dorsolateral, but overlapped by the postero-dorsolateral plate. Pectoral appendages at least as long as the armored trunk, segmented into a distal and proximal portion, the latter being much larger than the former, which is narrow and tapering; marginal scutes of the proximal portion meeting mesially, with a minute anconeal element only on the dorsal aspect; articular plates in contact for some distance above the external marginal on the outer aspect; marginal and central scutes of the distal portion more numerous than in Pterichthys. Tail naked; two dorsal fins.

A knowledge of the structure of this genus being indispensable for a correct understanding of the group, it is not surprising that the exquisitely preserved specimens of *B. canadensis,* from the Upper Devonian of Quebec, should have invited the most searching investigation on the part of palæichthyologists. The Canadian material is certainly unrivaled for exhibiting finer anatomical details, and but for the information so derived it would be difficult to interpret the poorly preserved remains occurring elsewhere in North America and in Europe. Bothriolepis is re-

garded as the characteristic Asterolepid genus of the estuarine aspect of the Upper Devonian, and is represented by four American and some half dozen foreign species in strata of that age.

Bothriolepis canadensis Whiteaves.

(Text-figs. 12, 13, 14)

1880. *Pterichthys* (*Bothriolepis*) *canadensis* J. F. Whiteaves, Amer. Journ. Sci. ser. 3, **20,** p. 132.
1881. *Pterichthys* (*Bothriolepis*) *canadensis* J. F. Whiteaves, Canad. Nat. n. s., **10,** pp. 26, 28.
1885. *Bothriolepis canadensis* E. D. Cope, Amer. Nat. **19,** p. 290.
1887. *Bothriolepis canadensis* E. D. Cope, Origin of the Fittest, p. 323, fig. 62.
1887. *Pterichthys* (*Bothriolepis*) *canadensis* J. F. Whiteaves, Trans. Roy. Soc. Canada, **4,** sect. 4, p. 101, pl. 6-9.
1888. *Bothriolepis canadensis* R. H. Traquair, Geol. Mag. dec. 3, **5,** p. 509, and Ann. Mag. Nat. Hist. ser. 6, **2,** p. 496, pl. 18, fig. 6.
1889. *Bothriolepis canadensis* J. F. Whiteaves, Trans. Roy. Soc. Canada, **6,** sect. 4, p. 91.
1892. *Bothriolepis canadensis* A. S. Woodward, Geol. Mag. dec. 3, **5,** p. 484.
1893. *Bothriolepis canadensis* H. S. Williams, Amer. Journ. Sci. ser. 3, **46,** p. 286, text-figs. 3-5.
1898. *Bothriolepis canadensis* E. D. Cope, Syllabus of Lectures on Vertebrata, p. 16, fig. 2.
1898. *Bothriolepis canadensis* A. S. Woodward, Outlines of Vertebrate Palæont. p. 14, text-figs. 13-15.
1904. *Bothriolepis canadensis* W. Patten, Biol. Bull. **7,** p. 113, figs. 1-6.
1904. *Bothriolepis canadensis* R. H. Traquair, Monogr. Fishes Old Red Sandstone, Palæont. Soc. Part 2, no. 2, p. 109, figs. 57-59.
1905. *Bothriolepis canadensis* W. Patten, Yearbook Carnegie Inst. Wash., no. 3, p. 140; no. 4, p. 284.
1907. *Bothriolepis canadensis* C. R. Eastman, Mem. N. Y. State Museum **10,** p. 43, text-figs. 10-12.
1908. *Bothriolepsis canadensis* J. F. Whiteaves, Trans. Roy. Soc. Canada, ser. 3, **1,** sect. 4, p. 249.

A species of moderate size, the head and trunk attaining a length of about 0.17 meter. Head much broader than long, about one-half as long as the dorsal armoring of the trunk; trunk broadly ovate, the sides overhanging the narrowly ovate ventral surface. Proximal segment of pectoral appendages broad, but elongated; distal segment relatively slender, only slightly ornamented, two-thirds as long as the proximal segment; outer and inner margins coarsely serrated. Anterior median dorsal plate as broad as long, more or less keeled in its posterior two-thirds; posterior median dorsal plate longitudinally keeled, the keel rising to a slight eminence near the posterior margin. Ornament

consisting of fine rounded tubercles fused into nodose, vermiculating ridges; those near the edges of the dorsal plates often displaying concentric arrangement. (Woodward.)

The following technical account of the structure of this extremely important species has been compiled chiefly from the recent papers of Traquair and Patten, cited in the above references to the literature.

The headshield occupies nearly one-third of the entire length of the armoring, and shows, on the upper surface, an orbital opening which is smaller and further back than in Asterolepis. The median occipital plate (text-fig. 12 *m. occ.*) has its lateral margin more perpendicular to the posterior one than in the last-named genus; its anterior aspect shows not merely a shallow re-entering angle for the postmedian plate, but a deep semi-elliptical notch or excavation, on each side of which it takes part in the formation of the posterior boundary of the orbit. Consequently the postmedian plate is small, entirely received in the aforesaid notch of the median occipital, and thus excluded from joining the laterals as in Pterichthys and Asterolepis. The lateral occipitals (*l. occ.*) and the angular (*ag*) do not call for any special comment, but the laterals (*l*) are much broader than in Asterolepis, while the extralaterals (*e. l.*) are very small, narrow, and pointed in front.

The orbital opening (*o*) is, as already mentioned, small compared with that of Asterolepis, and moreover, its anterior margin shows scarcely any re-entering flexure. Its right and left portions are almost completely filled by a system of sclerotic plates, the two inner ones being very considerably larger than the two outer; and the middle portion is covered by two loosely attached plates, namely, the median or pineal (*m*), and a very narrow T-shaped plate (called by Patten the "ethmoid") close in front of it. From the center of this narrow plate, as shown by Whiteaves and confirmed by Patten, a small linear process with expanded lower extremity passes down perpendicularly into the interior of the head, almost reaching a thin transverse shelf of bone which projects downwards from the under side of the premedian (*p. m.*). The space thus partitioned off beneath the premedian is interpreted by Patten as an "olfactory chamber",

and certain conjectures are hazarded by him as to the course of the olfactory nerves, which will be referred to presently. The median plate of the ocular opening is nearly perforated by a deep pineal foramen, similar to that occurring in Pterichthys, and often indicated by a low tubercle on the external surface. Two other pits, shallower than the first, and without any external indications of their presence, are symmetrically placed behind it on the under side of the small postmedian plate. The unpaired pit is in all probability to be regarded as the impression of the pineal body, but it is difficult to imagine what may have been the nature or function of the posterior pair. Analogy with all other vertebrates tends to discredit Professor Patten's suggestion that these three pits are all of the same nature and together indicate the presence of a triocular median eye.*

A matter of absorbing interest is the arrangement of the mouth parts in this species, now very satisfactorily known. Beneath the headshield at its front extremity (text-fig. 13) there is observed a pair of thin, concave plates of bone with free median and posterior margins, the latter being sharply bevelled and serrated. These plates are quite similar to those called the maxillae in Pterichthys (text-fig. 10 *mx,* page 77), but are less extensively in contact mesially, and are notched at the antero-external instead of at the postero-external angles. The greater part of the exposed surface of each plate is feebly rugose and marked by a sharply bent sensory canal, all appearances suggesting that they are purely dermal ossifications, and therefore of different origin and nature from the gill-arch jaws of higher vertebrates. The plates in question may be conventionally interpreted as maxillae, and are in fact so designated by Traquair, though Patten insists that they are mandibular. In the majority of specimens these so-called maxillary plates, and also the smaller, sigmoidal pair of mandibular elements, using both terms in the Traquairian sense, are more or less displaced; but this purely accidental feature furnishes no reason for supposing that the two pairs did not work directly against each other, or that the right and left halves of either pair were capable of independent motion, as in Arthropods. Finally it may be re-

* Patten, W., New Facts concerning Bothriolepis. Biol. Bull. 1904, **7**, p. 121.

marked that the appearance of these plates does not even remotely suggest comparison with the dentition of Arthrodires, and that structures corresponding to Dipnoan vomerine teeth do not occur in any known Asterolepid.

The pattern of the cephalic sensory canal system is considerably different from that in Asterolepis and Pterichthys. No transverse commissure unites the lateral canal of each side across the occipital plates; but in front, just at its incurved flexure on the lateral plate, a conspicuous branch is given off, which runs forwards and outwards to the margin of the shield, being very likely continuous with that on the maxillary plates on the lower side of the headshield. On the median occipital two fainter canals are observable, forming an angle with each other but not always uniting behind, and extending outwards and forwards over the lateral plates until they become confluent, or almost confluent, with the lateral canal near its central point of flexure. Near the same point, on the inner side of the main groove, a small ear-shaped mark is often, but not always to be seen. The main groove is continued nearly parallel with the periphery until it reaches the center of the premedian plate, where it is sometimes interrupted for a short distance.

The articulations of the body plates are as in Pterichthys, the anterior median dorsal (*a. m. d.*) overlapping the antero-dorsolateral (*a. d. l.*) of either side, but being itself overlapped by the postero-dorsolaterals (*p. d. l.*). On the under surface (text-fig. 13) the place of the two semilunars of Pterichthys is filled, according to Professor Patten, by at least three pieces, the posterior margins of which are assumed by this author to have been "freely movable in a dorso-ventral direction, like an operculum." * The course of the lateral sensory canals is exactly the same as in the body plates of Pterichthys, but in addition two shallow linear grooves diverge at a slight angle from about the center of the antero-dorsomedian plate, and extend across the postero-dorsolaterals.

The pectoral appendages are longer than the dorsal aspect of the body armor, and even pass beyond the termination of the ventral surface. The proximal portion is also longer than the

* Patten, W., Structure of the Ostracoderms. Science, n. s., 1903, **17**, p. 489.

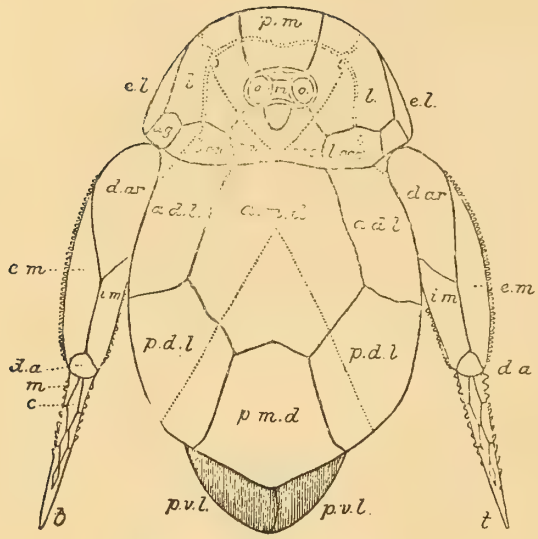


FIG. 12.

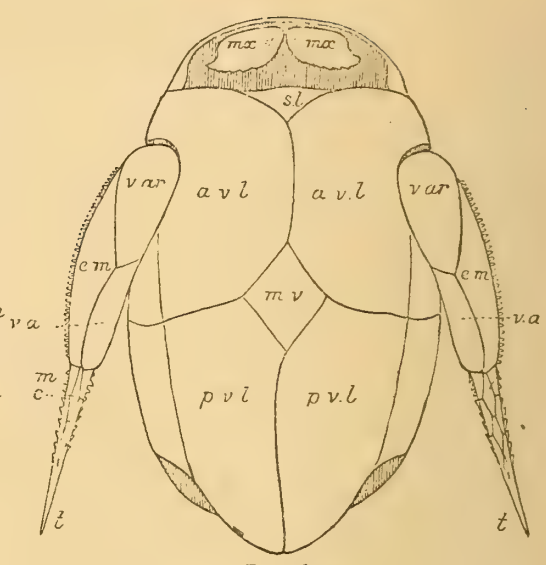


FIG. 13.

Fig. 12. *Bothriolepis canadensis* Whiteaves. Upper Devonian; Scaumenac Bay, Province of Quebec. Restoration of dorsal aspect, x $\frac{2}{3}$ (after Traquair).
m. occ., median occipital; *l. occ.*, lateral occipital; *ag.*, angular; *pt. m.*, post-median; *p. m.*, pre-median; *l.*, lateral; *e. l.*, extra-lateral; *m.*, median; *o.*, ocular; *a. d. l.*, anterior dorso-lateral; *a. m. d.*, anterior median dorsal; *p. d. l.*, posterior dorso-lateral; *p. m. d.*, posterior median dorsal; *d. a.*, dorsal anconeal; *d. ar.*, dorsal articular; *e. m.*, external marginal; *i. m.*, internal marginal; *c.*, centrals of lower arm; *m.*, marginals of lower arm; *t.*, terminal.

Fig. 13. The same from the ventral aspect, x $\frac{2}{3}$ (after Traquair). *mx.*, maxillary plate; *s. l.*, semilunar; *a. v. l.*, anterior ventro-lateral; *p. v. l.*, posterior ventro-lateral; *m. v.*, median ventral; *v. ar.*, ventral articular; *v. a.*, ventral anconeal; *c.*, centrals; *m.*, marginals of lower arm; *t.*, terminal.

distal, though the proportion seems to vary; roughly speaking, however, the difference between the two portions is less than one-third of the longer. The proximal portion is, like that of Asterolepis, trigonal in transverse section, and the plates of which it is composed are also similar in number and arrangement, save that the dorsal anconeal (*d. a.*) is a smaller rounded element placed just at the "elbow" joint, whereby the external and internal marginals are allowed to come together for a considerable distance between it and the distal extremity of the dorsal articular (*d. ar.*). The two articulars, as noted in the generic diagnosis, meet together on the outer aspect over the external marginal; this relation, however, is not always clearly visible in the Canadian specimens, though demonstrable in many fragments from Scotland and Russia. The lower or "fore" arm is slender and pointed, serrated along the external and internal margins, and composed of a greater number of pieces than in Pterichthys or Asterolepis.

For our knowledge of the trunk, caudal and two dorsal fins in this species, which is the only one of the genus showing these features, we are indebted to the painstaking investigation of Professor Patten, who has presented the following preliminary account of his observations:*

"The trunk was very slender and covered with a soft skin devoid of scales or of any other markings except those mentioned below. In spite of its delicate structure it is often only moderately compressed or distorted. In the region of the posterior dorsal, it may present a somewhat triangular cross-section, resembling that of Cephalaspis in a corresponding region, but without any traces of a lateral fold or of fringing processes [*i. e.,* fulcra, or marginal scales of other authors].

A few small irregular plates, with the typical sculpture of the buckler, are embedded in the skin along the dorsal surface, immediately in front of the anterior dorsal, and numerous minute ones are scattered irregularly over the flanks in the same region. One specimen shows indications of a lateral groove, and, dorsal to it, a few oblong folds suggestive of segmentation.

The anterior dorsal fin is low and elongated, the posterior one very high and rounded. Both fins are often preserved with wonderful clearness, but show no other detail than a faint striation probably due to the presence of delicate subdermal rays.

The elongated tail, with its axis slightly curved, terminates in a narrow band. The dorsal margin consists of a delicate membrane, strengthened by a row of curved rods lying close together and arranged with great regularity. The basal ends of the rods are swollen, and one is turned a little to the left, and the adjacent one, to the right of the median line. The rods extend on to the ventral margin of the terminal band, into the ventral lobe. The latter is faintly striated like the dorsal fins. Its anterior ventral margin appears to divide, as though it were continued forward into the lateral folds, although no such folds have been detected in the trunk region.

There are no indications whatever, either in surface views or in sections, of vertebral centra or arches, and the preservation of the specimens is so perfect that there is every reason to believe such structures, even if formed of cartilage only, were absent. Neither have we found any indication of a notochord, although one may infer from the outline of the trunk that a notochord was present. It was probably surrounded by a membraneous sheath of no more consistency, if as much, than that in Amphioxus."

*Patten, W., New Facts concerning Bothriolepis. Biol. Bull. 1904, **7**, p. 113, *et seq.*

FIG. 14.

Fig. 14. *Bothriolepis canadensis* Whiteaves. Lateral aspect of armor and body axis with two dorsal fins as restored by Dr. W. Patten. [The convolutions immediately behind the armoring on the ventral side, called "ventral frills" or "membranous folds", are apparently impressions of extruded viscera.] x ¾ (from Patten).

We may now return, finally, to a consideration of one or two doubtful matters. Neither on the dorsal nor ventral surface of the head region are there any certain indications of olfactory openings. It has been suggested by Smith Woodward, however, that the rounded notch occurring at the external angles of the maxillary plates in Pterichthys and Bothriolepis may indicate the opening of a nasal sac, and it is indeed difficult to conceive what other function it could have subserved. Professor Patten offers no explanation of the notches in question, and is forced to conclude from the absence of any other orifices that the orbital and nasal openings were confluent. The pineal plate and the T-shaped one in front of it, alongside of which the olfactory nerves are supposed to have passed according to Patten's conjecture, were capable (in this author's opinion) of sliding back and forth at the same time as the sclerotics, the eyes and olfactory pits being opened by one set of movements, and closed by a reverse set. It is to be regretted that there are no means of proving whether or not this ingenious contrivance ever existed. Real or imaginary, it had, however, this rather awkward defect: the creature possessing it could not smell with its eyes shut. Nature is not usually so economical that vertebrate organisms have the sense of sight and the sense of smell localized within a single opening. And the invariable position of the nasal openings in chordates is inferior, never on the dorsal aspect of the head.

As for the peculiar markings described by the Dartmouth author (*loc. cit.*, 1905) as "broad membranous folds, of unknown function, around the posterior end of the cephalic buckler", these are probably to be interpreted as impressions of the extruded viscera. It is stated in the same communication that certain specimens disclose the shape of the brain-chamber, an announcement which bids fair to yield interesting information.

Formation and locality. Upper Devonian; Scaumenac Bay, Province of Quebec, Canada.

Bothriolepis nitida (Leidy).

1856. *Stenacanthus nitidus* J. Leidy, Proc. Acad. Nat. Sci. Philad. **8**, p. 11, and Journal, ser. 2, **3**, p. 164, pl. 16, figs. 7, 8.
1856. *Holoptychius americanus* (*pars*) J. Leidy, *Ibid.*, p. 163, pl. 17, fig: 4.
1889. *Bothriolepis leidyi* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 111, pl. 18, fig. 2; pl. 20, figs. 1–5.
1891. *Holonema rugosa* E. D. Cope (*errore*), Proc. U. S. Nat. Mus., **14**, p. 456, pl. 30, fig. 7.
1893. *Bothriolepis canadensis* H. S. Williams (*errore*), Amer. Jour. Sci. ser. 3, **46**, p. 286, text-fig. 5.
1899. *Bothriolepis leidyi* C. R. Eastman, 17th Ann. Rept. N. Y. State Geol. p. 324.
1907. *Bothriolepis nitida* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 50, pl. 3, fig. 4; pl. 7, figs. 1, 3.

An imperfectly definable species, known only by fragments of the dermal armor and appendages. Superficial ornament consisting of fine stellate tubercles fused into nodose vermiculating ridges. Pineal plate relatively large and semi-circular in outline. Form and general proportions of pectoral appendages as in the preceding species, except that only the external margin is serrated.

This species appears to have equalled, or even exceeded the average of *B. canadensis* in size, and displays a similar ornamentation. The stellate character of the tubercles rarely appears in worn specimens, and the ornament is coarser in large-sized than in smaller or immature individuals. Only a few fragmentary examples of the headshield have been obtained, and nearly all of the detached body plates show evidence of post-mortem rolling and sorting by current action. As already noted by Newberry and Smith Woodward, the large antero-dorsomedian plate is numerically more abundant than any of the others. Its more frequent preservation is perhaps to be accounted for by the solidity imparted to it by the presence of a strong median carina along its visceral side. The plate immediately following behind is keelless, and as a corollary fact, is far less commonly preserved.

Formation and locality. Catskill of Tioga county, Pennsylvania, and same formation in Delaware county, New York.

Bothriolepis minor Newberry.

(Text-figure 15)

1889. *Bothriolepis minor* J. S. Newberry, Monogr. U. S. Geol. Surv. **16,** p. 112, pl. 20, figs. 6–8.
1892. *Bothriolepis minor* E. D. Cope, Proc. Amer. Phil. Soc. **30,** p. 224.
1899. *Bothriolepis minor* C. R. Eastman, 17th Ann. Rept. N. Y. State Geol. p. 324, text-fig. 5.
1907. *Bothriolepis minor* Leidy, C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 52, text-fig. 13.

This species is readily distinguished from the preceding by its smaller size and very much finer ornamentation, the external surface being covered with fine, closely crowded vermiculating ridges. Unfortunately, it is known only by detached plates, among which the headshield and pectoral limbs are excessively rare. The latter are of about the same proportions as in *B. nitida.* Concerning the headshield it is stated by Cope that "one of the characters of the species is seen in the fact that the sensory grooves of the median occipital plate do not extend to the smooth articular border, but are separated from it by a band of sculpture. The premedian plate is crossed by a groove which presents an abrupt loop backwards at the middle."

As is commonly the case with this class of remains, the antero-dorso-median plate is of much more frequent occurrence than any other, though seldom found entire. Its orientation may be easily determined by means of the V-shaped sensory canals which diverge from about the center of the plate, or, in case the

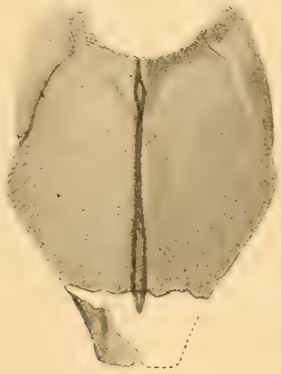


FIG. 15

Fig. 15. *Bothriolepis minor* Newb. Antero-dorso-median with denuded superficial ornament. Catskill, Delaware county, New York. x 1–1.

superficial ornament is denuded, by means of the longitudinal keel (text-fig. 15) which traverses the median line of the plate for about three-fourths of its length.

Formation and locality. Chemung group of Bradford county, Pennsylvania, and Catskill of Delaware county, New York. According to Newberry, the same or a very similar species occurs also in the Devonian of Belgium.

Bothriolepis coloradensis Eastman.

1904. *Bothriolepis coloradensis* C. R. Eastman, Amer. Jour. Sci. ser. 4, **18**, p. 254, text-figs. 2, 4.

1907. *Bothriolepis coloradensis* C. R. Eastman, Mem. N. Y. State Mus. **10** p. 53.

This, the largest known American species of Bothriolepis, is chiefly interesting on account of its geographical and geological occurrence, and for the evidence it furnishes regarding Asterolepid distribution. Considering that the genus is characteristic of estuarine deposits in the Upper Devonian of all parts of the world, it may be regarded as indicating the prevalence of Old Red Sandstone conditions in the corresponding formation of southwestern Colorado. The relations of this species seem to be rather with the Canadian than with either of the Chemung-Catskill forms occurring in the Atlantic Border States. Owing to the absence, however, of Asterolepid remains in any intermediate Upper Devonian locality, although other Chemung forms are present in abundance along the route, it is difficult to trace a line of migration directly connecting the Cordilleran species with those in New York and Pennsylvania. Assuming that the former is a European immigrant across the Atlantic, if the passage were not by way of the Dakotan sea we must suppose it to have entered either by skirting the land known as "Columbia" to the south, or that which has been termed "Laurentia" on the extreme north. The position of these Upper Devonic landmasses is indicated in the map given in Plate XVI.

Formation and locality. Elbert formation (Upper Devonian); Rockwood and Devon Point, Colorado.

Class **PISCES.**

Among the more distinctive characters of Fishes, as compared with all higher Craniates, may be mentioned the following:

Animals of this class are jaw-bearing chordates of fresh-water or marine habitat, which in their shape, locomotor and respiratory organs are completely adapted for an aquatic life. In all forms breathing is normally by gills, though in Dipnoans (or Lung-fishes) these merely assist the lungs. The gills are derived from the walls of the branchial clefts, and are supported by a series of branchial arches. The principal organ of locomotion is the powerful tail; in addition, however, there are paired fins, pectoral and pelvic, corresponding to the fore and hind limbs of the terrestrial Craniata, and possessing a supporting cartilaginous or bony skeleton ("ichthyopterygium") which cannot readily be compared with the limb-skeleton of the latter. Fishes also possess a system of median fins, supported by a special skeleton of their own. An exoskeleton of dermal spines or denticles, scales or bony plates, is usually present. Except in one group, the Dipneusti, the heart has but one auricle, and receives only venous blood, which it forces, first, through the blood-vessels of the gills, and thence, as arterial blood, through the vessels of the body generally. An air-bladder is frequently present, and serves as an hydrostatic organ or float, but in a few cases it may act as a lung, and helps the gills in the work of respiration. The paired olfactory organs rarely communicate with the oral cavity by internal nostrils. Peculiar cutaneous sense-organs are disposed in linear tracts along the sides of the body (lateral line sensory organs) and on the head, and appear to be specially associated with a life in water.

Subclass **ELASMOBRANCHII.**

Sharks and rays, both ancient and modern, agree in having the exoskeleton composed of a more or less uniform investment of dermal papillae or denticles called "shagreen". The term *placoid* is also sometimes applied to this type of cutaneous covering. The endoskeleton is wholly cartilaginous or partially calcified, and the skull is without either cartilage- or membrane-bones. The mode of attachment of the primitive upper jaw

to the skull is usually hyostylic, in that the hyomandibular and palato-quadrate form a freely movable support for the mandible. Only one or two genera form exceptions to this rule, where the condition is that which Huxley has termed amphistylic (see *ante*, p. 66), or as in the Port Jackson shark, there is a tendency toward that complete fusion of the palato-quadrate cartilage with the cranium which is known as autostyly,—when the mandible articulates directly with the cranium.* There are from five to seven branchial arches and clefts, and the latter are separated by complete interbranchial septa. Arches are present for the support of the paired fins; the pectoral pair is with rare exceptions uniserial, and the pelvic pair invariably so. The exoskeletal supports of all the fins consist of numerous slender horny fibres (ceratotrichia) and, when present, the fin-spines are invested by enamel. Claspers are generally present in the male.

Besides the foregoing definition, it may not be uninstructive to introduce at this point a few topics of general interest relating to modern sharks and rays, which are extracted in slightly abridged form from Professor Bridge's discussion in the Cambridge Natural History volume on Fishes (1904, p. 432).

The Elasmobranchs are for the most part predaceous fishes, living at different depths in the sea, from the surface to nearly a thousand fathoms, and ranging from mid-ocean to the shallower waters round the coasts in almost every part of the world. Although typically marine, they sometimes ascend rivers beyond the reach of tides, and a few are permanent inhabitants of fresh water. They are most abundant in tropical and subtropical areas, where they also attain their greatest size, and are numerous in temperate regions, but there are some species which are typically Arctic. None of them are small, and some of the sharks are the largest of living fishes. All are carniverous, but so diversified is their food that in different species it may range

* Dollo and some others are of the opinion that autostyly, whether incipient as in Cestracion, or complete as in Chimaeroids and Dipnoans, is a secondary modification, which may be independently acquired in widely different groups of fishes, and is usually associated with the need of a firm and rigid support for an exceptionally massive dentition. Dollo's remarks on this subject are given as follows:

"Sans vouloir absolument méconnaitre l'importance taxonomique de l'autostylie,—je ne puis la considérer comme un caractère fondamental. C'est une pure conséquence de l'adaptation à un régime triturateur très accentué (mylodonte),—dans un but de consolidation de l'appareil masticatoire."—*Sur la phylogénie des Dipneustes*, Bull. Soc. Belge Géol. etc. 1895, **9.** p. 109.

See also a more recent communication by the same author entitled "Sur quelques points d'éthologie paléontologique relatifs aux poissons." *Ibid.*, 1906, **20.** p. 1.

from other fishes of no mean size to mollusks, crustaceans and other invertebrates, or even to plankton. In their breeding habits the sharks and Dog-fishes present many interesting features. Unlike the generality of fishes, the eggs are fertilized internally as a sequel to the copulation of the sexes. For this purpose the males are furnished with special intromittent organs, the myxopterygia or so-called claspers, which are developed as modifications of the hinder portions of the pelvic fins. Each clasper is supported by an internal skeleton, consisting of several cartilages derived from the radialia of the fins, and is traversed along its inner aspect by a groove. When sexual congress takes place the claspers are thrust through the cloaca of the female into the oviductal orifices, and in some instances it is probable that they are retained in this position by hook-like denticles developed at their free extremities. The seminal fluid then flows along these conduits into the oviducts, in the upper portions of which it meets and impregnates the eggs. After fertilization the egg is enclosed in a dark brown horny egg-case, secreted by the oviductal gland.

Order **PLEUROPTERYGII.**

Notochord persistent; neural and haemal arches slender. Paired fins with basalia and radialia arranged much as in the median fins of recent fishes. Claspers not observed. Apparently a cutaneous flap much like an operculum covered the first of the gill slits, which were at least five in number, and perhaps seven. Jaws apparently hyostylic; lateral line an open groove.

The only known representative of this order, and at the same time, as indicated by the position of its paired fins and other features, the most primitive type of Elasmobranch yet discovered, is the Upper Devonian and Lower Carboniferous genus Cladoselache. Among all fossil fishes this genus is regarded as furnishing the most important testimony in favor of the lateral fin-fold hypothesis. In view of its extreme importance from a morphological and phylogenetic standpoint, it seems desirable to offer the following account of its organization, compactly drawn up by Smith Woodward:

"The fish (text-fig. 6, *ante,* p. 61) is elongated and round-bodied, with a short blunt snout, and forwardly placed eye. The precise characters of the cranium are unknown; but the olfactory capsules are large, placed close together, and terminal. The

mouth is also terminal, the upper and lower jaw being similar in shape and size, and supported by a slender elongated hyomandibular. The teeth are largest, longest, and most acutely pointed at the symphysis of the jaw, smallest and shortest at the angle of the mouth. The transverse series are closely apposed, and not separated as in the modern Chlamydoselachus; they are indeed tightly wedged together, and the cusps are frequently much abraded by wear. Every tooth has a principal cusp with variable smaller lateral cusps, and the broad base of each is overlapped by its successor behind. The number of gill-arches is uncertain, but five are known, and the presence of one or two others is suggested by some specimens. The neural and haemal arches of the axial skeleton have been observed only in the caudal region, where they are short tapering rods of cartilage, bifurcated at the base and distinctly corresponding in number with the calcified remains of the muscle plates. Intercalary cartilages are wanting.

The small basal cartilages of the paired fins seem to be embedded in the body wall, and the unjointed radial cartilages extend directly outwards to the edge of the membrane. There are no claspers in the pelvic fins, and both these and the pectoral fins were probably mere balancers directed somewhat downwards. Two low dorsal fins have been observed, both destitute of an anterior spine,* but strengthened by simple cartilaginous rays extending to the edge of the fin membrane. No anal fin has been distinguished. The caudal fin is strongly heterocercal and very remarkable. The neural arches seem to persist even to the end of the upturned axis, directly supporting the thick radial cartilages of the superior lobe of the caudal fin. The dermal membrane of the inferior lobe of the caudal fin is supported by simple cartilaginous rays only in its lower portion where they extend quite to the margin. The eye is surrounded by a double series of small dermal plates; but the remainder of the fish is covered only with minute lozenge-shaped denticles, which are apparently not enameled. The latter are slightly enlarged at the angles of the mouth, where they approximate in size and shape to the smallest of the teeth. The lateral line extends along the trunk between two series of the shagreen-like granules, and was thus presumably an open canal. A short dermal expansion forms a horizontal keel on each side of the caudal lobe just in advance of its upturned end. The largest known examples measure nearly 2 meters in length."

*This statement requires to be amended, Dr. Dean having discovered at least one specimen in which the anterior dorsal fin is provided with a powerful Ctenacanthus-like spine.

To the above description may be appended also the following paragraph from another article by the same author:*

"In conclusion, one word of protest against the American idea that the paired fins of Cladoselache can be compared with those of an Acanthodian.† We venture to maintain that these fins are fundamentally different in every respect. In Cladoselache the cartilages of the internal skeleton are well developed and support the whole fin membrane; in Acanthodians, whatever view we may adopt as to the naming of the parts, these cartilages are as much reduced as in a modern herring. Dr. Dean speaks of the "radials" of Cladoselache as if, by fusion, they might readily became a fin spine like that of the Acanthodian Parexus; but the former are cartilage and endoskeletal, the latter is merely the ordinary dentine and therefore presumably exoskeletal. The problem of the primeval sharks continues to present endless difficulties, but these are only multiplied by such comparisons. In the present writer's opinion, the pectoral of Cladoselache is more remotely connected with that of the Acanthodians than is that of a modern Siluroid with the pectoral of the Devonic Holoptychius. Everything still tends to show that the very highest Elasmobranchs lived simultaneously with almost the lowest in late Paleozoic times; while sharks and skates nowadays are a comparatively degenerate race."

We have already remarked that this genus furnishes important support for the doctrine of the evolution of fins, which now ranks as a fairly well demonstrated principle. In the first place, it is important to bear in mind that the paired fins of Cladoselache are the oldest known structures of their kind which are clearly observable; and secondly, they approach more closely than any others to the hypothetical primitive type from which all paired limbs have been derived. Briefly stated, the lateral fin-fold theory assumes that fishes originally possessed on each side of the body a continuous fold of the integument, strengthened by parallel cartilaginous rods extending outwards from the body wall, this fold becoming subdivided into the pairs of pectoral and pelvic fins as we know them in modern forms.

---

*Woodward, A. S., The Problem of the Primeval Sharks. Natural Science, 1895, **6**, p. 42.

†The Fin-fold Origin of the Paired Limbs, in the Light of the Ptychopterygia of Palæozoic Sharks. Anatom. Anzeig. 1896, **11**, p. 678.

Now it has been shown by Dr. Bashford Dean that in Cladoselache the paired fins were mere balancers with a more extended base line than is usual. The series of parallel cartilaginous rods, which in a primitive condition supported the lateral fin-fold, exist practically unmodified in the pelvic fins, simply clustered and partly fused within the body wall of the pectoral fins. Dean, Cope, and others are of the opinion that there is a tendency in the pectoral fin for the hinder end of the row of basals to rotate outwards—a process which would reduce the point of attachment of the fin to what was originally its front angle. The outwardly turned row of basals would in this case correspond with the median axis of the well known paddle in Ceratodus and Pleuracanthus, and one may without difficulty conceive of a fringe of cartilaginous rays developing quite secondarily along the hinder border of this axis. Hence, as argued by Dean and Cope, the modern tribasal or dibasal shark's fin cannot have evolved from the paddlelike "archipterygium", but these two kinds of fin must have arisen independently from the "ptychopterygium", as the arrangement has been appropriately termed by Cope.*

Complete skeletons of Cladoselache have been found only in the Cleveland shale (Upper Devonian) and Waverly of Ohio. Dismembered remains of the genus have been found also in the Portage of western New York State, and numerous detached teeth of the form common to both Cladodus and Cladoselache are distributed throughout the Carboniferous rocks of all parts of the world. Forerunners of Cladodus begin to appear as early as the Middle Devonian ("Corniferous" of Ohio), and various small, conical teeth that have been named Protodus, Doliodus, etc., are known from the Lower Devonian of Campbellton, New Brunswick. The precise position of these detached dental structures cannot be fixed with certainty, since there is reason to believe that several primitive genera, not necessarily of the

*For interesting discussions of this subject, one may consult the following: Mollier, S., Die paarigen Extremitäten der Wirbeltiere. I. Das Ichthyopterygium. Anatom. Hefte, **3**, 1893; Dean, B., Contributions to the Morphology of Cladoselache. Jour. Morphol. 1894, **9**, 87-114; A new Cladodont from the Ohio Waverly. Trans. New York Acad. Sci. 1894, **13**, 115-119; The Fin-fold Origin of the Paired Limbs, in the Light of the Ptychopterygia of Palæozoic Sharks. Anatom. Anzeig. 1896, **11**, 673-79; Woodward, A. S., The Problem of the Primeval Sharks. Nat. Sci. 1895, **6**, 38-43; *Ibid*, 1892, **1**, 28-35.

same family or even of the same order, were characterized by teeth of similar form. Owing to the resemblance between the Cladodont and Pleuracanthid type of dentition, it is customary to associate the "family" Cladodontidae provisionally under the same ordinal division as that which includes Pleuracanthus, Didymodus, etc. This has been called Ichthyotomi, in allusion to a curious, symmetrical fissuring of the skull as seen in some of the best preserved crania. No indications of Pleuropterygia have yet been found in the Devonian of Iowa or adjoining States.

Order **ICHTHYOTOMI.**

Notochord persistent; neural and haemal arches and intercalary cartilage present. Pectoral fin archipterygial; pelvic fins with claspers, caudal fin diphycercal. No placoid scales, but the head is covered with dermal ossifications.

This order is represented in the Devonian only by detached teeth similar to those characterizing well-known Pleuracanthid genera, and consisting of two or more sharp cusps, with or without intermediate denticles, attached to broad bases. While more specialzed than the preceding order, the fishes included in this group represent an extremely generalized type of Elasmobranch. Indeed, it has been justly said of Pleuracanthus, the typical genus, that "it is a form of fish which might with very little modification become either a Selachian, Dipnoan, or Crossopterygian" (Woodward). The general aspect of this creature has become familiar through the frequently copied restoration of Brongniart and Fritsch. During recent years a novel attempt at reconstructing its essential features has been made by Professor Otto Jaekel,* of Greifswald, whose illustration is reproduced herewith (text-fig. 16). It is intended to show an amphistylic skull, five branchial arches bearing clusters of minute denticles, no circumorbital plates, and continuous median fins.

* Jaekel, O., Neue Rekonstruktionen von Pleuracanthus sessilis etc. Sitzungsber. Ges. Naturforsch. Freunde, 1906, no. 6, pp. 155-159. Some comments on this figure, and also on Jaekel's restoration of Hybodus, are offered by E. Koken in his memoir "Ueber Hybodus", in Geol. u. Päl. Abhandl., 1907, n. f. **5**, Heft 4.

FIG. 16.

Fig. 16. *Pleuracanthus decheni* Goldfuss. Lower Permian; Lebach, Rhenish Prussia. Restoration by Dr. O. Jaekel of a primitive shark showing elongated dorsal; diphycercal caudal; two anal; and paired fins with segmented basal cartilages and actinotrichia. The branchial arches are believed by some authors to be seven in number, instead of five, as here shown. x ¼. (after Jaekel).

Family **PLEURACANTHIDAE.**

Body slender, but slightly depressed; mouth terminal; tail diphycercal. Dorsal fin elongate, low, continuous along the back from a point shortly behind the head; slender interneural cartilages more numerous than the neural spines. Pectoral fin with biserial arrangement of cartilaginous rays. (Woodward.)

Genus **PLEURACANTHUS** Agassiz.

The characters of this, the best known genus, have been briefly summarized by Smith Woodward as follows:

The fish is elongated and round-bodied, with a straight and tapering (diphycercal) tail. Fixed upon the occipital region of the cranium is a long and slender, bilaterally-symmetrical dermal spine, which is turned backwards when not erect, and does not appear to have supported a fin. The spine is hollow and is armed with a double longitudinal series of denticles or barbs. The foremost few neural arches are bent forwards, but from the origin of the dorsal fin backwards their direction is normal; the right and left halves of each remain separate. Ribs are rudimentary or absent; but in the caudal region the haemal arches are as large as the corresponding neurals. The branchial arches are believed to have been seven in number, though there may be only five. [Jaekel is positive that the latter number is correct.] The teeth are tricuspid, but the middle denticle is comparatively minute, and the name Diplodus, commonly applied to the isolated fossil teeth, is thus appropriate.

Very delicate dermal filaments (actinotrichia) are clustered round the supporting cartilages in all the fins. In the paired fins all the fringing cartilages are segmented; in the pectoral fin those of the anterior (preaxial) border are much more numerous and better developed than those of the hinder (postaxial) border. The dorsal fin is borne by a close series of slender cartilaginous suports, which are exactly twice as numerous as the neural arches to which they are apposed; each support is segmented into three pieces, of which the proximal element is short, the middle one very long, and the outermost again short, while the latter projects into the fin-membrane. The dorsal portion of the caudal fin is similarly supported, but its cartilages are equal in number to the neural arches. The ventral portion of the caudal fin has no supports beyond the haemal spines. The anal fin is curiously subdivided into two portions, of which the supports are crowded, partially fused together, and thus in

part branching; these exhibit more numerous segments than those of the other median fins. Complete skeletons of Pleuracanthus have been found only in the Coal Measures of Commentry, France, in the Lower Permian Coal Measures of Germany and Bohemia, and in the Lower Hawkesbury Formation of New South Wales; but detached spines and teeth indistinguishable from those of this genus occur also in the [Devonian, Mississippian and] Coal Measures of North America and in the lowermost Carboniferous strata of Scotland, while a few teeth have been found even in the Upper Trias (Keuper) of Somersetshire.

Genus DIPLODUS Agassiz.

Under this name are comprised a number of Palæozoic species founded only upon the evidence of detached teeth, hence the status of the genus is more or less provisional. This fact being understood, it is convenient to retain the generic title pending such time as our knowledge of the entire organization becomes more complete, notwithstanding the prior employment of Diplodus among modern bony fishes (porgies, bass). Mr. S. A. Miller, in his work on North American Geology and Palæontology, has proposed its replacement among fossils by Dissodus; and Dr. O. P. Hay prefers the substitution of the earlier synonym of Dittodus.

Diplodus pricus Eastman.

(Plate I, Figs. 5, 13)

1899. *Diplodus priscus* C. R. Eastman Journ. Geol. **7**, p. 490, pl. 7, figs. 1, 2.
1899. *Diplodus priscus* S. Weller, Journ. Geol. **7**, p. 484.
1907. *Diplodus priscus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 59, pl. 1, figs. 7, 8.

Teeth minute; the two principal cusps of dental crown divergent and slightly inclined backwards, robust, conical, circular in section, without lateral carinae; coronal surface marked with relatively few prominent, slightly curved striae extending from the base nearly to the extremities on the anterior face, but shorter and usually fainter on the posterior face. Median denticle slender, sometimes much reduced, or in one specimen wanting altogether. Anterior border of root slightly produced downward; lower surface concave, elliptical in outline; posterior button present.

This species, together with the one immediately to be described, is known by a number of examples of striated teeth from a peculiar deposit of the Upper Devonian in the vicinity of Elmhurst, Illinois. As described by Dr. Stuart Weller, who first noted the discordant relations of these beds, their contained fossils are deeply buried in fissures of Niagara limestone, appearances indicating that the joints were open, and became filled with sand and organic remains during the late Devonian. The same sort of unconformity has also been observed and described by Dr. J. M. Clarke at Buffalo, New York, between the uppermost Silurian and Oriskany sandstone.

Formation and locality. Upper Devonian; Elmhurst, Illinois.

Diplodus striatus Eastman.

(Plate I, Figs. 1, 16)

1899. *Diplodus striatus* C. R. Eastman, Journ. Geol. **7**, p. 490, pl. 7, figs. 3, 4.
1899. *Diplodus striatus* S. Weller, Journ. Geol. **7**, p. 484.
1907. *Diplodus striatus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 60, pl. 1, figs. 10, 11.

Of this species only a few fragmentary teeth were obtained by Dr. Weller from the same locality as the last, the largest and most perfect being represented in Plate I, figure 1. It attains apparently about twice the size of the preceding form, and is distinguished from it by its finer striation, shallower root, and somewhat compressed section of its principal cones. The striae on the anterior face all curve uniformly in a spiral direction, but on the posterior face their tendency is to curve outward on either side of the median line to the lateral margin of the cones, where they terminate, precisely as in some species of Cladodus. None of the specimens show the entire length of the median denticle, but it was apparently long and slender.

Formation and locality. Upper Devonian; Elmhurst, Illinois.

Genus **PHOEBODUS** St. John and Worthen.

Teeth differing from those of Diplodus in having three principal cones of about equal size, and from one to three very small intermediate cones.

Phoebodus politus Newberry.

(Plate I, Fig. 9)

1889. *Phoebodus politus* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 173, pl. 27, figs. 27-28*a*.
1899. *Phoebodus politus* C. R. Eastman, Journ. Geol. **7**, p. 491, pl. 7, fig. 5.
1907. *Phoebodus politus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 60, pl. 1, fig. 12.

Newberry's description of this rare and interesting form is as follows:

Teeth small, robust, breadth between tips of lateral cusps 6 to 12 mm, height from 4 to 8 mm, base broadly elliptical, thick, with a broad bilobed, padlike prominence in the middle portion of the upper surface, concave below, with a narrow arch between the cusps; cusps three, of nearly equal size, with minute rudimentary ones in the angles between them, all strongly recurved, flattened in front with salient, acute angles, rounded behind; surface smooth and polished, or bearing a few short, coarse striations.

The relations of this species have been commonly supposed to be with Cladodus, rather than with Diplodus, but recent discoveries of more perfect examples which display the characters of the root in this and other species leave no doubt as to the Pleuracanthid nature of these teeth. An illustration is given in Plate I Fig. 9 of one of the most perfect specimens of *P. politus* that have yet been obtained. The original is preserved in the Museum of Comparative Zoology at Cambridge, Mass., and is from the Cleveland shale of Lorain county, Ohio.

Formation and locality. Cleveland shale (Upper Devonian); Ohio.

Phoebodus macisaacsii St. John and Worthen.

1875. *Bathycheilodus macisaacsii* St. John and Worthen, Pal. Illinois, **6**, p. 252, pl. 1, figs. 1m, 13.
1889. *Phoebodus macisaacsii* A. S. Woodward, Cat. Foss. Fishes British Mus. part 1, p. 27.

A much smaller species than the preceding, and distinguished from it by its relatively elongated base and more extensively striated coronal surface. Length of base not exceeding 3 mm, and total height less than 1.5 mm. A pair of low, obtuse and striated

intermediate denticles in the angles between the principal cusps. Extremities of outer cusps slightly divergent.

These minute teeth are accompanied in the same formation by others of about the same size, but having the coronal cusps apparently smooth. Although regarded provisionally as pertaining to a distinct species, named *P. sophiae* by Messrs. St. John and Worthen, the authors admit the possibility of the two forms representing the upper and lower dentition respectively of one and the same species. Only one specimen has been figured of the smooth form designated as *P. sophiae,* and none have come under the observation of the present writer. But for the fact that the base is well defined, these minute teeth might readily be mistaken for Conodonts.

Formation and locality. Cedar Valley limestone; Waterloo, Iowa.

Family CLADODONTIDAE.

An indefinable family, apparently closely related to the Pleuracanthidae.

Genus CLADODUS Agassiz.

This typically Lower Carboniferous genus occurs sparingly in the Upper Devonian, and only two instances are known of its representation in the Middle Devonian, the species noticed immediately hereafter being found in the Columbus limestone (Ulsterian) of Ohio, and the next following in the Hamilton of Milwaukee, Wisconsin. It is quite possible that some detached teeth of similar nature which range upward into the Carboniferous belong in reality to Pleuracanthid sharks, whose earliest appearance is perhaps indicated by forms like Protodus and Doliodus in the Lower Devonian. Cladodont sharks of the Lower Carboniferous were apparently spineless, and in this respect differ from the spiniferous Cladoselache of the Upper Devonian and Waverly.

Cladodus prototypus Eastman.

(Plate I, Fig. 18)

1907. *Cladodus prototypus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 61, pl. 1, fig. 15.

Founded upon a single robust tooth of large size, the crown consisting of a stout, erect median cone and five lateral denticles on either side, not much compressed, and all delicately striated. The outer pair of lateral denticles is much the largest, and nearly circular in transverse section. The median cone is elliptical in cross-section, slightly recurved, without sharp lateral edges, and very broad across the base. Its total height, when complete, is estimated to have been about 3 cm.

The general appearance of the unique tooth answering to the above description is suggestive of *C. striatus* Agassiz, from the Lower Carboniferous limestone of Great Britain. The present example differs from the latter species, however, in the less compression of the crown, fewer lateral cones, and peculiar arrangement of the coronal striae. As many as thirty-five fine, parallel non-bifurcating striae are visible on the external face of the principal cone, those of the middle portion running vertically, and those along the sides curving gradually outwards and terminating in a faint ridge along the lateral margin. The apices of the median and nearly all of the lateral cones have unfortunately been broken away in the type specimen, and the root likewise is wanting. The length of the base in its present condition is 3.6 cm. Holotype preserved in American Museum of Natural History, New York (*ex* James Hall Collection).

Formation and locality. Columbus limestone (Ulsterian); Columbus, Ohio.

Cladodus monroei Eastman.

(Plate I, Fig. 17)

1900. *Cladodus monroei* C. R. Eastman, Journ. Geol. **8**, p. 36, text-fig. 2.
1907. *Cladodus monroei* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 62, pl. 1, fig. 5.

The holotype of this species is a small, imperfectly preserved tooth found by Mr. Charles E. Monroe in the Hamilton limestone of Milwaukee, Wisconsin. The median cone is robust, very

thick at the base, and indistinctly striated. The external denticles are also stout in proportion to the size of the principal cone, but the three intermediate denticles of either side are excessively small. The total height of the principal cone probably amounted to less than 1.5 cm, and the length of base is estimated to have been about 2.5 cm.

Formation and locality. Hamilton limestone; Milwaukee, Wisconsin.

Cladodus coniger Hay.

1889. *Cladodus carinatus* J. S. Newberry, U. S. Geol. Surv. Monogr. **16**, p. 103.
1899. *Cladodus coniger* O. P. Hay, Amer. Nat. **33**, p 783.

In the original description of this species, the teeth are stated by Newberry to be "less than half an inch in breadth and height, the base narrow, and bearing one central and four lateral cones, the exterior pair larger than the intermediate ones, but all much lower than the central denticle." The distinctive feature of the species is said to consist in the presence of four moderately strong carinations on the flattened posterior surface of the principal cone.

Teeth evidently belonging to this species are by no means uncommon in the Chemung of Warren county, Pennsylvania, but as a rule are imperfectly preserved. The general form is similar to that of *C. concinnus* Newberry, from the Huron shale of Ohio; and as in that species, the pair of intermediate denticles is sometimes absent. The external cones also diverge outwards at a considerable angle. The principal cone is strongly compressed, more or less recurved, with sharp lateral edges, and prominently striated on both faces. The number of carinae along the flattened, moderately convex anterior face is not limited to two pairs, however, some specimens displaying twice that number. These are symmetrically arranged on either side of the median line, the two innermost being nearly vertical and rather more prominent than the rest.

Formation and locality. Chemung beds (Chautauquan); Warren county, Pennsylvania. Also from the Meadville Upper Shale (Waverly series), near Meadville in the same State.

Cladodus formosus Hay.

1903. *Cladodus formosus* O. P. Hay, Amer. Geol. **30**, p. 373, text-fig. 1.

A small species resembling *C. concinnus* from the Huron shale of Ohio in general form, but the principal cone more robust, with rather strongly convex anterior face, the basal portion of which becomes somewhat flattened and at last indented. The anterior face is also more conspicuously striated than in the Ohio form, there being about twenty sharp carinations near the base, and half that number toward the apex. There are two pairs of divergent, striated lateral denticles, of which the internally situated one is the larger. Total height about 1.1 cm; length of base 1.5 cm.

Formation and locality. Ouray limestone (Upper Devonian); south slope of Needle Mountains, in Needles Mountain Quadrangle, Colorado.*

Cladodus urbs-ludovici, sp. nov.

(Plate III, Fig. 3)

A moderate-sized species, in which the teeth are composed of a robust and erect median cone without lateral denticles, supported by a small narrow base with gradually sloping lateral alae. Principal cone with gently convex faces and laterally compressed edges toward the apex, which is acute. Anterior face ornamented with numerous slightly wavy longitudinal striae, of which about twenty are to be counted toward the base; striae of posterior face not extending to the apex, which is smooth on that side. Total height of tooth in holotype, 1.6 cm; length of base 1.8 cm.

This species is founded upon a unique tooth of which the apical portion is preserved intact, but the basal portion of the crown is seen in impression and the root in cross-section, owing to fracture and subsequent weathering. Numerous Conodont teeth are associated with the specimen in the containing matrix. In

* The horizon immediately overlies the fish-bearing strata of the Elbert formation, described by Dr. Whitman Cross in the American Journal of Science for October, 1904. The upper part of the Ouray limestone carries a Mississippian invertebrate fauna, which has been described by Dr. G. H. Girty in Professional Paper No. 16 of the U. S. Geol. Survey, 1903.

general outlines and as regards absence of lateral denticles, the new form presents some resemblance to *C. pattersoni,* from the Waverly of Ohio. The latter, however, besides being from a later horizon, differs from the present form in having the principal cone strongly convex in cross-section, much reflexed and sigmoidally curved at the apex, and smooth and polished throughout.

The holotype was collected many years ago by Mr. W. N. Longworth, of Louisville, Kentucky, from whom it was obtained in 1867, along with other remains from the same locality, by the late Professor O. C. Marsh. Through exchange with the Director of the Peabody Museum at Yale, Professor Schuchert, it has become the property of the Museum of Comparative Zoology.

Formation and locality. New Albany or Genesee Black Shale (a horizon just above the Hamilton); near Louisville, Kentucky.

Cladodus springeri, exiguus, exilis, etc.

Under the above names have been described several varieties of Cladodont teeth whose relations are with typical Lower Carboniferous species, although they are accompanied in the same "fish-beds" of the Kinderhook limestone, near Burlington, Iowa, by other vertebrate and numerous invertebrate species of undoubted Devonian (Chemung) aspect. The dual nature of the Kinderhook fauna has been clearly demonstrated by Dr. Stuart Weller's recent investigations.* It will therefore be sufficient merely to record the presence of the above-mentioned Cladodonts as forming part of this complex assemblage, transitional between Devonian and Carboniferous, but having pronounced affinity with those later types of piercing teeth which are specially characteristic of the Mississippian series. The Belgian palæontologist, L. de Koninck, has suggested that the teeth named *C. alternatus, succinctus* and *wachsmuthi* are probably all identical with *C. springeri,* a conclusion that is fully approved by Smith Woodward. A similar form of tooth occurs

* Weller, S., The Northern and Southern Kinderhook Faunas. Journ. Geol. 1905, **13,** pp. 617-634. Kinderhook Faunal Studies. Trans. Acad. Sci. St. Louis, 1906, **16,** no. 7.

also in the Carboniferous limestone of the Government of Moscow, Russia.

Mention may also be made in this connection of the forms of pavement dentition known as *Helodus gibberulus* Agassiz, from the Chemung and Waverly rocks of several localities in Pennsylvania, and the newly described *H. comptus,* from the Meadville Upper Shale, in the vicinity of Meadville, western Pennsylvania. The latter exhibits characters transitional between Helodus and Orodus and is delicately plicated.

Order **ACANTHODII.**

Endoskeleton well calcified, with dermal and membrane calcifications in the regions of the skull and pectoral arch. Pterygoquadrate arcade movably articulated with the cranium (hyostylic). Orbit surrounded with a ring of thin plates of dentine. Teeth, when present, firmly fixed to the calcified sheathing plates of the pterygoquadrate and mandibular cartilages. Endoskeletal cartilages of all the fins much reduced, and the dermal expansion almost or completely destitute of rays; each of the fins except the caudal with a robust anterior spine implanted in the flesh. Pelvic fins of male without claspers. Dermal armature of trunk consisting of small, closely arranged quadrate granules, which also extend over the greater portion of the fins; lateral line passing between two series of granules.

This large and characteristic group of Palæozoic sharks is remarkable for developing membrane calcifications in the region of the skull and pectoral arch. The endoskeletal cartilage is also more or less permeated with granular calcifications, though the supports for the fins are never preserved. Two families of Acanthodian fishes are commonly recognized, one distinguished by the presence of a single, and the other by two dorsal fins. Both families are represented in the American Palæozoic, though their remains are infrequent, and as a rule imperfectly preserved. In Europe the Acanthodidae range from the Lower Devonian to the Permian inclusive, but the Diplacanthidae are limited to the uppermost Silurian and Lower Devonian. It has long been considered probable that the detached fin-spines known as Machaeracanthus belong to members of this order, and thanks to the

discovery of complete skeletons of Gyracanthides, from the Carboniferous of Australia, the Acanthodian nature of the Gyracanthus type of fin-spines has been positively established within the past year or two.*

Acanthodes (*?*) *pristis* Clarke.

1885. *Acanthodes ? pristis* J. M. Clarke, Bull. U. S. Geol. Surv., no. **16**, p. 42.
1891. *Acanthodes ? pristis* A. S. Woodward, Cat. Foss. Fishes Brit. Mus. pt. 2, p. 15.
1902. *Acanthoëssus ? pristis* O. P. Hay, Bull. U. S. Geol. Surv., no. **179**, p. 273.
1907. *Acanthodes ? pristis* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 64.

Founded upon a considerable portion of the shagreen of an undoubted Acanthodian fish, the family position of which, owing to non-preservation of the fins, is uncertain. In the solitary known specimen, the greater number of scales have retained their natural exceedingly compact arrangement, and are so minute as to indicate a species of very diminutive proportions. Their characters are given in the original description as follows:

"The scales are very small, measuring .5 mm on the edge, square or slightly sub-rhomboidal in outline, and one-fourth as thick as wide. The adjacent edges at about two-thirds the distance from the upper surface are strongly grooved by a single deep furrow. The upper surface of the scales is smooth and slightly convex."

Formation and locality. Rhinestreet shale of the Portage beds; near Sparta, New York.

Genus **MACHAERACANTHUS** Newberry.

Spines, so far as known, elongated, tapering, more or less curved and somewhat laterally compressed, with sharp edges and a very large longitudinal ridge on each side; central cavity extending nearly to the apex; external surface covered with a thin layer of ganodentine, smooth, finely punctate, or sometimes longitudinally striated.

*Woodward, A. S., On a Carboniferous Fish-fauna from the Mansfield District, Victoria. Mem. Nat. Mus. Melbourne, 1906, **1**, pp. 1-32. See also Bashford Dean's recent paper: Notes on Acanthodian Sharks. Amer. Journ. Anat. 1907, **7**, pp. 209-222.

Spines belonging to the typical species, *M. peracutus* Newberry, occur in the Columbus and Delaware limestones of Ohio, and the equivalent Onondaga limestone of New York State. *M. sulcatus* (Plate III, Fig. 4) is more widely distributed in rocks of the same age, and its persistence at different levels (Logan's Divisions 1 and 6) of the Gaspé series* in eastern Canada apparently indicates a migration northward beyond the confines of the Appalachian basin. *M. longaevus* is a Hamilton species, occurring typically in western New York, but may be represented also by a few doubtful fragments in the Hamilton limestone of Milwaukee, Wisconsin. No indications of this genus have been discovered as yet in the Iowa Devonian.

Genus GYRACANTHUS Agassiz.

The paired fin-spines of this genus have not been found associated with other parts of the skeleton in any instance thus far reported, but their position and mode of attachment are readily to be divined from analogy with the remarkable Australian form described by Smith Woodward under the name of *Gyracanthides murrayi.* Two Devonian species of Gyracanthus are already known from the rocks of this continent: *G. incurvus* Traquair, from the Lower Devonian of Campbellton, New Brunswick; and *G. sherwoodi* Newberry, from the Chemung-Catskill of New York and Pennsylvania. An illustration of the latter form is given in Plate III, Fig. 1. A notice of a third species immediately follows.

Gyracanthus primaevus, sp. nov.

(Text-fig. 17)

Founded upon a unique fin-spine of relatively small size, the total length being probably not more than 8 cm, and maximum width in antero-posterior direction 0.75 cm. Slender in form and of graceful proportions, the spine is much laterally compressed, regularly and rather strongly arched, and gradually tapering to an acute apex. The ornamentation consists of numerous fine

*Geology of Canada, 1863, p. 395.—Palæozoic Fossils, 1874, part 1, **2**, pp. 3, 4. —Lankester, E. R., Geol. Mag. 1870, **7**, p. 398, text-fig. 3.—Clarke, John M., Evidences of a Coblenzian Invasion in the Devonic of Eastern America. A. von Koenen's Festschrift, 1907, p. 359. *Idem*, Early Devonic History of New York and Eastern North America. Mem. N. Y. State Mus. **9**, 1908, p. 76 ff.

slightly waved, delicately crenulate or tuberculate costae, which pass with a very slight obliquity over the face of the spine, this obliquity increasing toward the base as well as toward the anterior margin, where the ridges are also somewhat coarser and more widely separated than either distally or posteriorly. A noteworthy feature of these ridges is that they terminate before reaching the anterior margin, leaving a smooth and highly pol-

FIG. 17.

Fig. 17. *Gyracanthus primaevus*, sp. nov. Stafford limestone (Marcellus division of the Erian); Stafford, New York. Lateral aspect of fin-spine, x 3-2.

ished enamelled band adjacent to the front margin or cutwater. As many as 22 of these ridges terminate along the oblique line of insertion, and here the evidence of minute tuberculation is more distinct than in the more distal portion. About midway the length of the spine an imperfect division or branching of the costae is to be observed. How far the internal cavity is open along the posterior face cannot be ascertained, but the oblique

termination of the costae suggests that it was exposed for a considerable distance. The distal third of the posterior face is armed with a double series of stout, decurved hook-like denticles, of which 16 may be counted in the actual condition of the specimen. The extreme apex of the spine is wanting, and the distal portion for the space of about 2 cm is preserved in impression.

This elegantly formed and beautifully enamelled ichthyodorulite has been only recently brought to light by Dr. J. M. Clarke, the accomplished New York State geologist, to whom we are indebted for the privilege of studying and describing it. Found in the Stafford limestone at Stafford, New York, a rock which lies within the black Marcellus shales and carries in fine development the first clear representation of the Hamilton fauna which develops more profusely above, the present example not only acquaints us with a new species of Acanthodian sharks, but also one that is eminently *proemial*, according to Dr. Clarke's definition of the term. That is to say, the species which is here found at the base of the Erian marks the initial occurrence of a group which reappears sparsely from time to time at different intervals in the Devonian, but does not acquire ascendency in the western hemisphere until during the Carboniferous. It should be said, however, that this statement would need qualification in case the suspected Acanthodian affinities of Machaeracanthus should be definitely established by future discoveries. Account should also be made of the fact that the Lower Devonian fish-bearing horizon at Campbellton, New Brunswick, has not been precisely correlated with the Appalachian formational series, nor has intermigration of the vertebrate elements been shown to take place between the two provinces.

At this point, however, it is pertinent to recall that several undoubted Acanthodian species, including one of Gyracanthus, have been described from the Campbellton locality in New Brunswick, and that, judging from Traquair's rather meagre description, the spine called by him *G. incurvus* presents some similarity to the new form from the Marcellus made known above. Dr. Traquair's specimen barely exceeds 5 cm (2⅛ inches) in length, and its distinguishing feature is stated to consist in "an antero-posterior curvature of a very much stronger and more pro-

nounced description than is found in the young forms of any hitherto described species, and this together with the great delicacy of its ornamentation distinguishes it as new." * The author further remarks in the same connection that "Gyracanthus has hitherto not been known to exist below the horizon of the Carboniferous rocks. Its occurrence in the Lower Devonian of Canada is therefore as interesting a fact as the occurrence of Cephalaspis in the Upper Devonian of the same country." Newberry, however, in his Monograph of 1889, had founded the species *G. sherwoodi* upon the evidence of ten spines contained in an erratic block seven by nine inches in dimensions, within which were also embedded teeth and scales of Holoptychius, the whole easily recognizable as having been derived from the Catskill sandstone in Pennsylvania. More recently the same species has been found in the Chemung of Cattaraugus county and elsewhere in the state of New York. Hence there are at present three clearly distinct species of Gyracanthus ranging from the supposed Lower to the uppermost Devonian in eastern North America. The association in the same matrix of as many as ten spines belonging to at least half as many individuals, assuming that they were all pectoral fin-defenses, and the inclusion therewith of remains of a large Crossopterygian fish is indeed a remarkable circumstance. A convenient explanation of the facts would be to suggest that the spines are preserved as part of the stomach contents of the larger fish whose remains are indicated by scales and teeth, and whose food-habits might well have included such prey as Acanthodian sharks.

Formation and locality. Base of Marcellus division of the Erian (Middle Devonian); Stafford, New York. Holotype preserved in the New York State Museum at Albany.

Subclass HOLOCEPHALI.

Skeleton entirely cartilaginous, in which no true bone is developed; mandibular suspensorium and pterygoquadrate cartilage fused with the cranium (autostylic); exoskeleton, when present, structurally identical with the teeth. Tail heterocercal, gill-slits

*Traquair, R. H., Notes on the Devonian Fishes of Scaumenac Bay and Campbelltown in Canada. Geol. Mag. 1890, dec. 3, vol. **7**, p. 21.—Whiteaves, J. F., Supplementary Notes. Trans. Roy. Soc. Canada, 1908, ser. 3, **1**, sect. 4, p. 258.

four in number, externally covered by a membranous fold, so that but one opening appears on the outside; pelvic fin of male with clasper.

We may profitably insert here the following paragraph from Smith Woodward relating to the Holocephali, and also a few general remarks from the same source regarding Chimaeroids, living and fossil. For further details one may consult the elaborate monograph on Chimaeroids by Professor Bashford Dean, published by the Carnegie Institution of Washington, 1906.

Dental plates essentially similar to those of the existing Chimaeroid fishes are met with in rocks as early as the Middle Devonic; but there is still no evidence of any member of the Holocephali which can not be included in the surviving order of Chimaeroidei. Some of the early forms were certainly armed with dermal plates; but palæontology as yet lends no support for the theory that the Chimaeridae are degenerate descendants of fishes once possessed of membrane bones. The earliest known complete skeletons are unfortunately only Liassic.

Order **CHIMAEROIDEI.**

In all known Chimaeroids, whether recent or extinct, the notochord is persistent and at most only partially constricted, the calcifications in the sheath, when present, consisting of slender rings more numerous than the neural and haemal arches The pectoral fins are abbreviate, without segmented axis; and the pelvic fins in the male are produced into a pair of claspers. In the extinct forms there is no trace of any dermal plate developed in the opercular flap.

The only clear evidence of evolution hitherto observed concerns the development of the peculiar dental plates. In each of the four known families the dentition consists of a few large plates of vascular dentine of which certain areas ("tritors") are specially hardened by the deposition of salts within and around groups of medullary canals, which arise at right angles to the functional surface. In most cases there is a single pair of such plates in the lower jaw, meeting at the symphysis, while two pairs (the so-called vomerine and palatine plates) are arranged to oppose these above. A permanent pulp remains under each plate, and growth thus takes place continually within as the

oral surface is triturated by wear. In the surviving family of Chimaeridae these dental plates are much thickened, while the hinder upper pair ("palatines") are both closely apposed in the median line and considerably extended backwards.

The dental plates named Ptyctodus, from the Devonian of Russia, Rhenish Prussia and North America, are essentially similar to those of modern Chimaeroids, but there are no representatives of the vomerine pair. The tritors, one only in each plate, are well differentiated, consisting of hard, punctate superimposed laminae, arranged obliquely to the functional surface. The contemporaneous teeth known as Rhynchodus and Palæomylus, however, exhibit more indefinite tritoral areas, or none. The symphysial facette is always distinct.

Spines which may be compared with those of modern Chimaeroids are also known from the Devonian and Carboniferous systems, and Harpacanthus and Cyrtacanthus may perhaps be cited as examples of head spines. No Chimaeroid skeletons, however, have hitherto been satisfactorily determined from Palæozoic rocks, save for the possible exception of Menaspis.* The fragmentary remains known as *Dictyorhabdis priscus,* from the Ordovician of Canyon City, Colorado, are of extremely problematical nature, and it is even questioned by some authors whether they are vertebrates.

The most recent and thoroughgoing discussion of the relations between fossil and recent Chimæroids is that of Professor Bashford Dean, in publication No. 32 of the Carnegie Institution of Washington, 1906. His more general conclusions are summed up in the following paragraph (p. 155):

Chimæroids, accordingly, are widely modified rather than primitive forms. The evidence contributed by anatomy, embryology and palæontology is unmistakably in favor of this interpretation. And there can be no doubt that the recent forms retain less perfectly the general characters of the ancestral gnathostome than do living sharks. On the other hand, it must be admitted that Chimaeroids have retained several characters of their Palæozoic Selachian ancestors which modern sharks have lost. According to many converging lines of evidence we may

* Skeletal portions in natural association with the dental plates of the type specimen of "Rhamphodus" are reported, but have not yet been described, by Dr. Otto Jaekel.

indeed go so far as to conclude that the ancestral Holocephali diverged from the Selachian stem near or even within the group of the Palæozoic Cestracionts. Indeed, the recent Chimaeroids and Cestracionts retain many features of kinship. Among these need only be mentioned at the present time approximations in dentition, labial cartilages, articulation of mandibles, structure of fins, and urogenital system. Even the complicated egg-capsule of Chimaeroids finds its nearest parallel in the recent Cestraciont, a comparison often lost sight of on account of the spiral arrangement of the lateral webs in the capsule of the latter form.

From the standpoint of taxonomy, on the other hand, it must be clearly recognized that the Chimaeroids have been separate from the early sharks for so long a time and have acquired such different characters that they are to be given a high rank among the divisions of the subclass Elasmobranchii, the equivalent, let us say, of such groups as Pleuracanths or Pleuropterygians.

Family PTYCTODONTIDAE.

A family at present indefinable, of doubtful ordinal position, known only by remains of the dentition and associated dermal ossifications. A single pair of large, laterally compressed dental plates present in each jaw, united but not fused at the symphysis, and either with trenchant oral margin, or developing one or more tritoral areas posteriorly.

Rhynchodus undoubtedly represents the most primitive condition of dental plates, the tritors of Ptyctodus and Palæomylus arising at a subsequent stage, and indicating greater specialization. The two last-named genera are exclusively Devonian, Rhynchodus alone persisting as late as the Waverly (Lower Carboniferous).

Ever since Pander's investigations of Ptyctodus, in 1858, the opinion has prevailed among authors generally, until very recent times at least, that the Ptyctodont type of dentition affords positive indications of Chimaeroid or Chimaeroid-like fishes during the Palæozoic. So far as reliance can be placed upon detached dental elements, unaccompanied by other parts of the skeleton, this determination of their nature is eminently justifiable, inasmuch as no essential differences are to be observed between the dental plates of Ptyctodus and its congeners, and those of modern Chimaeroids. Palæomylus differs from the typical genus

only in having the tritoral areas more diffuse and indefinite, and in Rhynchodus they are compacted into a narrow band close to the rim of the plates so as to form an extended sectorial margin.

Following Newberry's description of these plates, Sir Philip Grey Egerton expressed the opinion, in 1875, that "they are unquestionably those of Chimaeroid fishes." * The shape of the Meckelian cartilage in Rhynchodus, and the association with this genus or with Ptyctodus of detached dermal ossifications not unlike those of Myriacanthus, are regarded by Dean† as characters which "yield strong evidence in favor of their Chimaeroid nature." Yet on the other hand, the same author continues, "we must admit the possibility that they may have belonged to some early specialized offshoot of a Selachian stem which may not have given rise to true Chimaeroids." Dean's attitude in regard to the problem at large is thus stated by him:

"The main virtue in the study of Ptyctodontids is to the writer this—that they present some evidence (1) that Chimæroids are of Devonian stock; (2) that at this early period their dental plates were still but four in number, representing the dental structures of the jaw-halves of sharks; and (3) that the tritors existed as small points forming together a texture in the dental plates which is well known among early sharks. The evidence, in short, leads us to conclude with fair probability that the vomerine plates of Chimæroids were a later acquisition."—(*loc. cit.* p. 136.)

Among other participants in the discussion of Ptyctodont relations within recent years should be mentioned Professor Otto Jaekel, of Griefswald, and Dr. Louis Dollo, of Brussels. The former of these palæontologists, in the course of his description of "Ramphodus" (afterwards emended to Rhamphodus), made the following statement in regard to Ptyctodus, overlooking the fact that its complete dentition had already become known:‡ "Da wir von der Zahnform und dem Gesammtgebiss von *Ptyctodus* noch nichts genaueres wissen, so können wir ihn

* Quoted by Newberry in Rept. Geol. Surv. Ohio, Palæont. 2, p. 59.

† Dean, B., Chimaeroid Fishes and their Development. Pub. no. 32, Carnegie Inst., Wash. 1906, p. 136. See, however, his subsequently somewhat modified opinion as expressed in *Science* for February 7, 1908, p. 204.

‡ Jaekel, O., Ueber Ramphodus nov. gen., etc. Sitzungsber. Ges. naturforsch Freunde, 1903, p. 392.

auch noch nicht mit genügender Sicherheit den vorhergenannten [Rhynchodus, Palæomylus, etc.] anreihen. Vielleicht ist Ptyctodus schon ein echter Vertreter der sechszahnigen Holocephalen.''

Again, in a communication published three years later (March, 1906), the same author reports the following additional features:*

''Es liegen mir ferner mehrere Arten der bereits von mir beschriebenen Gattung *Ramphodus,* von der ein neues Fundstück auch rudimentäre palatinale Zahnplatten und andere gänzlich unerwartete Skeletteile zeigt. Ebenfalls zu den Chimaeren, aber nicht zu obiger Form dürfte ein Rückenstachel gehören.''

Finally, in July, 1906, the Griefswald professor declares that he has found reason to modify his previous views, and is now of the opinion that Ptyctodonts belong to the Sturgeon tribe of ganoid fishes, and that Sturgeons themselves are related to ''Placoderms'' (*i. e.* Arthrodires plus Asterolepids). His conclusions are thus formulated:†

''Die neuen Funde bestätigen nun zunächst (1), die Richtigkeit meiner ersten Auffassung der Zahnplatten im Gebiss und begründen (2), die Zugehörigkeit der Rhynchodonten zu den Stören (*Acipenseroidei, Chondrostrei*); und (3) die Beziehung der *Chondrostei* zu den Placodermen, mit denen die devonischen Rhynchodonten noch viele Ubereinstimmungen erkennen lassen.''

Dollo's contributions to Ptyctodont literature are contained in two papers already published, and a third is announced as shortly to be forthcoming. In the first,‡ dated June, 1906, it was merely declared that Ptyctodonts are not of Chimaeroid nature (''Les Ptyctodontes ne sont pas des Holocéphales''). In the second,§ published March, 1907, arguments were presented in

---

*Jaekel, O., Neue Wirbeltierfunde aus dem Devon von Wildungen. Sitzungsber. Ges. naturforsch. Freunde, 1906, no. **3**, p. 75.

†Jaekel, O., Einige Beiträge zur Morphologie der ältesten Wirbeltiere. Sitzungsber. Ges. naturforsch. Freunde, 1906, no. **7**, p. 180.

‡Dollo, L., Sur quelques points d'éthologie paléontologique. Bull. Soc. Belge Géol. etc., 1906, **20**, p. 1.

§Dollo, L., Les Ptyctodontes sont des Arthrodères. Bull. Soc. Belge Géol. etc., 1907, **21**, pp. 1-12.

support of the contention that Ptyctodonts are Arthrodires, and that modern Chimaeroids are specialized descendants of Cochliodont sharks. The capital point which influenced him in favor of the former of these theses, as the author admits, depended upon Jaekel's unconfirmed statement that a bony shoulder-girdle was present in "Rhamphodus" the elements of which were thought to be disposed somewhat after the pattern of Coccosteid dermal plates. Evidence will be presented hereinafter to show that both Jaekel and Dollo are mistaken in their interpretation of the elements forming a supposed pectoral arch, and that real homologies do not exist between these external ossifications and parts of the Arthrodiran system of body-armoring.

Genus **RHYNCHODUS** Newberry.

(Syn. *Rhamphodus* Jaekel *non* Davis.)

Functional margin of dental plates simply trenchant, without tritoral areas. Upper and lower dental plates of similar form, except that in some species the symphysial margin of the lower plates is produced downward into a spiniform process. Indications of cartilaginious union between each pair of dental plates are distinctly shown on the inner symphysial facettes.

Rhynchodus secans Newberry.

1873. *Rhynchodus secans* J. S. Newberry, Rept. Geol. Surv. Ohio, **1**, pt. 2, p. 310, pl. 28, fig. 1; pl. 29, figs. 1, 2.
1889. *Rhynchodus secans* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 47, pl. 28, figs. 1-3.
1898. *Rhynchodus secans* C. R. Eastman, Amer. Nat. **32**, pp. 485, 546.
1906. *Rhynchodus secans* B. Dean, Carnegie Inst. Wash. Pub. no. 32, p. 139, text-fig. 127.
1907. *Rhynchodus secans* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 67.

This species, which is the type of the genus, is not uncommon in the Columbus and Delaware limestones of Ohio, and is interesting for having furnished a group of four teeth preserved in natural association, evidently representing the complete dentition of a single individual. In this the mandibular dental plates are easily recognized as such by reason of their having retained an impression showing the entire outline of the Meckelian cartilage. Aside from this, there is but little difference in the form of

upper and lower dental plates, though the latter are as usual somewhat deeper, and both terminate anteriorly in prominent beaks. The latter character is probably a generic one, and is obviously correlated with their adaptation "au régime conchifrage", as Dollo calls it, together with a prehensile habit of plucking hard-shelled food from the bottom. An excavation is noted just back of the beak in the upper dental plate where the terminal point of the lower came in contact with it, thus proving that the relations between the parts functioned in the same manner as in Ptyctodus.

Formation and locality. Columbus and Delaware (="Corniferous") limestone; Ohio.

Rhynchodus excavatus Newberry.

(Text-fig. 18)

1877. *Rhynchodus excavatus* J. S. Newberry, Geol. Wisconsin, **2**, p. 397.
1878. *Rhynchodus excavatus* J. S. Newberry, Ann. N. Y. Acad. Sci. **1**, p. 192.
1878. *Rhynchodus occidentalis* J. S. Newberry, Ann. N. Y. Acad. Sci. **1**, p. 192.
1889. *Rhynchodus excavatus*, Monogr. U. S. Geol. Surv. **16**, p. 50, pl. 29, fig. 1. (The original of this figure is the type specimen of the so-called *R. occidentalis.*)
1898. *Rhynchodus excavatus* C. R. Eastman, Amer. Nat. **32**, p. 486.
1907. *Rhynchodus excavatus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 68.

A comparison of the type specimen of the so-called *R. occidentalis,* shown in text-fig. 18, with an extensive series of dental plates from the Hamilton of Wisconsin, agreeing with Newberry's description of *R. excavatus*, leads to the conclusion that the two forms are identical. Indeed, it appears almost certain that their identity had suggested itself to Newberry, since he inadvertently confused the types of the two species at the time of preparing his Monograph on Palæozoic Fishes of North America. In point of fact, the original exemplar of *R. excavatus* has never been figured, and its actual whereabouts are unknown. On the other hand, the specimen serving for the original description of Newberry's *R. occidentalis* is now preserved in the American Museum of Natural History in New York. The writer is indebted to Dr. L. Hussakof, of that institution, for calling his attention to the fact that this is the very specimen which New-

FIG. 18.

Fig. 18. *Rhynchodus excavatus* Newberry. Cedar Valley limestone (Meso-Devonian); Waverly, Iowa. The dental plate here shown is the holotype of Newberry's so-called *R. occidentalis*. Original in American Museum. Natural size.

berry unwittingly figured under the name of *R. excavatus* in his Monograph of 1889.

That others may judge of the propriety of uniting the two species, we append herewith the original description of *R. occidentalis:*

Teeth of small size, much compressed. Anterior margin slightly curved, but nearly vertical. Superior margin gently arched downward from the prominent anterior point, forming a much compressed triturating surface or edge. Posterior portion of upper margin acute-edged. Exterior lateral surface striated obliquely backward. Basal margin formed by the edges of external and internal laminae, of which the edges are broken and irregular. From the Hamilton limestone, Waverly, Iowa.

Little need be added by way of supplementing the above description. The total length of the dental plates rarely exceeds 5 or 6 cm, though in one specimen in the Cambridge Museum it amounts to 8 cm. There is much similarity between upper and lower dental plates, barring the not uncommon circumstance that the symphysial margin of the lower is produced into a long and slender descending spiniform process, and the sectorial edge of the upper is somewhat less arched or "excavated" (whence the specific title), than in the lower dental plates. As shown by marks of wear, the tips of the lower dental plates closed outside and slightly behind those of the upper, after the same manner as in Ptyctodus. An extensive series of specimens, collected many years ago by Mr. Orestes H. St. John from the Cedar Valley limestone near Waterloo and Waverly, Iowa, is now preserved in the Museum of Comparative Zoology at Harvard College.

The dental plates of this species are accompanied both in the Cedar Valley limestone, and in the Hamilton of Milwaukee by numerous detached scale-like dermal ossifications, somewhat suggestive of those of Myriacanthus,* but presenting much closer affinities with the contemporary "genus" Acanthaspis. As indicated by their almost lamellar thinness and tuberculate ornamentation, these plates were without doubt externally situated, possibly in the vicinity of the pectoral fin. An average-sized plate of this kind, from the Hamilton of Milwaukee, is shown in Plate II, Fig. 18. Plates exhibiting the same form, which is constant, some of equal size and others one-quarter to one-third larger, but all extremely tenuous, occur in the Cedar Valley limestone. They are clearly of identical nature with the element designated as "cleithrum" by Jaekel, found in natural association with the dentition of his so-called *Rhamphodus tetrodon,* and interesting for the enlightenment it furnishes in regard to the so-called Acanthaspis of Newberry. One or two examples of the smaller structure interpreted by Jaekel as "clavicula" are also known from the Waterloo locality. These bodies will be referred to more particularly under the head of

* A good example is figured by Smith Woodward in his Cat. Foss. Fishes Brit. Mus. 1891, pt. 2, pl. 2, fig. 2*a*.

the following species, and the accompanying fin-spines of the form known as Heteracanthus will be noticed under a separate caption.

Formation and locality. Cedar Valley limestone; Waverly and Waterloo, Iowa. Hamilton limestone; Milwaukee, Wisconsin.

Rhynchodus major Eastman.

(Plate III, Fig. 8)

1898. *Rhynchodus major* C. R. Eastman, Amer. Nat. **32,** p. 487, text-fig. 42.
1900. *Rhynchodus emigratus* F. von Huene, Neues Jahrb. für Mineral. **1,** p. 65, text-fig. 2.
1900. *Rhynchodus major* C. R. Eastman, Centralbl. für Mineral. p. 177.
1900. *Rhynchodus major* C. R. Eastman, Amer. Geol. **25.** p. 392.
1903. *Ramphodus tetrodon* O. Jaekel, Sitzungsber. Ges. naturforsch. Freunde, p. 392, text-fig. 1.
1904. *Rhynchodus major* C. R. Eastman, Amer. Nat. **38,** p. 296, text-fig. 1.
1906. *Rhamphodus tetrodon* O. Jaekel, Sitzungsber. Ges. naturforsch. Freunde, pp. 75, 181, text-figs. 1, 3, 5.
1907. *Rhamphodus tetrodon* L. Dollo, Bull. Soc. Belge Géol. **21,** p. 1, pl. 2.
1907. *Rhynchodus major* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 69.
1907. *Rhamphodus* sp. O. Jaekel, Sitzungsber. Ges. naturf. Freunde, no. **6,** p. 8.
1908. *Rhamphodus* sp. B. Dean, Science, n. s. **27,** p. 204.

A species somewhat exceeding in size both *R. excavatus* and *R. rostratus,* and distinguished from them by slight differences in contour, especially by the more strongly convex anterior margin of both upper and lower dental plates. Upper dental plate of considerably less vertical height than the lower, with more slender and acutely pointed symphysial beak, and more retreating anterior margin; the sectorial margin strongly excavated immediately behind the anterior beak.

Lower dental plate relatively deep, with prominent, slightly prehensile symphysial beak, behind which the sectorial margin is regularly but not very deeply concave. Anterior margin boldly and uniformly convex, produced downward into a long, backwardly curved spiniform process similar to that in some species of Ptyctodus. External surface smooth, or with only fine concentric markings due to increment in growth, or occasionally faint rugae.

This species is interesting in the same way as are *R. secans* and the two species respectively of Ptyctodus (*P. calceolus* and *P. ferox*) and Palæomylus (*P. crassus* and *P. greenei*), in which the complete dentition is known. The first-named of these species furnishes reliable criteria for distinguishing between upper and lower dental plates, a group of four naturally associated dental plates being preserved, in which the entire outline of the Meckelian cartilage is shown by the mandibular pair. The lower plate is invariably deeper, and in some forms also somewhat longer than the upper. It usually shows conspicuous symphysial facettes for the lodgment of cartilage holding the jaw-parts together in front. Occasionally, too, it develops a downwardly directed, recurved spiniform process, whose function seems to have been to strengthen the symphysial union, and to form a rigid "chin," so to speak, the front profile of the lower jaw being about as steep as in recent Chimaeroids. The presence of this process can hardly be regarded as a generic character, since it is common to different species of both Ptyctodus and Rhynchodus, though it has not been observed in any example of Palæomylus. Morphologically the anterior process is equivalent to the distinct chisel-shaped presymphysial tooth of Myriacanthus and Chimaeropsis, from Jurassic rocks. Jaekel's novel interpretation of this structure, and of the symphysial facettes (which he thinks served to lodge the nasal capsules), is due to his confusion of upper and lower dental plates in the species we are considering. We have amended his proposed arrangement by restoring the elements to their normal position, as shown in our Plate III, Fig. 8.

Remains of this species occur typically in the Middle Devonian of the Eifel District, in Rhenish Prussia, and so far as can be determined from published figures and descriptions, also in the Upper Devonian of Wildungen, Waldeck. Jaekel himself fails to note any characters which separate his so-called "*Rhamphodus tetrodon*" from the type of Baron von Huene's earlier described *Rhynchodus emigratus,* due regard being paid to the fact that in the figured example of the latter the anterior spiniform process is missing, and has probably been broken away. The Baron has since stated in correspondence that the only reason which

suggested to him the propriety of recognizing the type of his *R. emigratus* as a distinct species is because, at the time of preparing his paper, he was misled into supposing that *R. major* and *R. rostratus,* with which he compared it, were strictly North American species, whereas in point of fact both are from the Eifel Devonian. Owing to similarity in form and identical provenience, the Baron now agrees (*litt.*) with the present writer in regarding *R. emigratus* as synonymous with *R. major.* That the so-called "Rhamphodus" is not entitled to rank as an independent genus will be evident from a comparison of the illustration given in Plate III, Fig. 8 with typical Rhynchodonts, and awarding full value to the original description, which is as follows:*

"*Ramphodus* [=*Rhamphodus*], *n. g.* mit Praemaxillarzähnen, die zusammen die Form eines Papageischnabels und am inneren Vorderrand einen tiefen Ausschnitt besassen, hinter dem an der Innenseite ein flügelförmiger Fortsatz nach hinten und aufwärts [in reality, downwards] gerichtet war. Mandibularzähne schmal, vorn scarf zugespitzt, mit glattem, Tritoren entbehrendem Schneiderand und unten einer schwachen Ausbuchtung am äusseren Vorderrand. Eine oberdevonische Art, der Typus der bevorstehenden Beschreibung, *R. tetrodon n. spec.*"

It has already been remarked that the dental plates of "Rhamphodus" (the statement lacks confirmation that these consisted of more than two pairs)† are acompanied by a series of scale-like ossifications showing precisely the same configuration and tuberculated ornament as certain detached structures which have long been known to accompany Ptyctodont remains in the Middle Devonian of Iowa and Wiscinsin,‡ and being further-

Loc. cit., 1903, p. 392. It may be recalled in passing that the same generic title, with the type species of *Rhamphodus dispar*, was previously proposed by J. W. Davis for certain Cochliodont teeth from the Lower Carboniferous limestone of Armagh. This fact seems to have been generally overlooked by recent writers on Rhynchodus and related forms.

†Dollo's remarks upon this matter may be quoted in slightly condensed form as follows: "Il n'est pas définitivement établi que Rhamphodus a une deuxieme paire de plaques dentaires supérieures. M. O. Jaekel mentionne, il est vrai, une telle paire, mais à l'état rudimentaire. Cependant, il ne l'a pas figurée jusqu'à présent, bien qu'il ait répresenté deux fois la dentition de Rhamphodus, et il n'en parle plus dans sa dernière communication." *Loc. cit.*, 1907, pp. 1, 7.

‡Dean refers these dissociated remains to Ptyctodus at page 136 of his Chimaeroid Memoir published by the Carnegie Institution of Washington, 1906.

more remarkably suggestive of the spiniferous plates described as *Acanthaspis armata* and *A. pruemensis.* The last-named form, it should be remarked parenthetically, is found in the same horizon with Rhynchodus dental plates in the Lower Devonian of the Eifel District, and the former accompanies the type species of Rhynchodus in the Middle Devonian of Ohio.

That these plates were externally situated, and therefore not to be interpreted as parts of a primary pectoral girdle (such as occurs in ganoids and teleosts), is patent from their extreme tenuity, fragility, tubercular ornamentation, and the dense, brittle and close-grained texture of their superficial layer, which has the glistening appearance of vasodentine. Were they the parts of an osseous secondary girdle, such as we are acquainted with in dipnoans, ganoids* and teleosts, we must suppose them to be membrane bones developed on the outer side of the primary girdle and re-enforcing it. But as shown by examination of a large series of detached plates presumably belonging to *R. excavatus,* there is absolutely no indication that they were attached on their inner or visceral side to any other structures, as they must needs have been according to this idea of their nature. On the contrary, all appearances indicate that the series of scale-like plates which Jaekel identifies as a secondary bony shoulder-girdle in "Rhamphodus" were merely dermal ossifications, loosely supported in the integument, and forming an osseous chain or band arranged transversely in advance of the pectoral fin and back of the head-region, but having nothing whatever in common with the cartilaginous pectoral arch, and in nowise homologous with the lateral body-armoring of Arthrodires. Evidence is wanting which justifies an association of Ptyctodonts with Arthrodires, and the known evolutionary history of Chondrostei will not permit us to affiliate them with modern Sturgeons.

On the assumption that Ptyctodonts are of Arthrodiran nature we should expect to find wherever their remains are favorably preserved, (1) above all things an ossified headshield; (2) two pairs of dental elements in the upper jaw, one of them cor-

* For a discussion of the secondary shoulder-girdle in Chondrostei see R. Wiedersheim's "Das Gliedmassenskelet der Wirbelthiere," 1892, pp. 155-160. Consult also the literary references given in this and other works by the same author.

responding to vomerine teeth or "premaxillaries" as they are sometimes called; and (3) a system of dorsal and ventral armoring in the abdominal region, the former articulating with the headshield by a movable joint. None of these structures are found in association with Ptyctodont remains, however, even under the most favorable conditions of preservation. Jaekel, for instance, does not mention an ossified headshield in "Rhamphodus," but notes explicitly that the cranial roof is "composed of calcified cartilage", as is the invariable rule among Elasmobranchs.* Moreover, there is considerable reason to suppose that Ptyctodonts were armed with dorsal fin-spines of the forms known as Heteracanthus, Phlyctaenacanthus, etc., the like of which is unknown among Arthrodires. Problematical as may be the nature of Ptyctodonts, their interpretation as Elasmobranchs still remains the most satisfactory that has been proposed.

Formation and locality. Middle Devonian; Eifel District, Rhenish Prussia. Upper Devonian; Wildungen, Waldeck.

Rhynchodus pertenuis Eastman.

(Text-figure 19)

1904. *Rhynchodus pertenuis* C. R. Eastman, Amer. Nat. **38,** p. 297, text-fig. 2.
1906. *Rhynchodus pertenuis* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **3,** p. 113, text-fig. 7.
1907. *Rhynchodus pertenuis* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 69, pl. 2, fig. 5.

Dental plate narrow and elongate, with sharp and extended sectorial margin and knifeblade-like cross-section; anterior beak prominent, no descending symphysial spiniform process, external surface smooth.

The unique dental plate upon which this species is founded was obtained from the Chemung of Franklin, New York, and is now preserved in the Albany Museum. The general outlines and proportions of this plate differ from those of all other species, and the absence of a spiniform anterior process is a character affiliating it with the type of the genus, *R. secans,* and at the

**Loc. cit.* 1901, p. 183.

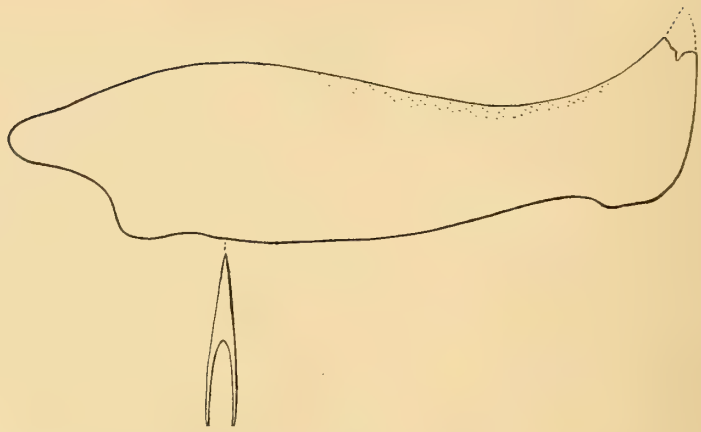


FIG. 19.

Fig. 19. *Rhynchodus pertenuis* Eastm. Chemung; Delaware county, N. Y. Lower dental plate of holotype, slightly less than natural size.

same time separating it from the group represented by *R. excavatus, R. major,* etc. But for the trenchant functional margin and blade-like cross-section, the specimen might readily be mistaken for a lower dental plate of Ptyctodus, instead of Rhynchodus. That it is properly a mandibular element, and referable to the latter genus, seems to admit of no question. The depth of the longitudinal cavity along the base indicates the extent to which the plate was embedded in the supporting cartilage of the jaw. The total length is 9 cm.

Formation and locality. Chemung beds; Franklin, Delaware county, New York.

Rhynchodus sp. ind.

Dental plates of an undetermined species of Rhynchodus are reported by Dr. J. M. Clarke * as occurring in the High Point (Chemung) fauna near Naples, New York. An undescribed member of the group represented by *R. excavatus, R. major,* etc., is also known from the base of the Waverly in Boyle county, Kentucky.

*Bull. U. S. Geol. Surv. 1885, no. 16, p. 72.

Genus **PTYCTODUS** Pander.

Oral surface triturating, the single tritoral area of each dental plate well differentiated, and consisting of hard, punctate, superimposed laminae arranged more or less obliquely to the functional surface. Lower dental plates with upturned symphysial beaks, which, as shown by marks of wear, closed against the outer margin of the upper dental plates. Anterior margin of lower plates sometimes produced downwardly as a slightly recurved spiniform process.

Ptyctodus punctatus Eastman.

(Plate III, Fig. 6)

1907. *Ptyctodus punctatus* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 70.

This species is readily distinguished from all others previously described by the comparative coarseness and peculiar arrangement of the medullary canals passing through the tritoral areas. The sides and triturating surface of the latter are completely covered by a network of small polygonal pittings, formed by the termini of the medullary canals. As these are not grouped in parallel lines, there is no surface indication of laminar structure. The simpler arrangement of the medullary canals in this species, and the fact of its greater antiquity as compared with other known species, are taken as indicating the primitive character of the present form.

Formation and locality. Onondaga limestone (Ulsterian); Le Roy, New York, and corresponding formation in Ohio.

Ptyctodus calceolus Newberry and Worthen.

(Plate V, Figs. 1-17)

1866. *Rinodus calceolus* Newberry & Worthen, Rept. Geol. Surv. Illinois, **2,** p. 106, pl. 10, fig. 10.
1870. *Ptyctodus calceolus* Newberry & Worthen, Rept. Geol. Surv. Illinois, **4,** p. 374.
1875. *Ptyctodus calceolus* J S. Newberry, Rept. Geol. Surv. Ohio, Palæont. **2,** pt. 2, p. 59, pl. 59, fig. 13.
1897. *Ptyctodus calceolus* S. Calvin, Proc. Iowa Acad. Sci. **4,** p. 18.
1898. *Ptyctodus calceolus* C. R. Eastman, Rept. Geol. Surv. Iowa, **VII,** p. 115, text-fig. 10*a*.
1898. *Ptyctodus calceolus* C. R. Eastman, Amer. Nat. **32,** p. 476, figs. 1-17.

1899. *Ptyctodus calceolus* S. Weller, Journ. Geol. **7**, p. 484.
1906. *Ptyctodus* sp. B. Dean, Carnegie Inst. Wash. Pub. no. 32, p. 137, text-fig. 116.
1906. *Ptyctodus calceolus* W. H. Norton, Rept. Geol. Surv. Iowa (1905), **XVI**, p. 356.
1907. *Ptyctodus calceolus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 71.

Dental plates compressed into a thin cutting edge shortly behind the symphysis, but widening gradually, becoming more or less outwardly curved, and the functional surface occupied for nearly its entire width by the tritoral area, the inner margin of which is more strongly curved than the external. Laminar structure of the tritors indicated superficially by fine punctae arranged in parallel rows which are directed obliquely across the triturating surface. The compressed edge in advance of the tritor in the lower dental plate slopes rapidly upward and terminates in a strong anterior beak, beneath which the front margin is continued downwards in a short, blunt process. Upper dental plates similar in a general way to the lower, except that the symphysial margin is rounded and not produced into a beak.

Notwithstanding the extraordinary abundance of this species in various Middle and Upper Devonian localities of the Mississippi Valley, as indicated by thousands of detached tritors, complete dental plates are very rare, their structure being on the whole frail and liable to injury. Of widespread distribution in the Hamilton, the species is most profuse in limited areas of the Upper Devonian, certain layers of no great thickness being fairly charged with their broken and abraded tritors. Nowhere have similar remains been found in such abundance as in the old State Quarry beds * near North Liberty, in Johnson county, where a single exposure only a few yards square has yielded countless fragments of the dentition, including a score or more nearly perfect plates. They are plentiful, though generally of smaller size, in the contemporaneous Sweetland Creek beds of Muscatine county; fine specimens have been obtained from the Upper Devonian Lime Creek shales of Cerro Gordo county, and perhaps the most perfect of all from the Cedar Valley limestone of Bremer county, Iowa. Well preserved dental plates of

*Calvin, S., Geology of Johnson county. Rept. Geol. Survey Iowa, 1897, **VII**, pp. 74-76. Also Proc. Iowa Acad. Sci. 1897, **4**, pp. 16-21.

this species, some of considerable size, are occasionally found in the New Albany (=Genesee) Black Shale near Louisville, Kentucky, and more rarely in the Genesee of western New York State. At least one instance is reported of its occurrence in the Portage fauna of the Agoniatite or Parrish limestone near Naples, New York. Its accompaniment by fin-spines of the form described as Heteracanthus, and other detached structures, is noted below.

Formation and locality. Middle Devonian of Iowa, Illinois, Missouri, Wisconsin and Manitoba. Upper Devonian of Iowa and Elmhurst, Illinois. Genesee of Louisville, Kentucky, and near Buffalo, New York. Portage beds of Naples, New York.

Ptyctodus compressus Eastman.

(Plate V, Figs. 18-27)

1898. *Ptyctodus compressus* C. R. Eastman, Amer. Nat. **32,** p. 479, text-figs. 18-27.

The tritors of this species are relatively longer and narrower than in the preceding, and the oral margin in advance of the triturating surface is developed into a long, keen trenchant edge. In all other species this sectorial margin is shorter than the tritoral area, but in the present form it is invariably longer, sometimes even as much as one-fourth longer than the tritor. The dental plates are as a rule less curved than those of *P. calceolus,* and the symphysial beak of the lower elements is less produced.

Formation and locality. State Quarry beds (Upper Devonian); North Liberty, Johnson county, Iowa.

Ptyctodus ferox Eastman.

(Text-figures 20-22)

1898. *Ptyctodus ferox* C. R. Eastman, Amer. Nat. **32,** p. 480, text-figs. 35-40.
1899. *Ptyctodus ferox* C. R. Eastman, Journ. Geol. **7,** p. 282.
1906. *Ptyctodus* sp. B. Dean, Carnegie Inst. Wash. Pub. no. 32, p. 139, text-fig. 126.
1907. *Ptyctodus ferox* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 72.

Dental plates unusually large and massive, attaining a total length of about 14 cm, and exhibiting but slight lateral curvature. Lower dental plates with stout symphysial beak, the front

margin projecting downward as a long spiniform process. Anterior margin of upper dental plate regularly arched, not produced into a beak or spinous process, and showing on the outer face marks of contact with the opposing dentition. Inner surface of both upper and lower dental plates with a roughened, deeply incised triangular symphysial facette.

FIG. 20.

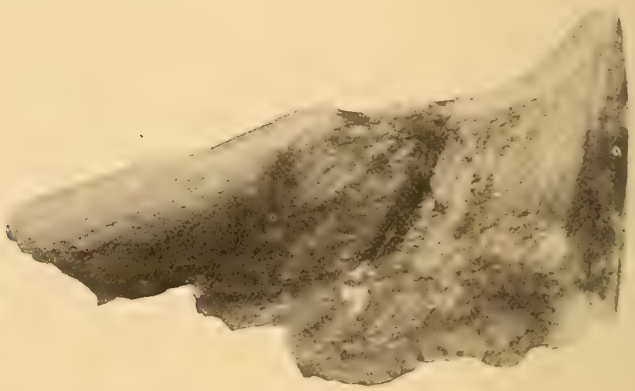


FIG. 21.

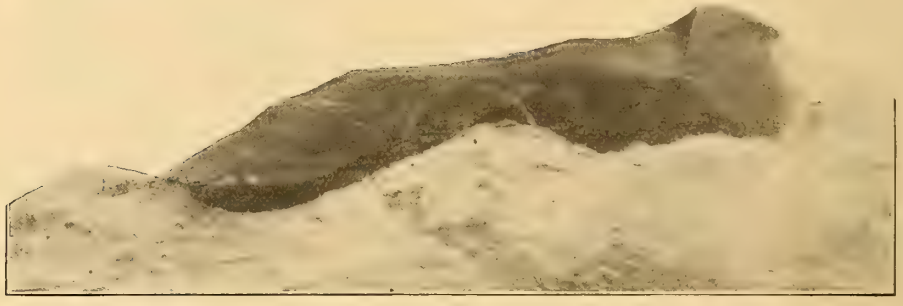


FIG. 22.

Fig. 20, 21.—*Ptyctodus ferox* Eastm. Hamilton; Milwaukee, Wis. To the left is shown an immature lower dental plate with well preserved descending process at the front margin; to the right an older and much worn lower dental plate from which the descending process and a portion of the inferior border have been broken away. Both plates have distinctly marked tritoral areas with obliquely directed punctae, x 1-1.

Fig. 22.– *Ptyctodus ferox* Eastm. Hamilton; Milwaukee, Wis. Left upper dental plate showing facet due to wear against the lower dentition. x 1-1.

The fact that the smaller and younger plates belonging to this species have a decidedly Rhynchodus-like aspect (text-fig. 20), indicates that the functional margin in immature teeth was simply trenchant, the tritors not being developed until a comparatively late period. Rhynchodus, therefore, represents a more primitive stage than either Ptyctodus or Palæomylus in the

development of dental plates, its relations to contemporary types being closely paralleled by Rhinochimaera among recent genera.* There is excellent reason for believing that the fin-spines known as Heteracanthus or "Gamphacanthus" are truly referable to the species under discussion, their size being commensurate, and though not actually associated with the dentition in any instance thus far reported, they invariably accompany it in the Middle Devonian of Wisconsin and Iowa. Other accompanying remains will be noticed later under a separate heading.

Formation and locality. Hamilton limestone; Milwaukee, Wisconsin. Cedar Valley limestone; Waverly and Waterloo, Iowa. State Quarry beds (Upper Devonian); North Liberty, Iowa.

Ptyctodus eastmani Weller.

1906. *Ptyctodus eastmani* S. Weller, Trans. Acad. Sci. St. Louis **16**, p. 462, pl. 1, figs. 31, 32.

The geological occurrence of this species is interesting as indicating the survival of a characteristic Devonian genus as late as the dawn of the Carboniferous. Its presence in the Kinderhook is paralleled by the persistence of Rhynchodus in the basal portion of the Waverly in Boyle county, Kentucky. The distinguishing features of this species are given in the original description as follows:

"Occasional abraded tritors of a species of Ptyctodus occur in the Glen Park limestone, and one nearly perfect specimen of a complete dental plate has been observed. . . . The most notable characteristic of the Glen Park species as distinguished from *P. calceolus,* is in the lower margin of the tooth, this margin describing a continuous slightly concave curve from the posterior to the anterior extremity, while in *P. calceolus* this margin is convex from the posterior extremity to a conspicuous sinus below the anterior extremity of the tritor, and then convex again nearly to the anterior extremity of the symphysial beak where there is a conspicuous downward extension of the tooth. The upper [=oral] surface also differs from *P. calceolus* in having a less conspicuous differentiation between the tritoral and the symphysial regions."

*Garman, S., Chimaeroids, especially Rhinochimaera and its Allies. Bull. Mus. Comp. Zool. 1906, **41**, p. 246.—Dean, B., *Loc. cit.* p. 128.

Some of the above-mentioned differences may be due in part to conditions of preservation, but one important characteristic, as appears from the illustration, is found in the absence of a descending spine, or even a blunt projection, at the anterior margin of the lower dental plate.

Formation and locality. Glen Park limestone (Kinderhook); Glen Park, Jefferson county, Missouri.

Accompanying Detached Parts, presumably referable to Ptyctodonts.

1. DORSAL FIN-SPINES.

Genus **HETERACANTHUS** Newberry.
(Syn. Gamphacanthus Miller)

Spines of moderate size, broad and laterally compressed at the base, but soon becoming subtriangular in cross-section, nearly rectilinear, and gradually tapering toward the acute apex. Internal cavity relatively large, extending nearly to the apex, and open along the posterior margin for a considerable distance. No anterior keel; posterior denticles not observed. Exserted portion ornamented with finely crenulated longitudinal ridges which become smooth and flat with wear, and are separated by fine, denticulate intercostal grooves.

Heteracanthus politus Newberry.

1889. *Heteracanthus politus* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 66, pl. 21, figs. 4, 5.
1892. *Gamphacanthus politus* S. A. Miller, North Amer. Geol. and Pal. p. 715.
1898. *Heteracanthus politus* C. R. Eastman, Amer. Nat. **32**, p. 552.
1899. *Heteracanthus politus* C. R. Eastman, Journ. Geol. **7**, p. 282.
1907. *Heteracanthus politus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 82.

Spines attaining a total length of about 20 cm, very broad at the base, and with Ctenacanthus-like ornamentation. The longitudinal costae, which are rather numerous and closely crowded, become perfectly smooth in the worn condition, their presence being indicated only by the fine and deep intercostal grooves,—the so-called "sinuous or denticulate longitudinal sutures" of Newberry. More or less variation in size and number of the costae is to be observed among different examples. The basal

portion is somewhat produced anteriorly, but to a less extent than in *H. uddeni,* and without forming a very conspicuous "shoulder" or Physonemus-like projection in front.

Bilaterally symmetrical as these dermal defenses undoubtedly are, their position must have been in the median line of the body, and not, as suggested by Newberry and others, along the front margin of the pectoral fins. That they were borne by Chimaeroids (Ptyctodonts) seems very probable from the fact that they are a constant accompaniment of the dental plates of Ptyctodus and Rhynchodus in the Middle Devonian of Iowa and Wisconsin. The longitudinal extension of the base is a feature which suggests comparison with the supporting cartilage of the dorsal fin-spines in all recent Chimaeroids, and even the triangular cross-section agrees with modern Chimaeroid conditions. Both Rohon and Jaekel have noted the accompaniment of European Ptyctodont remains by detached fin-spines, but no specimen has been described in which they are seen to be naturally associated.

The present form of ichthyodorulite is a characteristic Middle Devonian species, and rather widely distributed. Numerous specimens have been obtained from the Cedar Valley limestone of Waverly and Waterloo, Iowa, and from the Hamilton of Milwaukee, Wisconsin. One very well preserved spine showing the closely spaced and finely denticulated costae is to be seen in the State Museum at Albany, having been derived from the Hamilton of Canandaigua Lake; and another is said to have come from the Naples shale of the western part of New York State.

Formation and locality. Hamilton; Milwaukee, Wisconsin, and corresponding Cedar Valley limestone of Bremer county, Iowa; also Hamilton and Naples shale (Portage) of New York State. Doubtful indications also in State Quarry beds of Johnson county, Iowa.

Heteracanthus uddeni Lindahl.

1897. *Heteracanthus uddeni* J. Lindahl, Journ. Cincinnati Soc. Nat. Hist. **19,** p. 95, pl. 6.
1898. *Heteracanthus uddeni* C. R. Eastman, Amer. Nat. **32,** p. 557.
1899. *Heteracanthus uddeni* C. R. Eastman, Journ. Geol. **7,** p. 282.
1907. *Heteracanthus uddeni* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 83.

Spines of moderate size having the distal portion essentially as in the preceding species, but the basal or inserted portion curving forward and extended into a rounded anterior projection or "shoulder", comparable in a way to that observed in Stethacanthus and some species of Physonemus. The longitudinal costae are finer and more numerous than in the typical species, and are slightly sinuous in direction toward the base.

Formation and locality. Hamilton limestone; Milwaukee, Wisconsin, and corresponding Cedar Valley limestone of Buffalo, Waterloo and Waverly, Iowa.

Genus ACANTHOLEPIS Newberry.

Spines in reality compound, consisting of two closely applied segments, a small spatulate anterior and a major, regularly arched posterior portion, the latter representing the usual type of dorsal fin-spine, and the former corresponding to its supporting cartilage, as seen in modern Holocephali. The major segment, or fin-spine proper, sometimes attains a large size, is of triangular section in that the anterior margin is acute, the lateral faces flattened and slightly divergent from each other toward the base, and the posterior face abruptly truncated or becoming slightly hollowed toward the line of insertion, where the walls of the basal portion suddenly flare outwards on either side, and form a subpyramidal figure. Seen in profile, the exserted portion is gently arcuate, tapering distally to an acute point, its sides ornamented with numerous, closely spaced, finely stellate tubercles, which sometimes exhibit an arrangement parallel to successive growth-lines. Tubercles along either side of the posterior margin enlarged so as to form a double row of denticles directed at right angles to the margin.

Inserted portion of major segment slightly curved backward and gradually narrowing, with gently rounded proximal extremity, and line of apposition with anterior spatulate segment nearly rectilinear. The smaller anterior segment has the distal portion, which is partially exserted, gradually tapering, and the inserted proximal portion evenly rounded; its ornamentation identical with that of the major portion, or fin-spine proper. Lateral walls of both segments very thin, and hence usually found closely

appressed in the fossil condition, although specimens that have escaped deformation show that the cross-section is acutely triangular along the line of insertion in the integument.

The above definition has been emended and amplified in the light of a fresh examination of Newberry's type material, and of newly discovered specimens both of the present form and of the closely allied Hamilton species known as *Phlyctaenacanthus telleri,* in which the characters of the basal portion are well displayed. Heretofore doubt has prevailed as to whether the spines referred to these provisional, and possibly identical genera, were in reality segmented, this being a most unusual condition among ichthyodorulites. This doubt is now dispelled. During the past year an exceptionally perfect example of Phlyctaenacanthus has been described and figured by Mr. Edgar E. Teller, of Milwaukee, which clearly demonstrates the dual nature of the Hamilton species named in his honor. A reference to his paper is given below. Likewise, one of Newberry's originals of the Corniferous form we are considering (that figured in Plate 31, fig. 5, of his Monograph of 1889), may be considered as proving that the "scutes", as Newberry calls them, of *A. fragilis* are disposed in dual series, but not in groups of more than two, as the original author imagined.

The characters of the basal portion are well displayed in the extremely small and no doubt immature spine shown in Plate III, Figs. 5 and 5*a* of the present contribution. The original is from the "Corniferous" limestone of the Falls of the Ohio, and is preserved in the Museum of Comparative Zoology. It shows, as do also some undeformed specimens of Phlyctaenacanthus, that the tenuous walls of the basal portions of both segments were laterally expanded, and inserted in the soft parts in a manner analogous to that seen in Stethacanthus. On decomposition of the soft parts, the hollow cavity contained between the lateral faces yielded to mechanical pressure, in the generality of cases at least, thus bringing the walls of either side in contact, and presenting a very deceptive appearance. This state of affairs was remarked upon by Newberry, but somewhat differently interpreted by him, in the following terms:

"In some instances the plates [*i. e.*, fin-spines] are triangular in outline, and seem to have been thin cones of bone or enamel, supported by cartilaginous centers. As the latter are decomposed, the sides, which were once widely separated, were brought together or crushed in like broken shells."—(Palæozoic Fishes N. America, p. 35.)

Acantholepis fragilis Newberry.

(Plate III, Figs. 5, 5*a*)

1857. *Oracanthus fragilis, granulatus, abbreviatus* J. S. Newberry, Proc. Nat. Inst. n. s., **1**, p. 126.
1875. *Acantholepis pustulosus* J. S. Newberry, Rept. Geol. Surv. Ohio, Palæont. **2**, pt. 2, p. 38, pl. 56, figs. 1-6.
1889. *Acantholepis pustulosus* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 34, pl. 31, fig. 5.
1889. *Eczematolepis pustulosus* S. A. Miller, North Amer. Geol. and Pal. p. 586, text-fig. 1098.
1891. *Acantholepis pustulosus* A. S. Woodward, Cat. Foss. Fishes Brit. Mus. pt. 2, p. 129.
1907. *Acantholepis fragilis* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 79, pl. 3, fig. 1.

Major segment of detached fin-spines attaining a total length of about 25 cm, and exhibiting the characters of the "genus". Minor anterior segment spatulate in form, in general like that of Phlyctaenacanthus, and with same tubercular ornamentation as the principal spine. Arrangement of tubercles often varying considerably, sometimes paralleling concentric growth-lines, and generally finer and more closely crowded in small, immature spines than in fully grown examples.

The spines which are included under this provisional title,* were first associated with Oracanthus by Newberry, but subsequently interpreted by him as dermal plates or scutes of "Placoderms", and supposed to be of similar nature as those which have received the name of Acanthaspis. Subsequently their resemblance to the triangular ichthyodorulites of Psammosteus was pointed out by Smith Woodward, before the true nature of the latter genus had been ascertained. They are here interpreted

*For the designation Acantholepis, preoccupied among insects, the late Mr. S. A. Miller proposed the not too aesthetic sobriquet of "Eczematolepis", a procedure that proves the truth of Pope's lines:

* * * Index-learning turns no student pale,
Yet holds the eel of science by the tail.

as dermal defenses of Ptyctodonts, partly on account of their being a frequent accompaniment of Rhynchodus and Palæomylus in the Corniferous and Hamilton respectively of Ohio and Wisconsin, and partly because their triangular cross-section and segmented structure suggest comparison with modern Chimaeroids more readily than with other forms. The comparison becomes effective only in so far as the anterior segment of the fossil forms is brought into relation with the supporting cartilage of the single dorsal fin-spine in modern Chimaeroids.*

Formation and locality. Onondaga limestone (Ulsterian) near Buffalo and Le Roy, New York, and Columbus and Delaware limestones ("Corniferous") of Ohio. Fragmentary remains either of this or a very similar form occur in the Hamilton limestone (Erian) of Milwaukee, Wisconsin, and one nearly perfect specimen, now preserved in the State Museum at Albany, is interesting for having been derived from the Ithaca beds (recurrent Meso-Devonic fauna in the Portage) near Truxton Corners, Cortland county, New York.

Genus PHLYCTAENACANTHUS Eastman.

Distinctly segmented arcuate spines of large size, with flattened lateral faces which meet at an acute angle in front along the line of insertion, and diverge outwardly and downwardly on either side toward the proximal, inserted extremity, so that the basal pirtion is triangular or even subpyramidal in outline. Relations of the two segments and their general form very similar to those of Acantholepis, and manner of their insertion recalling the corresponding portion of Stethacanthus.

Phlyctaenacanthus telleri Eastman.

1898. *Phlyctaenacanthus telleri* C. R. Eastman, Amer. Nat. **32**, p. 551, text-fig. 49.
1899. *Phlyctaenacanthus telleri* C. R. Eastman Journ. Geol. **7**, p. 283.
1906. *Phlyctaenacanthus telleri* E. E. Teller, Bull. Wisconsin Nat. Hist. Soc. **4**, p. 162, pl. 1-5.
1907. *Phlyctaenacanthus telleri* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 80.

*The mode of attachment of the dorsal fin-spine and condition of the axis in Rhinochimaera and Callorhynchus of existing seas is well shown by S. Garman in Bull. Mus. Comp. Zool. 1904, **41**, no. 2, plates 1 and 2.

The spines assigned to this species are scarcely distinguishable from those of Acantholepis, such differences as are to be noted in form, segmented structure and tuberculate ornamentation being only of minor importance. These Hamilton spines are evidently constructed upon the same peculiar pattern as those that occur typically in the Onondaga of New York and Ohio, described by Newberry as Acantholepis. Ignorant as we are, however, of their precise relations, it seems advisable to maintain a provisional distinction between the two genera and species, until such time at least as an identity is established between slightly dissimilar spines occurring in different divisions of the Middle Devonian. The species which is thus conventionally distinguished under the above name is not known to occur elsewhere than in the Hamilton limestone of Milwaukee, Wisconsin. *Palæomylus greenei* appears also to be limited to the same horizon and locality, and other species of Palæomylus, *P. crassus* and *P. frangens,* accompany the spines of Acantholepis in the Ohio Onondaga. The coincidence suggests with some plausibility that Palæomylus may have been armed with segmented spines of this character.

Formation and locality. Hamilton limestone; Milwaukee, Wisconsin.

Genus ACANTHASPIS Newberry.

A purely provisional classificatory title which may for the present be conveniently retained for certain spiniferous plates occurring in the Lower and Middle Devonian of this country and Europe, but known as yet only in the detached or dissociated condition. There are, however, excellent reasons for supposing these structures to be dermal ossifications belonging either to Rhynchodus or some closely related genus, although heretofore they have been variously classed with Cephalaspids, Bothriolepids and Arthrodires, especially such forms among the last-named as Phlyctaenaspis.

The chief reason for supposing the spiniferous bodies described under this name and the dental plates of Rhynchodus to belong to one and the same sort of creature depends upon the recognition of homologies between the plates known as Acan-

thaspis and certain very similar structures that have been described by Jaekel in natural association with the dentition and other parts of the skeleton of "Rhamphodus", a name which we have shown to be synonymous with Rhynchodus. Attention has also been called to the fact that plates of almost identical conformation, and without doubt of the same nature as the dermal ossifications described by Jaekel, are an invariable accompaniment of *Rhynchodus excavatus* in the Middle Devonian of Iowa and Wisconsin. A like coincidence is to be noted in the distribution of the so-called *Acanthaspis armata* and the type species of Rhynchodus (*R. secans*); and as regards the two or three Eifelian species of Rhynchodus, these are accompanied by the dissociated spiniferous bodies known as *Acanthaspis pruemensis* Traquair* and *A. tuberculatus* Eastman.† On the other hand, the peculiar Asterolepid described by Smith Woodward‡ from the Lower Devonian of Spitzbergen, and characterized by having a fixed spinous appendage, must be regarded as of totally different nature, whose distinctness from either Phlyctaenaspis- or "Acanthaspis"-like forms is best indicated by making it the type of an independent genus. For this the name of Arctolepis is proposed, in allusion to its hyperborean habitat. Besides the type species, *A. decipiens* (Woodward), it is possible that a second Spitzbergen species, described by Smith Woodward under the name of *Acanthaspis minor,* should also be referred to the same genus. The correctness of Woodward's reference of these forms to the Asterolepidae apparently admits of no question.

Acanthaspis armata Newberry.

(Plate I, Fig. 14)

1875. *Acanthaspis armatus* J. S. Newberry, Rept. Geol. Surv. Ohio, Pal. **2,** pt. 2, p. 37, pl. 53, figs. 1-6.

1889. *Acanthaspis armatus* J. S. Newberry, Monogr. U. S. Geol. Surv. **16,** p. 36, pl. 31.

1894. *Acanthaspis armata* R. H. Traquair, Ann. Mag. Nat. Hist. ser. 6, **14,** p. 371.

*Traquair, R. H., Notes on Palæozoic Fishes. Ann. Mag. Nat. Hist. 1894, ser. 6, **14,** p. 370.

†Eastman, C. R., Devonische Fischreste aus der Eifel. Centralblatt für Mineral. 1900, p. 178. Also in Amer. Geol. 1900, **25,** p. 392. Original figured by F. Roemer, Lethæa Geognostica, 1876, **1,** pl. 31, fig. 10.

‡Woodward, A. S., The Devonian Fish-Fauna of Spitzbergen. Ann. Mag. Nat. Hist. 1891, ser. 6, **8,** p. 4, pl. 1.

1896. *Acanthaspis armata* E. W. Claypole, Amer. Geol. **17**, p. 354.
1906. *Acanthaspis* sp. L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9**, p. 132, text-fig. 16.
1907. *Acanthaspis armata* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 117, pl. 2, fig. 2.
1907. *Acanthaspis armata* O. Jaekel, Sitzber. Ges. naturf. Freunde, no. **6**, p. 8, text-fig. 4.

The spiniferous plates which are known under this provisional designation have not been found in natural assemblage with other parts of the skeleton of forms accompanying them in the same horizon, but it is to be noted that they are an invariable accompaniment of Rhynchodus dental plates, and as essentially similar structures have recently been described by Jaekel in undoubted association with the dentition, calcified cranial roof and other parts of the anatomy of *Rhynchodus major* (type of his so-called "Rhamphodus"), the most satisfactory interpretation of their nature seems to be to regard them as dermal ossifications of the same genus.

All of the specimens thus far brought to light are of fairly uniform configuration, and agree in being composed of two portions: (1) a thin, almost lamellar and more or less flattened plate, finely tuberculated on the external surface in larger examples, but smooth or with but few scattered tubercles in those of smaller dimensions; and (2) an elongate, tapering, gently curved and feebly denticulate spinous process, which is immovably attached to the supporting lamellar plate by an oblique suture. This suture may be indistinct in small-sized examples, but is usually conspicuous in those whose larger size may be considered as indicating adult individuals. The interior of the spinous portion is hollow throughout, subcircular in cross-section, although frequently deformed by the fossilization process, and along the line of its attachment with the basal plate is sometimes to be seen a double row of perforations which communicate with the internal cavity.

Formation and locality. Onondaga limestone; Le Roy, New York, and the nearly equivalent Columbus and Delaware limestones of Ohio.

2. VERTEBRAL CENTRA.

It is a well known fact that the usual condition of the vertebral axis in Palæozoic fishes was notochordal, and even in the most advanced forms ossification seldom progressed so far that the vertebral bodies were more than hollow rings. The earliest Elasmobranch bodies of this nature known to Agassiz were of Jurassic age, and the total absence of ossified centra in Palæozoic ganoids, even in the most exquisitely preserved Palæoniscid skeletons, impressed this ichthyologist as a very singular fact. Inclined at first to attribute their absence to defective preservation, or to post-mortem destructive agencies, such as chemical solution, he afterwards adopted the opinion that is now generally entertained, namely, that in the aggregate of Palæozoic fishes the axis never passed beyond the cartilaginous stage. Even in Devonian Lung-fishes, such as Dipterus, Scaumenacia, etc., there were no ossified centra, and the perforated bodies from the Devonian of Novgorod, Russia, that were tentatively regarded as of Dipterine nature by Pander * have been excluded from such association by Traquair after an examination of a large quantity of Scottish material.†

Under these circumstances it is interesting to record the fact that a single well preserved vertebral centrum has been brought to light during the spring of last year from the Upper Devonian near Solon, in rocks of the same age as the State Quarry beds north of Iowa City. Mr. J. H. Hoats, one of Professor Calvin's students in geology at the State University, was fortunate enough to discover the specimen while collecting in Johnson county, and the thanks of the writer are due to both master and pupil for the privilege of describing it. An illustration of it is given of the natural size in Plate XII, Fig. 16.

This unique example of a detached vertebral body is chiefly interesting on account of its geological antiquity. There are no similar contemporaneous structures with which it may be compared, and in the absence of other naturally associated parts, its systematic position can only be conjectured. Ptycto-

* Pander, C. H., Ueber die Ctenodipterinen des devonischen Systems. St. Petersburg, 1858.

† Traquair, R. H., On the genera Dipterus, Palædaphus, etc. Ann. Mag. Nat. Hist. 1878, ser. 5, **2**, p. 10.

dont remains being represented in far greater abundance in the same formation than any other group of fishes, and tritors of *P. calceolus* surpassing all the rest in point of numbers, there is a strong temptation to make this theoretical association of parts.

The specimen is here considered under the head of detached parts accompanying Ptyctodont remains because this is a convenient place to speak of it, and also because it does not seem to us a too remote contingency that the body actually belongs to Ptyctodus or one of its congeners. At the same time it must be acknowledged as a very remarkable fact that similar bodies have not been brought to light elsewhere in association with Ptyctodont remains, especially in localities where these remains are well preserved, as at Waterloo, or Milwaukee, or the Upper Devonian of Wildungen, Germany. And above all we must not be forgetful that this elongate centrum is strikingly dissimilar to the narrow "rings" observed in those Chimaeroids where the axis is segmented, and that in the existing Callorhynchus no trace of axial segmentation is to be seen at all. Hence the occurrence of calcified vertebral bodies in Ptyctodonts, of the form presented by Mr. Hoats' specimen, would be a character difficult to reconcile with their supposed Chimaeroid affinities. The centrum *looks* as if it belonged to fishes of a higher grade than Chimaeroids, or even Dipnoans, but as we know of absolutely no other remains with which they might be theoretically associated, the conjecture is allowed to stand that it *may* be of Ptyctodont nature.

The original specimen obtained by Mr. Hoats is now deposited in the Museum of Comparative Zoology. It is of moderate or rather small size, measuring 1 cm in length, and approximately 1.2 cm in diameter, allowing for a slight deformation due to mechanical pressure prior to or during fossilization. The intervertebral faces are deeply biconcave, and apparently perforated by a small central opening for passage of the notochord. In the present condition of the specimen, however, it cannot be positively determined whether the orifices seen on either face are continuous throughout the substance of the vertebral body. Some of the problematical Russian specimens are completely perfo-

rate, others not. Dorsally are seen two longitudinal fossae which mark the position of the neural arches. The texture is everywhere quite compact, that of the intervertebral faces being especially dense, yet exhibiting under the lens the structure of calcified cartilage.

3. TUBERCULATED DERMAL PLATES.

Different varieties of detached tubercles, some of them of large size, and other dermal ossifications evidently of Elasmobranch (and possibly Holocephalic) nature are found in considerable abundance in the Kinderhook limestone near Burlington, LeGrand, and elsewhere in Iowa. Some of these tuberculated plates and spiniform bodies bear a strong resemblance to those found in natural association with Myriacanthus, as figured by Smith Woodward (Cat. Foss. Fishes Brit. Mus. pt. 2, pl. 3, fig. 4, and Quart. Journ. Geol. Soc. 1906, *62,* pl. 1, figs. 4, 5), and on that account may be provisionally referred to Palæozoic Chimæroids,—that is to say, Ptyctodontidae. That members of this family were in existence as late as the dawn of the Carboniferous is proved by the occurrence of *Ptyctodus eastmani* in the Glen Park limestone (Kinderhook) of Jefferson county, Missouri, and by the presence of an undescribed species of Rhynchodus in the Waverly of Boyle county, Kentucky. These Lower Carboniferous forms are to be regarded, however, as archaic survivals of late Upper Devonian fish faunas.

An idea of the general appearance of the tuberculated dermal plates occurring in the Iowa Kinderhook, and tentatively regarded as of Chimaeroid nature, may be had from an inspection of the illustrations given in Plate II, Figs. 12 and 15, the originals of which are preserved in the Museum of Comparative Zoology. In the same category should be placed the curious spiniform bodies described under the name of *Erismacanthus barbatus,* and the small falcate spines called *Physonemus pandatus* and *P. hamus-piscatorius.** Dean and others have suggested with much plausibility that the defenses known as *Cyrtacanthus dentatus,* from the Ohio Corniferous, and the Lower Carbonifer-

*Bull. Museum Comp. Zool. 1903, **39,** no. 7.

ous species of Harpacanthus, are in reality the head-spines of Palæozoic Chimaeroids.*

ICHTHYODORULITES.

As remarked by Smith Woodward, the characters of the dermal spines and tubercles of cartilaginous fishes vary so much in the different genera, and are sometimes so completely identical when other parts are quite distinct, that all fossils of this nature hitherto discovered in an isolated condition may be conveniently grouped together under the denomination of Ichthyodorulites. The term was first employed by Buckland and De la Beche, who were the earliest to discover the true nature of these fossils; it was subsequently applied by Agassiz to all fossil spines of Elasmobranch and Chimaeroid fishes, whether correlated with the teeth or not; and still later was restricted by Smith Woodward to those detached spines, tubercles and plates which exhibit the microscopical structure of vasodentine, but whose precise systematic position cannot be determined. It is in the latter sense that the term is here employed to include isolated dermal structures that are probably of non-Chimaeroid nature.

Genus ONCHUS Agassiz.

Spines of small size, laterally compressed; sides of exserted portion ornamented with smooth or faintly crenulated longitudinal ridges; no posterior denticles. In all, two Silurian and one Devonian species are known from North American Palæozoic rocks, and an undescribed form is also reported from the Niagara of Cumberland, Maryland. The Devonian spine may be briefly indicated as follows.

Onchus rectus Eastman.

(Plate III, Fig. 9)

1899. *Onchus rectus* C. R. Eastman, 17th Ann. Rept. N. Y. State Geol. p. 323, text-fig. 4.

1907. *Onchus rectus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 74, text-fig. 16.

Spines attaining a total length of about 5 cm, nearly rectilinear, and tapering gradually to an acute point. Inserted portion round in cross-section, very delicately striated; exserted

* Carnegie Inst. Wash. Pub. no. 32, 1906, p. 136.

portion laterally compressed, without trace of posterior denticles, the sides traversed by about ten fine longitudinal costae. The latter are non-bifurcating, regularly spaced, and of uniform size with the exception of the large triangular one along the anterior margin, which is twice the width of the others.

Formation and locality. Chemung group; Delaware county, New York.

Genus **HOMACANTHUS** Agassiz.

This genus, which strongly resembles Ctenacanthus, is thus defined by Smith Woodward: "Dorsal fin-spines of small size, slender, more or less arched, laterally compressed, and gradually tapering distally; sides of exserted portion ornamented with few, large, smooth, widely-spaced longitudinal ridges; a similar ridge also forming a large anterior keel; posterior face with a double series of large, downwardly curved denticles."

American species that were formerly referred to Homacanthus, have, with but two exceptions, since been removed to other genera; but at least one Devonian representative of this genus seems to be indicated by the spines described in the following paragraph.

Homacanthus acinaciformis Eastman.

(Plate III, Fig. 10)

1903. *Homacanthus acinaciformis* C. R. Eastman, Bull. Mus. Comp. Zool. **39**, p. 218, pl. 5, fig. 58.

1907. *Homacanthus acinaciformis* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 75, pl. 1, fig. 16.

Spines comparatively small, slender, gradually tapering, gently and regularly arcuate; lateral surface with five or six continuous longitudinal ridges; posterior denticles slender, rather widely spaced.

The small, gracefully curved spines referred to this species are more strongly arched than those found in the Lower Carboniferous limestone of this country and Great Britain, but according to J. W. Davis, much variation in curvature is to be observed in spines belonging to a single species. Some resemblance is to be noted between the present form and the Upper Devonian spines from Ohio described by Newberry under the

name of *Hoplonchus parvulus*. According to Smith Woodward, the so-called *Homacanthus gracilis* of Whiteaves, from the Lower Devonian of Campbellton, New Brunswick, may belong to an Acanthodian resembling Climatius.

Formation and locality. Chemung Group; Warren, Pennsylvania.

Homacanthus delicatulus Eastman.

1903. *Homacanthus delicatulus* C. R. Eastman, Bull. Mus. Comp. Zool. **39**, p. 218, pl. 3, fig. 28, pl. 5, fig. 59.

Spines very diminutive, erect, deeply inserted; base of exserted portion relatively broad, distal extremity acute, sides ornamented with not more than five or six straight longitudinal costae.

The holotype is a unique specimen from the Kinderhook limestone of LeGrand, Iowa, where it occurs in company with a number of typically Mississippian species, though probably itself representing a survival of the Upper Devonian fish-fauna. Appearances suggest that it does not belong to a young individual, but to an adult of very small, even dwarfish proportions.

Formation and locality. Kinderhook limestone; LeGrand, Iowa.

Genus **CTENACANTHUS** Agassiz.

Spines robust, those of the first dorsal fin often attaining a large size, laterally compressed; sides of exserted portion ornamented with longitudinal ridges, usually crenulated or denticulated, rarely smooth; posterior face flat or concave, with a series of small denticles along each margin. Spines of the second dorsal fin characterized by their abbreviate, stumpy proportions and oblique angle of insertion in the integument; ornamentation as in the longer, more gracefully curved ones of anterior dorsal fin.

It is certain that spines of this character were common to more than one genus of Palæozoic sharks. Reference has already been made to the occurrence of spines indistinguishable from those of this genus in Cladoselache, and Newberry was strongly inclined to believe, owing to the discovery of associated fragments from the Ohio Waverly, that the spines called

Ctenacanthus belonged to sharks having the dentition of Orodus, in which case the two generic terms apply to one and the same kind of fish.

Of primary importance in the distinction of species is the general conformation of the spines, especially their curvature, nature of cross-section, and length of inserted portion. Next in order of importance are the number, shape and direction of the longitudinal costae, their mode of origin, whether by bifurcation or implantation, together with their finer ornamentation; and still further distinctive characters are to be found in the nature of the posterior face and the sometimes keeled or otherwise differentiated anterior margin, or "cutwater". A class of spines agreeing in their short, stocky proportions, and very oblique insertion in the integument, is probably to be correlated with the posterior dorsal fin. They contrast strongly with the group of slender, elongated and tapering spines whose position was undoubtedly in advance of the first dorsal fin.*

Ctenacanthus wrighti Newberry.

1884. *Ctenacanthus wrighti* J. S. Newberry, 35th Rept. N. Y. State Mus. p. 206, pl. 16, figs. 12-14.
1889. *Ctenacanthus wrighti* J. S. Newberry, Monogr. U. S. Geol. Surv. **16,** p. 66, pl. 26, fig. 4.
1907. *Ctenacanthus wrighti* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 76.

An examination of the peculiarly shaped and unusually large fin-spine serving for the type of this species, now preserved in the American Museum of Natural History in New York, confirms the entire accuracy of Newberry's description, which is as follows:

Spine of large size, long triangular in outline; anterior margin straight, laterally compressed; medullary cavity large, open posteriorly to the middle of the spine; posterior face traversed above by a strong rounded ridge; [posterior] denticles small; surface of exposed portion entirely covered with pectinated ridges of nearly uniform width on the front and sides, becoming narrower and less distinctly pectinated near the posterior margin.

The spines of this species are very striking in their characters as regards both form and markings. The anterior margin seems

*Science, n. s., 1901, **14,** p. 795.

to have been absolutely straight from base to summit. Along the line of junction between the enameled and buried portions the spine must have been 2 inches wide, but it tapered rapidly upward, terminating in a slender, acute point. The exposed surface is more completely covered with ridges similar in character, and the pectination is more crowded than in any other species known to me. In its broad base and its general and uniform ornamentation this spine has some resemblance to *C. speciosus* St. J. & W., specimens of which have been in my hands, but the line of demarcation between the ornamented and buried portions is less oblique, showing that the spine was more erect [and hence referable to the anterior dorsal fin]; the ridges are considerably coarser and the form is straighter. The pectination is also less oblique and close, compared with the coarseness of the ridges.

Formation and locality. Moscow shale (Hamilton division of the Erian); Kashong creek, Yates county, New York.

Ctenacanthus randalli Newberry.

1889. *Ctenacanthus randalli* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 105.

1907. *Ctenacanthus randalli* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 77.

This species, which has never been illustrated, is founded upon the proximal portion of an extremely large spine, estimated to have been at least 30 cm in length. The original description is here reproduced as follows:

Dorsal fin spines 12 inches or more in length by 1½ inches in width at base of ornamented portion; form slightly curved backward, sides compressed, basal portion conical, smooth or finely striated longitudinally; line of demarcation between ornamented surface and base strongly marked, inclined downward and forward at an angle of 30° with the axis of the spine; ornamented surface near base formed by about 40 parallel, subequal, closely crowded ridges on each side of the median line, and these bear small rounded closely approximated tubercles.

Formation and locality. Olean conglomerate (Chemung group); near Warren, Pennsylvania.

Ctenacanthus chemungensis Claypole.

1885. *Ctenacanthus chemungensis* E. W. Claypole, Proc. Amer. Assoc. Adv. Sci. 33d meeting, p. 490 (name only).

1907. *Ctenacanthus chemungensis* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 77, pl. 7, fig. 3.

This name was applied by Professor Claypole without definition or illustration to small fin-spines obtained by him from the Chemung of Bradford county, Pennsylvania, whose length was stated to be "less than half that of *Ct. vetustus*".

To this species are probably to be referred a number of small, gently arcuate, finely ornamented spines which were collected by the late Professor Charles E. Beecher and others from the Chemung of Warren county, Pennsylvania, examples of which are preserved in the Yale and Harvard Museums. Spines of the same general character have also been obtained from two or three localities in New York State, as for instance between Friendship and Nile, and along the bank of Fall creek near Ithaca, at different levels in the Chemung Group.

None of these spines appear to have exceeded 10 cm in total length and they are frequently much shorter, their form being narrow and gradually tapering. The flattened sides are covered with numerous filiform costae, as many as twenty being observed toward the base, and these are for the most part continous; when new longitudinal costae are formed their origin is by implantation. The costae are finely pectinated at intervals varying from twice to three times their own width, thus giving rise to a finely punctuate appearance when seen in impression as is usually the case.

Formation and locality. Chemung group; New York and Pennsylvania.

Post-Devonian Species of Ctenacanthus.

More than a dozen species of this genus have been founded upon detached fin-spines occurring in the Kinderhook limestone near Burlington, LeGrand, and other localities in Iowa, but without exception their relations seem to be rather with Carboniferous sharks (Cochliodonts?) than with Devonian Pleuropterygii. An interesting correlation has been established between two distinct series of fin-spines and their probable position in advance of the anterior and posterior dorsal fins, as already noted. In the following list, the series formed by *C. varians, spectabilis, deflexus, solidus, clarki* and *brevis,* all char-

acterized by abbreviate, stumpy proportions, and by a very oblique line of insertion in the integument, are referable with considerable probability to the posterior dorsal fin. They contrast strongly with the group of slender, elongate and tapering spines represented by *C. formosus, sculptus, depressus, venustus, vetustus, denticulatus* and numerous others, which evidently belonged to the first dorsal fin. The distribution of spines pertaining to this genus in the Lower Carboniferous of this country is shown by the following table:

LIST OF SPECIES OF CTENACANTHUS OCCURRING IN THE MISSISSIPPIAN SERIES.

	Name of Species	Kinderhook	Burlington	Keokuk	St. Louis	Chester
1.	*Ctenacanthus coxianus* St. J. and W.	x	—	x	—	—
2.	" *decussatus* Eastm.	x	—	—	—	—
3.	" *depressus* Newb.	x	—	—	—	—
4.	" *longinodosus* Eastm.	x	—	—	—	—
5.	" *lucasi* Eastm.	x	—	—	—	—
6.	" *sculptus* St. J. and W.	x	—	—	—	—
7.	" *semicostatus* (St. J. and W.)	x	—	—	—	—
8.	" *solidus* Eastm.	x	—	—	—	—
9.	" *spectabilis* St. J. and W.	x	—	—	—	—
10.	" *varians* St. J. and W.	x	—	—	—	—
11.	" *venustus* Eastm.	x	—	—	—	—
12.	" (?) *burlingtonensis* St. J. and W.	—	x	—	—	—
13.	" *gradocostatus* St. J. and W.	—	x	—	—	—
14.	" *acutus* Eastm.	—	—	x	—	—
15.	" *cylindricus* Newb.	—	—	x	—	—
16.	" *excavatus* St. J. and W.	—	—	x	—	—
17.	" *keokuk* St. J. and W.	—	—	x	—	—
18.	" *xiphias* (St. J. and W.)	—	—	x	—	—
19.	" *costatus* Newb. and W.	—	—	—	x	—
20.	" *deflexus* St. J. and W.	—	—	—	x	—
21.	" *gemmatus* St. J. and W.	—	—	—	x	—
22.	" *gurleyi* Newb.	—	—	—	x	—
23.	" *harrisoni* St. J. and W.	—	—	—	x	—
24.	" *littoni* Newb.	—	—	—	x	—
25.	" *pellensis* St. J. and W.	—	—	—	x	—
26.	" *angulatus* Newb. and W.	—	—	—	—	x
27.	" *canaliratus* St. J. and W.	—	—	—	—	x
28.	" *similis* St. J. and W.	—	—	—	—	x

Subclass DIPNEUSTI.

(Dipnoans or Lung-Fishes.)*

Fishes with partially ossified skeleton, numerous membrane or dermal bones, and persistent notochord; skull autostylic; dentition confined to inner bones of the mouth; premaxillae and maxillae absent; gill-clefts feebly separated, opening into a cavity protected by two opercular plates; paired fins archipterygial or reduced; tail diphycercal or heterocercal, median fins often subdivided; exoskeleton consisting of true bony tissue; sensory canals well developed; nostrils inferior; claspers absent; a cloaca present, air-bladder single or paired, functioning as a lung.

The few existing Dipnoan species, comprised by the fresh-water genera Neoceratodus, Protopterus and Lepidosiren, form a well-nigh inappreciable remnant of a once flourishing and highly diversified race of Lung-fishes, whose acme of development, specialization and numerical superiority occurred during the Devonian. One remarkable order comprising huge armored fishes passed entirely out of existence at the dawn of the Carboniferous, without leaving descendants. Such, at least, appears to be the most satisfactory interpretation of the group now commonly known as Arthrodira. Another division, Ctenodipterini, was conspicuous throughout the Palæozoic, and attained a higher degree of specialization along certain lines than is evinced by later forms. The geological history of the Sirenoid order, to which Ceratodus and its modern descendants belong, is not traceable with certainty earlier than the Trias, although it is not unlikely that some Palæozoic remains, known chiefly by the dentition, should properly be included here. That primitive members of the Sirenoid order were in existence at least as early as the Lower Devonian follows as a necessary consequence of regarding it as ancestral to both Arthrodires and Ctenodipterines. This view of their relations, however, is novel, and the considerations which make for its acceptance, and com-

* As pointed out by Haeckel, Boulenger and others, the term Dipnoi, first applied by Johannes Müller in 1845 for the group of Lung-fishes, is improperly so used, having been previously chosen by Leuckart as a name for Amphibians. There is no objection, however, to retaining the name Dipnoan as a vernacular equivalent of Dipneusti, and it is here employed in that sense.

pel us to look upon Neoceratodus as an archaic survival of the primal Dipnoan stock, will be discussed under the caption of Arthrodires immediately following.

Order **ARTHRODIRA.**

Dipnoans having a reduced number of dermal bones forming the cranial roof, arranged after essentially the same pattern as in Ceratodonts, and the dentition also paralleling that of modern forms. Dermal armor of abdominal region consisting of large plates, either in simple apposition with the headshield, or more commonly articulated with its posterior border by a pair of movable ginglymoid joints placed dorso-laterally. Column notochordal, but with distinct neural and haemal arches. Tail apparently diphycercal in the best known forms (Coccosteus and Dinichthys); pectoral fins wanting, and only obscure traces of the pelvic pair observed; pelvic arch represented by a pair of sigmoidal or club-shaped plates, sometimes (Dinichthys) with an anterior ventral projection.

The remarkable group of armored Coccosteus-like fishes was originally united with Asterolepids by M'Coy, in 1848, in a single "family Placodermi", and for more than forty years this arrangement was adhered to by writers generally, save for slight changes in the rank assigned to the main divisions. To Professor E. D. Cope belongs the credit of having been the first naturalist to recognize the heterogeneous nature of this assemblage, and to initiate its disruption. In 1889, he proposed the removal of Asterolepids from the class of Fishes altogether, and at the same time referred Coccosteans provisionally to the Crossopterygii, or "fringe-finned ganoids".* Shortly thereafter, however, following Smith Woodward's suggestion, the several families of Coccosteus-like fishes were grouped, under Woodward's new name of Arthrodira, in a distinct order of Dipnoans.† This arrangement obviously implied, though it had not at that time been demonstrated, that the Arthrodiran skull was truly autostylic, and that a maxillary arch was not devel-

* Cope, E. D., Synopsis of the Families of Vertebrata. Amer. Nat. 1889, **23**, p. 856.

† *Ibid*, 1891, **25**, p. 647. Also Syllabus of Lectures on Geology and Palæontology, p. 14. Phila. 1891.

oped. Another feature which influenced the novel association of Arthrodires with Dipnoans was the parallelism, previously noted by Dr. Theodore Gill, and by him called to the attention of Professor Newberry,* between the dentition of Dinichthys and that of the modern Protopterus. The absence of any indication of a hyomandibular bone, even in the most admirably preserved specimens, and of more than a single ossification in the lower jaw, were considered sufficient reasons for excluding Arthrodires from Teleostomes.

This provisional association of Arthrodires with Dipnoans met with an indifferent reception on the part of most palæontologists, and was afterwards rejected by some of its early supporters, notably Drs. Traquair and Bashford Dean. It was even conceded by Smith Woodward himself, a few years later, that "the systematic position of this extinct order is indeed doubtful."† Traquair's defection dates from 1900, when he declared, in his Bradford address,‡ in favor of considering Arthrodires as "Teleostomi belonging to the next higher order, Actinopterygii." The following year Dean expressed the radical view that they were not true fishes at all, but representatives of a distinct class, called by him Arthrognathi, and conceived by him to have possible kinship with the Ostracophori.§ It was even allowed that subsequent researches might demonstrate a union between Arthrognaths and Ostracophores, whereby the time-honored group of Placodermata would be restored. This last was a complete reversal of his former view that the "jaws, specialized dentition, fin-spines and highly evolved pelvic fins completely separate this group [Arthrodira] from the lowly Ostracoderms."‖

By far the most comprehensive use of the term Placodermata is that adopted by Otto Jaekel, in 1902, whereby the Pteraspids, Trematapids, Cephalaspids, Asterolepids and Coccosteans were

*Newberry, J. S., Descriptions of Fossil Fishes. Rept. Geol. Surv. Ohio, 1875, **2**, pt. 2, Palæont. p. 15. The suggestion is here advanced that Protopterus and Lepidosiren are lineal descendants of "Placoderms".

†Woodward, A. S., Outlines of Vertebrate Palæontology. 1898. p. 64.

‡Traquair, R. H., Vice-Presidential Address. Rept. Brit. Assoc. Adv. Sci., Bradford meeting, 1900, p. 779.

§Dean, B., Palæontological Notes. Mem. N. Y. Acad. Sci. 1901. **2**, p. 113.

‖Dean, B., Fishes, Living and Fossil. New York, 1895. p. 130.

all embraced within a single group.* This assemblage was modified a twelvemonth later, however, in that the two last-named families were bracketed together under the head of "Temnauchenia", all of the others, together with Drepanaspids, Coelolepids and Birkeniidae being collectively designated as "Holauchenia."† Placoderms in this broadened sense were all considered by Jaekel to belong to fishes proper,‡ and it was further maintained by him that Coccosteans were ancestral to Chimaeroids, an opinion in which he clearly stands alone. The only other author who has ventured to recognize any descendants from Arthrodires whatsoever is Newberry, who, as we have seen, imagined Protopterus to be a modern lineal descendant of Dinichthys.

We may now pass rapidly in review the minor fluctuations of opinion that are apparent during the last few years. Dr. O. P. Hay, in his "Catalogue of Fossil Vertebrata of North America," employs the term Placodermi for both Arthrodires and Asterolepids, placing them in the same subclass with Dipnoans. Arthrodires and Ostracophores are awarded each the rank of a separate subclass in the English edition of von Zittel's "Text-book of Palæontology", the lamented author having disapproved of uniting Coccosteans with Dipnoans. In a remarkable paper published by Mr. C. T. Regan in 1904, the Placodermi are re-established so as to include Coccosteidae, Asterolepidae and Cephalaspidae, all being placed in a single order of Teleostomes.§ During the same year Professor T. W. Bridge expressed the view, in the volume on "Fishes" in the Cambridge Natural History, that Coccosteans are "a highly specialized race of primitive Teleostomi," and compared their cranial roofing bones with those of typical bony fishes. The idea of a relation between Coccosteans and Lung-fishes is dismissed in the following passage, found at page 537 of the work cited:

*Jaekel, O., Ueber Coccosteus und die Beurtheilung der Placodermen. Situngsber. Ges. naturforsch. Freunde, 1902, p. 103.

†*Idem*. Ueber die Organisation und systematische Stellung der Asterolepiden. Zeitschr. deutsch. geol. Ges. Mai-Protokoll, 1903, **55**, p. 58.

‡This view as to the truly piscine character of "Placoderms", together with the descent of Coccosteans from Cephalaspids is reaffirmed in his recent paper on Pholidosteus, published in 1907.

§Regan, C. T., The Phylogeny of the Teleostomi. Ann. Mag. Nat. Hist. 1904, ser. 7, **13**, p. 346.

The Arthrodira have been regarded as armoured Dipneusti, a view which is mainly based on their supposed autostylism and the nature of the dentition. But this autostylism has yet to be verified, and, if proved, the possibility that it may be a secondary feature, associated with the evolution of a peculiar dentition, must not be forgotten. Much more may be said for their claim to be regarded as a highly specialized race of primitive Teleostomi. Besides a well developed lower jaw, bones comparable to the elements of a secondary upper jaw are known, and in a general way the disposition of the cranial roofing bones, and the arrangement of the endoskeletal elements of the pelvic fins, tend to conform to the normal Teleostome type. In fact, Dr. Traquair has expressed the opinion that the Arthrodira are Teleostomi and Actinopterygii.*

In several recent papers published by Dr. L. Hussakof, of the American Museum, the group of extinct forms we are considering is designated as "Placoderms" and excluded from association with Pisces proper.† With regard to their position, Mr. E. Ray Lankester is entirely non-committal in his interesting lectures on "Extinct Animals", recently published in book form.‡ Dr. Frederic A. Lucas' popular treatise on "Animals before Man in North America" places them in association with Lung-fishes in accordance with Smith Woodward's idea. Still another useful handbook deserves mention, whose scope includes not only recent fishes and fish-like vertebrates but treats of their fossil allies as well and ranks as a standard modern authority. We refer to President D. S. Jordan's "Guide to the Study of Fishes," published in 1905. At the time of preparing this treatise the author considered Arthrodires to be of extremely problematical position, but has since expressed himself in favor of the view that they are specialized Dipnoans.

Finally, reference may be made to several papers published by the present writer§ during recent years, in which fresh arguments were advanced, based upon newly discovered evidence, to show that the dentition of Arthrodires belongs distinctly to

*In his latest reference to this subject, however, Dr. Traquair admits that Arthrodires are of uncertain subclass. Compare, for instance, his description of *Coccosteus angustus* in Trans. Roy. Soc. Edinburgh, 1903, **40**, p. 732.

†Hussakof, L., Articles 4 and 25 of Bull. Amer. Mus. Nat. Hist. 1905, **21**, pp. 27-36, and 409-414; also memoirs of same institution, 1906, **9**, pp. 105-154.

‡Lankester, E. R., Extinct Animals, p. 256. New York, 1905.

§Article 9 in American Journ. Sci. 1906, **21**, p. 131; also Nos. 1 and 7 in Bull. Mus. Comp. Zool. 1906-7, **50**, pp. 1-29 and 211-228.

the Dipnoan type, and that veritable homologies exist between their cranial roofing plates and those of the living Neoceratodus. This position is maintained in the following discussion of the group, as it seems to be most nearly in accord with the preponderance of known facts.

FIG. 23.

Fig. 23. *Mylostoma variabile* Newb. Cleveland shale; Sheffield, Ohio. Complete tritoral dentition arranged in natural position, but the elements of both pairs of palato-pterygoid plates belonging to different individuals. The presence of a third pair of vomerine elements in advance of the two here shown has not yet been established by positive evidence. x 1-1.

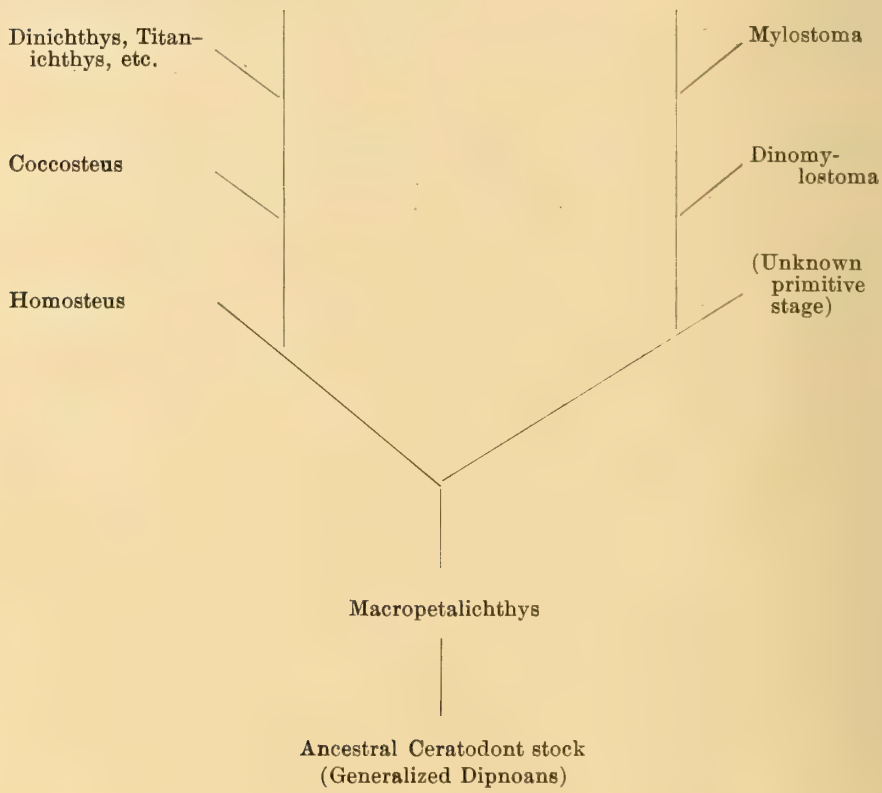
Concerning the systematic arrangement of Arthrodires, it need only be said that, owing to faulty preservation, we are still too imperfectly acquainted with the details of structural organization in different families to permit of more than a provisional scheme for illustrating successive stages of advancement. Analogy with other, and especially higher, groups leads one to expect the dentition to furnish not only reliable clues as to relationship, but also a convenient and serviceable basis of minor classification. Experience proves that the expectation is only partially justified. As between the two well-marked types of dental structure, which find close parallels in the existing Neoceratodus and Protopterus respectively, there need be little hesitation in recognizing the former, or triturating type, as the more primitive, it being one of the most constant, persistent and distinctive features of the Dipnoan stem. Nothing is more natural than to regard the trenchant or sectorial type

of dental plates, whether we find it already in vogue during the Devonian, or developed independently from the main stock in the Permian,* or again in evidence at the present day, merely as a derivative of the more simple, earlier, or perhaps even original type—the crushing or triturating type—which apparently resulted from the concresence and fusion of hardened shagreen granules. The Mylostomid type of dental plate is, therefore, as implied by its structure, of more primitive nature than the Coccostean or Dinichthyid type, and more faithfully reproduces the ancestral condition of things. On the basis of the dentition alone members of the latter category signalize themselves as more highly modified than the former. But other parts of the organization and the very similar structure of the headshield and body armoring in both Mylostomids and Coccosteids prove that these families have become relatively further advanced in certain directions than contemporary or earlier families (those typified by Macropetalichthys and Homosteus, for instance) of whose dentition we know little or nothing. In a word, the evidence of dental characters is decisive and positive enough so far as it goes, but should be supplemented by our knowledge of associated skeletal details before determining the precise rank of different families and genera. Present information, however, regarding these concomitant characters is in many cases meagre or very deficient.

Under these circumstances it is evident that data are wanting for a detailed classification of Arthrodires, and even a genetic grouping can only be provisionally outlined. As already intimated, the general indications (apart from dental characters) are that Macropetalichthys and Homosteus represent earlier and less advanced stages of evolution than the grade of typical Coccosteus-like forms. In case the former of these genera were eventually found to possess the triturating type of dentition, it would fulfil very satisfactorily the requirements of an exceedingly primitive phase of Arthrodires, approximating closely to the primal Dipnoan stem. It is even conceivable that body armoring is absent from this phase, in consonance with its primitive condition; and certain it is that the genus itself pre-

*The reference is to *Sagenodus pertenuis*, from the Permian of Texas and Russia described in Amer. Nat. 1903, **37**, p. 493.

sents no indications of having had the abdominal region protected by a system of dermal plates. We may assume, provisionally, that this Meso-Devonian genus does indeed represent the most primitive known stage of evolution among Arthrodires; and in this case we may fix upon Homosteus as occupying an intermediate position between it and typical Coccosteans. These latter forms represent the terminal members of a divergent series that agree with Mylostomids as regards cranial pattern and arrangement of body armoring, but differ from them in respect to the dentition. A graphical representation of these stages is attempted in the following scheme, with what claims to verisimilitude we leave others to judge. It will at least serve to emphasize the point that in any conjectural line of descent two divergent series of Arthrodires must be recognized, agreeing more or less as regards cranial pattern, but differing with respect to the dentition.



In conclusion, a brief rejoinder may be offered at this point to certain objections that have been raised against the above inferential line of descent. Dr. Bashford Dean, for instance, contends in two recent articles in Science * that Arthrodires cannot have been derived from ancestral Ceratodonts for the following reasons: (1) Writers who dissent from Dollo's theory of the phylogeny of Dipnoans—that is to say, the majority of modern students—are not justified in considering Neoceratodus to be of primitive or ancestral nature as compared with Ctenodipterines, since the modern genus may be supposed with even greater plausibility to have been descended from Ctenodipterine stock; (2) in case an ancestral line of Ceratodont lung-fishes had been in existence from the Devonian onwards down to the present day, it is inconceivable that the palæontological record should be destitute of all traces of it prior to the Triassic; and (3), accepting the view that a close kinship exists between Arthrodires and Ostracoderms ("bothriolepids and cephalaspids" as Dean terms them), it is difficult to imagine that the latter are also descended from a Ceratodont ancestor. Whence it follows that if these forms are not so descended, neither are their allies.

Dean's pronunciamento in regard to Neoceratodus, namely, that "there is, indeed, no reason evident why it should not have descended from an ancestor resembling Uronemus or Phaneropleuron," seems to us to be negatived by the conclusive arguments brought forward by Bridge, Fürbringer and other leading opponents of Dollo's theory.† Once this theory is discarded, the case of Neoceratodus becomes identical with that of Sphenodon and other late survivals of a generalized stock which must of necessity have had an earlier origin and longer geological history than more specialized derivatives of the same stock, whether still existing or long since extinct. Sphenodon, for instance, is

---

*Dr. Eastman's recent papers on the Kinship of Arthrodires. Science, 1907, **26**, pp. 46-50.—Studies on fossil fishes during the year 1907. *Ibid.*, 1908, **27**, pp. 202-204.

† See especially: Bridge, T. W., On the morphology of the Skull in the Paraguayan Lepidosiren. Trans. Zool. Soc. London, 1898, **14**, p. 372. Fürbringer, K. Beiträge zur Morphologie des Skeletes der Dipnoer. Jena Denkschr. 1904, **4**, p. 481. Agar, W. E., Development of the skull and visceral arches in Lepidosiren and Protopterus. Trans. Roy. Soc. Edinb., 1906, **45**, pp. 49-64. *Ibid.*, 1907, pp. 611-641.

known only in the modern fauna, yet the evidence of comparative anatomy forces us to conclude that it has come down to us practically unchanged from Permian times, and that its immediate ancestors gave rise to all reptiles with two cranial arches (Archosauria or Diapsida), and possibly to a Dinosaur-avian offshoot as well. Similarly, if modern Ceratodonts can be shown to possess a more primitive organization than Palæozoic Ctenodipterines and Arthrodires, with which groups they are evidently related, it becomes a logical necessity for us to suppose the more primitive group to have antedated and perhaps even to have given rise to the more highly specialized. The truth of this hypothesis does not require confirmation by positive evidence such as might be furnished by the palæontological record, its validity being established upon well ascertained principles of comparative anatomy. Our concern is neither to impugn nor to exalt the adequacy of the palæontological record. We have merely to take it as we find it, and where its continuity is broken, characters obliterated, and the chain of organic forms interrupted, there is no recourse but to fill in the lacunae as best we may through exercise of the trained imagination.

What weight should be assigned to Dean's third objection depends upon whether or not we adopt the view that Arthrodires and Ostracophores are closely related, and that both are distinct from Pisces proper. The problem may be still unsolved, yet it must be remarked that very few morphologists favor a separation of Arthrodires from ordinary fishes, and the idea that "bothriolepids and cephalaspids" share close affinities with Coccosteus-like forms may be likened to a goal that is unattainable except after having penetrated a Daedalian labyrinth of uncertainties and possibilities. It may be pertinent to recall, furthermore, that Patten's recent studies of Bothriolepis have convinced him that the lowly group to which it belongs should be separated further than ever from true fishes, and elevated to the rank of a new and independent class. This implies, of course, an effectual separation between the two groups which Dean and Hussakof unite in their understanding of the term Placodermata. We may close this phase of the discussion by quoting Professor Patten's latest utterance in regard to the

position of Bothriolepis, which is summed up as follows: "The structure of the gills, anus, anal fin and other organs indicate that the Ostracoderms must be separated from all other known subdivisions of the Chordata and raised to the dignity of a separate class." *

Family MACROPETALICHTHYIDAE.

Cranial shield much arched from side to side, completely enclosing the orbits, and extending over the nuchal region posteriorly. External surface covered with fine stellate tubercles which conceal the underlying sutures between dermal plates. Median series of the latter but two in number, narrow and elongate; external occipitals large; centrals divided, the two pairs on either side not meeting their fellows in the median line. Pineal foramen inconspicuous, situated slightly in advance of a line joining the anterior borders of the orbits. Sensory canals forming large tubular excavations in the bone, opening at the external surface by a continuous narrow slit or by a double series of pores. Parachordal cartilage and notochordal sheath calcified. Nature of dentition unknown, although there is apparently an articular cavity for the lower jaw. No indications of abdominal armoring.

The typical genus of this family is Macropetalichthys, known by a single American, and two or three European species. In addition, an undescribed species is reported by Jaekel from the Middle Devonian of the Eifel District, in Rhenish Prussia, the type of which is in the Senckenburg Museum at Frankfort, and at the same time the form described by Kayser in 1880 as *M. pruemensis* is made by Jaekel the type of a distinct genus.† All these forms evidently stand in close relation to Homosteus as regards number and general arrangement of cranial roofing plates, position of the orbits, and in having the headshield prolonged posteriorly over the nuchal region. It is perhaps of some significance to note that the median series of cranial plates are reduced to the same number as in Neoceratodus, and are fewer than in Dipterus.

---

* Science, 1905, **21**, p. 297.—See also Yearbook Carnegie Inst. Wash. 1904, no. 3, p. 140, where the same conclusion is presented.

†Jaekel, O., Ueber Coccosteus und die Beurtheilung der Placodermen. Sitzungsber. Ges. Naturforsch. Freunde, 1902, p. 113.—*Ibid.*, 1906, pp. 73-85.

Genus MACROPETALICHTHYS Norwood and Owen.

This genus, certainly one of the most primitive of Arthrodires, is represented in this country by the typical species, which was first described under the name of *M. rapheidolabis.** Subsequently, two new specific titles, *M. sullivanti* and *M. manni,* were proposed by Newberry for cranial shields that presented no important differences from the type, and it was afterwards proved that no constant distinctive features exist. Hence only the name originally proposed for the type species is entitled to recognition. The same author also pointed out that the so-called *Placothorax agassizii* of Hermann von Meyer, published at the same time as Norwood and Owen's description, and more fully illustrated the following year, was founded upon a denuded headshield of Macropetalichthys. The so-called "Physichthys" of von Meyer was also shown by Smith Woodward to be a composite aggregation including fragments belonging to Macropetalichthys, Rhynchodus and *Pterichthys rhenanus.*† A review of the more recent literature of the genus has been given by the writer in another place, and need not be repeated here.‡

Macropetalichthys rapheidolabis Norwood and Owen.

(Text-figure 24)

1846. *Macropetalichthys rapheidolabis* Norwood and Owen, Amer. Journ. Sci. ser. 2, **1,** p. 371, text-figs. 1, 2. Also separate folio.

1851. "Buckler of ganoid fish," L. Agassiz, Proc. Amer. Assoc. Adv. Sci. **5,** p. 179.

1852. *Macropetalichthys* sp. J. S. Newberry, Annals of Sci. **1,** p. 12.

1857. *Agassichthys sullivanti* J. S. Newberry, Bull. Nat. Inst. p. 124.

1857. *Agassichthys manni* J. S. Newberry, Bull. Nat. Inst. p. 122, woodcut.

1862. *Macropetalichthys manni* and *M. rapheidolabis* J. S. Newberry, Amer. Journ. Sci. ser. 2, **34,** pp. 75, 76, woodcut.

1873. *Macropetalichthys sullivanti* J. S. Newberry, Rept. Ohio Geol. Surv., Palæont. **1,** pt. 2, p. 294, pl. 24, 25, fig. 1.

1889. *Macropetalichthys sullivanti* J. S. Newberry, Monogr. U. S. Geol. Surv. **16,** p. 44, pl. 38, figs. 1, 2.

1890. *Macropetalichthys sullivanti* E. D. Cope, Amer. Nat. **24,** p. 846.

---

*Amer. Journ. Sci. 1846, ser. 2, **1,** pp. 367-72. Also a separate abstract in folio, published at Madison, Iowa, under date of February 16, 1846, a copy of which is preserved in the library of the Museum of Comparative Zoology at Cambridge (*ex bibl.* N. S. Shaler).

†Woodward, A. S., Vertebrate Palæontology in some American and Canadian Museums. Geol. Mag. 1890, Dec. 3, **7,** p. 459; also Cat. Foss. Fishes Brit. Mus. 1891, pt. 2, p. 303.

‡Mem. N. Y. State Mus. 1907, **10,** pp. 100-103.

1891. *Macropetalichthys sullivanti* and *M. rapheidolabis* E. D. Cope, Proc. U. S. Nat. Mus. **14**, pp. 449, 455, pl. 29, 30, fig. 5.
1897. *Macropetalichthys sullivanti* and *M. rapheidolabis* C. R. Eastman, Amer. Nat. **31**, pp. 493, 499, pl. 12.
1901. *Macropetalichthys* sp. B. Dean, Mem. N. Y. Acad. Sci. **2**, p. 119, text-fig. 12.
1903. *Macropetalichthys* sp. O. Jaekel, Neues Jahrb. für Mineral. **1**, p. 342.
1907. *Macropetalichthys rapheidolabis* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 103, pl. 9. fig. 5, pl. 11.
1907. *Macropetalichthys sullivanti* E. Hennig, Centralbl. für Mineral. p. 587, text-fig.

Headshield suboval, regularly arched in a transverse direction, attaining a maximum length of about 25 cm and width across the posterior border of about 17 cm, but often considerably flattened by pressure. Ornamentation consisting of fine, closely crowded tubercles with stellate bases, sometimes displaying concentric arrangement. Of the two pairs of small centrals, which are separated from contact with each other by the intervention of the median occipital, the anterior takes part in forming the orbital border and is not traversed by sensory canals. Pineal plate pierced by an inconspicuous foramen, and apparently equivalent to the so-called anterior median element or "mesethmoid" of Neoceratodus, or to the corresponding undivided area in Dipterus. Parasphenoid (or the element interpreted by Cope as such) much expanded in front, posteriorly produced, resembling in a general way the corresponding membrane bone of Ctenodipterines and Sirenoids, but considerably less ossified. Preorbital sensory canals lyrate, and confluent in the middle line with the sharply angulated exoccipito-central system. The postorbital canal extends from the inferior border of the orbits to the center of the marginal plates, where it turns abruptly inward and continues in a straight line to meet the exoccipito-central canal at the point of its angulation. The latter canal disappears beneath the surface of the external occipital plate on either side close to the hinder margin of the headshield, passing obliquely downward and inward below the cranial roof, and in the living state presumably communicated with the internal auditory sense organs.

Speaking entirely within bounds, it is not too much to say that the characters of this long misunderstood genus and species

fail of comprehension, or at least of satisfactory analysis, save as they are brought into relation with those of modern Dipnoans and interpreted through comparison with them. Many students have puzzled over the cranial structure of Macropetalichthys and the allied genus Asterosteus, of which only the median series of plates are known; but accumulation of details has resulted only in greater perplexity. A serious obstacle to their understanding has been the absence of a standard of comparison or trustworthy clue by means of which their characters acquire significance; they must needs remain unintelligible until brought into harmonious adjustment with other established facts.

Newberry, with an abundance of well preserved material at his command, went widely astray in imagining these forms to be ancestral to modern sturgeons. Cope's keen insight led him immediately to perceive the community of structural plan between Macropetalichthys and Dinichthys; and in suggesting a comparison of the former with Neoceratodus, he actually hit upon a solution of the whole matter, though unfortunately he did not rigorously apply it. He correctly identified the parasphenoid as such—a membrane bone that appears to have been incompletely formed in Arthrodires generally—and noted that it displayed the usual Dipnoan outline; but he was less happy in explaining the nature of the so-called "cerebral chamber" of Newberry, and other internal structures termed by him "nuchal elements".

Cope's "nuchal plate", or so-called "dorsal plate" of Dean and Eastman, was further misinterpreted by the last-named authors in that it was held to represent collectively the dorsal body plates of other Arthrodires. Dean's definition of "Anarthrodira" was, in fact, based upon this erroneous view.* Indeed, it must be frankly acknowledged that serious misapprehension has prevailed among all students, including the present writer, concerning the septate structures within the interior of the headshield of Macropetalichthys. As in the case of the cranial buckler itself, the conformation of the inner parts be-

*As pointed out by O. Jaekel in the *Neues Jahrbuch* for 1903 (**1**, p. 342), the definition embraces structural characters which in reality do not exist.

comes intelligible only through comparison with surviving Dipnoans, and without such aid must remain an enigma *sui generis*. The pertinency of this statement will appear from the following description of the headshield.

Cranial characters.—The arrangement of dermal roofing plates in the headshield of Macropetalichthys is shown in the accompanying restoration (text-fig. 24), which may be profitably compared with the diagram given on page 197 (text-fig. 29) of the cranial roof of Neoceratodus. One perceives that there is a general correspondence between the two genera as regards cranial pattern, and especially noteworthy is the similar disposition of the median series of plates, the more posterior of which is elongated nearly to the same extent as in Homosteus. Other points of agreement between the form under discussion and Homosteus consist in the elongation of the external occipitals, and enclosure of the orbits within the headshield. In more specialized forms, the preorbital and postorbital plates are merely notched externally, but in Macropetalichthys, Homosteus, and presumably also in Asterosteus, these two plates are in contact with each other externally so as to form the inferior border of the orbits.

A conspicuous difference between Macropetalichthys and other Arthrodires, one which has proved a stumbling-block to a correct understanding of the cranial osteology, lies in the fact that the central elements are divided so as to form *two* small plates on either side of the headshield back of the orbits. These more or less rounded plates are placed one behind the other, the two pairs being separated from contact with each other in the median line by the elongated median occipital plate (*MO,* text-fig. 24), very much as is the single pair of corresponding plates in Neoceratodus (text-fig. 29). That the plates here called the centrals are correctly determined as such is evident from the following reasons: First, the two pairs together occupy the usual position of the centrals with reference to the preorbital plate in front, and to the postorbital and marginal plates externally; and secondly, they are proved to be such by the disposition of the sensory canals. Imagining the suture line as obliterated between the two independently ossified plates on either side, we shall have

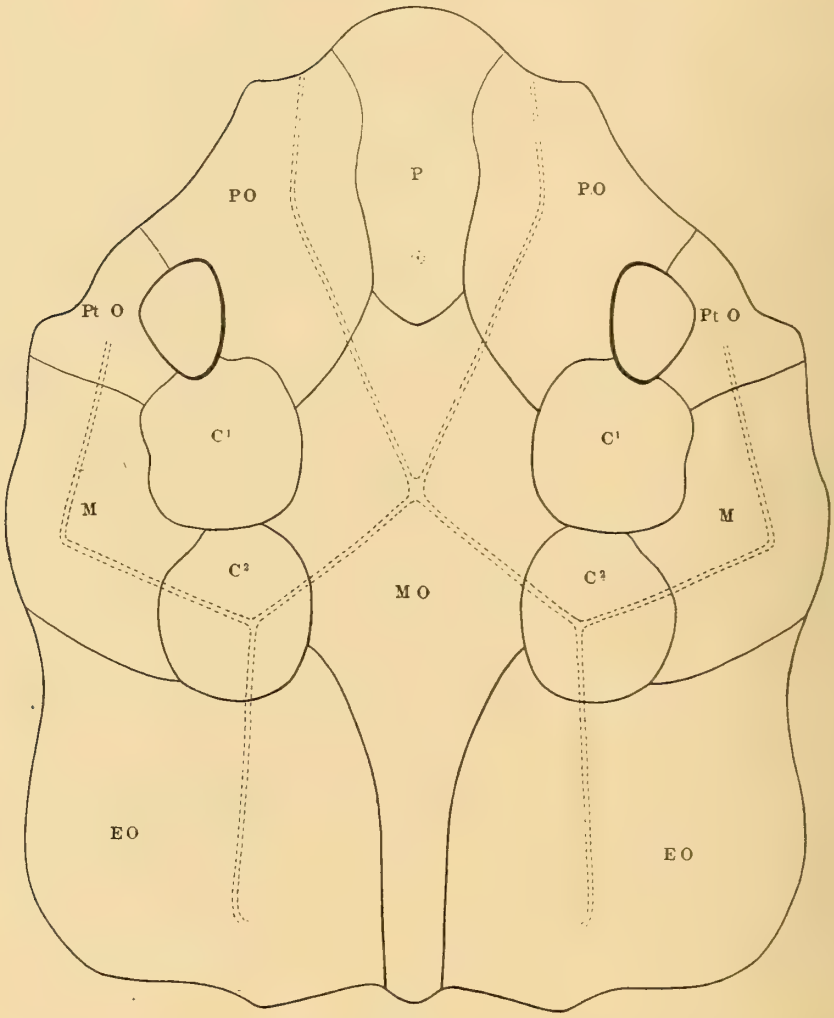


FIG. 24.

Fig. 24. *Macropetalichthys rapheidolabis* Norw. & Owen. Middle Devonian; Indiana, Ohio and New York. Restoration of headshield showing arrangement of cranial plates and course of sensory canals. x ½.

*C*¹, *C*², divided centrals; *EO*, external occipital; *M*, marginal; *MO*, median occipital; *P*, combined pineal and rostral, corresponding to the anterior median unpaired plate ("mesethmoid") in Neoceratodus; *PO*, preorbital; *PtO*, postorbital plate.

a single pair of elements occupying the same relative position as in Homosteus. The posterior moiety of this plate is seen to be traversed by three distinct canal systems, identifiable with those called by Dean the preorbital, postorbital and occipital. Now, in the headshield of all Arthrodires so far as known, the central

is the only plate traversed by all three of these canals. The pre- and post-orbital systems are sometimes confluent in other forms, but the occipital (or more properly, the occipito-central) does not unite with these other systems save only in Macropetalichthys.

Evidence of the primitive nature of this genus, as compared with other Arthrodires, is furnished by the following characters, which are strongly indicative of embryonic or ancestral conditions: (1) continuity of the sensory canal systems; (2) discreteness of the central elements and their separation on either side of the middle line by the elongated median occipital; (3) reduced number of median series of plates; (4) complete enclosure of the orbits within the headshield; and (5), absence of any evidence of articulation, overlap, or other connection between the headshield and a system of dorsal body plates.

That the headshield was produced posteriorly over the nuchal region, similarly, and in fact to about the same extent as in Homosteus, is apparent from the configuration of the under surface and structures seen within the interior of the cranial buckler. An interesting feature first noted by Cope is that a passageway for the notochord is provided by an ossified tubular sheath of small diameter, which is supported by the narrow posterior extension of the parasphenoid, and perforates by means of a triangular orifice the thin, vaulted and backwardly sweeping partition or septum depending from the under side of the occipital plates, and interpreted by the present writer as the ossified posterior wall of the chondrocranium. That this septum actually closed the chondrocranium behind seems extremely probable both from its form and position, which are highly suggestive of the conditions observed by Traquair * in Dipterus; and by its suspension from the cranial roof in a manner recalling that in Neoceratodus. The septum is, however, very thin-walled, and there is no evidence of separately ossified exoccipital plates adjacent to the triangular foramen magnum. Another thin transverse septum depends vertically from the posterior border of the headshield, and like the first, is rigidly united with the narrow extension of the parasphenoid

* Ann. Mag. Nat. Hist. 1878, ser. 5, **2**, p. 5, pl. 3, fig. 1.

below. It is along the plane of this septum that the exoccipito-central canals penetrate obliquely downward from the outer surface by means of funnel-shaped openings, the interior of which is filled with cancellated bony tissue. The function of the hinder transverse septum seems to have been to impart rigidity to the arch of the headshield, and to serve as a partial support for the parasphenoid. The space included between the two septa just described is that which Newberry designated as a "cerebral" and Cope as a "nuchal chamber," both authors apparently regarding it as closed along the sides as well as at either end. It was, however, only partially enclosed, its middle portion alone being floored by the parasphenoid, or backward prolongation of that element. No known organ could have been lodged in this partially enclosed space, and in all probability it merely contained fatty matter.

We have already had occasion to speak of the element called by Cope the parasphenoid, and in our opinion correctly identified by him as such. In form this very tenuous plate resembles in a general way the familiar lozenge-shaped bone in Dipterus, Ctenodus and modern Dipnoans, but it is remarkable for its great expansion in front, where it occupies nearly the entire width of the headshield. Becoming rapidly constricted in the occipital region, it extends backward over the space separating the two transverse septa already mentioned in the form of an arched laminar plate, not unlike that of Neoceratodus in form, and serves as a floor for the parachordal cartilages and notochordal sheath.

This hinder portion of the parasphenoid was interpreted by Cope as consisting of a pair of distinct elements, called by him the "lateral alae of the axis", and in another place, "descending osseous laminae"; but it is clear from well preserved specimens that only a single ossified element is concerned in flooring the cartilaginous cranium and projecting backward as far as the extreme posterior margin. A right understanding of this feature shows that in the form under discussion the parasphenoid is produced posteriorly to the same extent as in Neoceratodus and Lepidosiren; hence Cope's statement requires rectification when it is said that the corresponding bone in modern forms is abnor-

mally produced behind.* The extreme thinness of the bone in its anterior portion forms a decided contrast to the solidly ossified plate of Ctenodipterines, and it is further noteworthy that no specimen has yet enlightened us as to its relations with the palato-pterygoid cartilages. Near the point of its greatest constriction, in what corresponds to the position of the quadrate element in Dipterus, is a well-marked oval concavity, described by Cope as a "glenoid fossa"; and this may not improbably be looked upon as having served for articulation with the mandibular suspensorium. Nothing whatever is known of the quadrate, mandibles, or nature of the dentition. These parts must necessarily have existed, and our ignorance of them is attributable to failure of preservation.

Formation and locality. Onondaga limestone; Le Roy, New York. Columbus and Delaware limestones; Ohio. "Corniferous" limestone of Indiana, and said to have been obtained also from equivalent strata in Canada. Although listed among Kentucky Devonian fossils, its reported occurrence within the limits of that State probably rests upon erroneous identification.

Macropetalichthys agassizi (von Meyer).

1845. *Asterolepis hoeninghausii* L. Agassiz (*errore*). Poiss. Foss. V. G. R. p. 130, 147, pl. 30*a*, fig. 10.
1846. *Placothorax agassizi* H. von Meyer, Neues Jahrb. p. 596.
1847. *Placothorax agassizi* H. von Meyer, Palæontogr. **1**, p. 102, pl. 12, fig. 1.
1855. *Physichthys hoeninghausii* H. von Meyer, Palæontogr. **4**, p. 80, pl. 15, figs. 1-5 (*non* figs. 6-11).
1857. *Agassichthys agassizi* J. S. Newberry, Bull. Nat. Inst. p. 119.
1873. *Macropetalichthys agassizi* J. S. Newberry, Rept. Ohio Geol. Surv., Palæont. **1**, pt. 2, p. 291.
1895. *Macropetalichthys agassizi* A. von Koenen, Abhandl. Ges. Wis. Göttingen, **40**, p. 22, pl. 4, fig. 3.
1907. *Macropetalichthys agassizi* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 112.
1907. *Macropetalichthys hoeninghausii* and *Placothorax agassizii* E. Hennig, Centralbl. für Mineral. Geol. und Pal. no. 19, p. 587.

Reference has already been made to the fact that the type of Hermann von Meyer's *Physichthys hoeninghausii* is now the property of the Museum of Comparative Zoology at Cambridge,

* Cope states that "the parasphenoid in both Lepidosiren and Ceratodus is produced abnormally, and it is only necessary to imagine this part to be reduced to its normal length to have the conditions found in Macropetalichthys."—Proc. U. S. Nat. Mus. 1891, **14**, p. 455.

Mass. Although incomplete, the part that is preserved shows several of the cranial elements very distinctly, and also the narrowed posterior portion of the parasphenoid which supports the notochordal sheath. This is deeply channeled in the median line for the passage of the notochordal sheath, and is concentrically striated in the same manner as the vertical lamina which descends from the posterior margin. The sheath itself exhibits no trace of segmentation, and, like that in the type species, is of remarkably small diameter.

Formation and locality. Middle Devonian; Eifel district, Rhenish Prussia.

Macropetalichthys pelmensis Hennig.

1907. *Macropetalichthys pelmensis* E. Hennig, Centralbl. für Min. Geol. Pal. no. 19, p. 589, text-figs. 1-3.

Under the above name has been recently described a new species of Macropetalichthys which agrees very closely in form, size and general appearance with the type of *M. agassizi* (von Meyer), and indeed is only distinguishable from it by means of its finer ornamentation and gently ridged condition of the headshield over the occipital region. The cross-section of the latter shows that the cranial roof rises into a low peak in the median line, and slopes away rather abruptly laterad of the occipital sensory canals. The latter are conterminous with the posterior margin of the headshield, at which point they are deflected abruptly downward and also at a slight angle inward, being encased in a funnel-shaped duct which is partially filled with cancellated tissue. Identical conditions have been observed in the type species of Macropetalichthys, and also in *M. agassizii.* The peculiar structures in question are in nowise homologous with the articular sockets for antero-dorso-lateral plates in other Arthrodires, as supposed by Hennig, but are clearly the continuation of the sensory canals from the cranial roof downward into the interior of the headshield, where they were probably in communication with the internal auditory organs. According to this interpretation the funnel-shaped orifice would correspond to the *ductus endolymphaticus,* which in modern Elasmobranchs opens on the dorsal surface of the head by an

obliquely placed mouth, but in higher fishes is closed or ends blindly.

Formation and locality. Upper division of the Middle Devonian; Pelm, near Berlingen, Eifel District, Rhenish Prussia. Holotype preserved in Museum of Berlin University.

Family **MYLOSTOMATIDAE.**

Headshield and abdominal armoring constructed essentially as in typical Coccosteids, but with dentition adapted to crushing instead of cutting. Upper triturating dentition consisting of two pairs of Ceratodont-like palato-pterygoid dental elements, with non-denticulate margins. Well-developed vomerine teeth present in the earlier, but not yet observed in later forms.

Genus **DINOMYLOSTOMA** Eastman.

A genus transitional between Mylostoma and Dinichthyids, as its name implies, and partaking of the characters of both. Mandibles with slightly prehensile symphysial beak, and broad, flattened, regularly excavated functional margin, showing marks of contact with dental plates of the opposite jaw, the latter essentially as in Mylostoma. Vomerine teeth subtrihedral, slightly prehensile.

Dinomylostoma beecheri Eastman.

1906. *Dinomylostoma beecheri* C. R. Eastman, Amer. Jour. Sci. ser. 4, **21**, p. 83, text-fig. 2.
1906. *Dinomylostoma beecheri* C. R. Eastman, Bull. Mus. Comp. Zool. **50**, p. 23, pl. 1, figs. 4, 5; pl. 2, figs. 13, 14, 16, 17; pl. 4, 5.
1906. *Dinomylostoma beecheri* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9**, pp. 119, 123.
1907. *Dinomylostoma beecheri* C. R. Eastman, Bull. Mus. Comp. Zool. **50**, p. 226.
1907. *Dinomylostoma beecheri* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 151, pl. 14, figs. 5, 6; pl. 15.
1908. *Dinomylostoma* [*beecheri*] B. Dean, Science, n. s., **26**, p. 50.

The specific characters of this primitive form are included in the foregoing generic diagnosis. It may be noted, however, that its particularly distinctive feature consists in the acute termination of both mandibles and vomerine teeth in front, together with the deeply concave or excavated functional margin of the lower dental plates. The triturating surface of all the dental elements is narrower than in Mylostoma, thus making some ap-

proach to Dinichthys-like conditions, and a still further resemblance to the latter is observed in the form of the vomerine teeth. The latter, if found in the detached state, might readily be mistaken for the commonly so-called "premaxillary" teeth of typical Dinichthyids. In addition, the dorsomedian and other plates of the abdominal armoring are indistinguishable from those of Dinichthys.

The mandibles of this species, which are extremely well preserved in the holotype, bear a superficial resemblance to the lower dental plates of Palæomylus, especially *P. greenei,* and they are constructed more nearly after the pattern of Dinichthys than of Mylostoma. Their anterior extremities are elevated into a rather obtuse symphysial beak, which rises but little above the broad, flat, deeply excavated functional surface. The latter displays a single inconspicuous eminence or tubercle close to the external margin, situated about midway the length of the oral surface; and at some distance behind this elevation is a second, larger tubercle, rather elongate, and externally situated like the first. This posterior prominence fits snugly against the single large rounded boss of the opposing palato-ptyergoid dental plate, thus determining the orientation of the latter with utmost nicety, and affording a certain clue to the position of the corresponding element in Mylostoma.

The splenial is developed as a long, slender shaft of bone, resembling that of Dinichthys, but relatively deeper. In the type specimen, preserved in the Yale Museum, both the right and left elements are preserved in natural association with the articular cartilage. This last has become more or less compressed through fossilization, but remains attached to the outer face of the bony shaft near its posterior extremity. There is no separate angulare, nor dentary bone, the mandible being reduced to its lowest terms and consisting, as is usual among Arthrodires, of merely the splenial and dental plate.* The vomerine teeth are prehen-

*Jaekel's claim to have discovered a well differentiated angulare in the mandible of his so-called "Pholidosteus", in reality a synonym of Brachydirus, is discredited by Dean (Science, 1908, **27**, p. 203), who suggests that the structure in question may be a displaced portion of the well known interlateral plate. Jaekel's supposed articular element Dean likewise interprets as a detached portion of the antero-ventro-lateral plate. It is indeed noteworthy that the former of these alleged mandibular components shows a strongly tuberculated surface, which is scarcely reconcilable with its assignment by Jaekel to an internal position.

sile to about the same degree as the symphysial beaks of the lower jaw, against which they closed. Their posterior face is smooth and slightly hollowed, thus indicating that they were in direct contact with the anterior pair of palato-pterygoid plates, which are missing in the original example. The posterior pair, however, is admirably preserved, and on being brought into adjustment with the opposing lower dentition, it is a comparatively easy matter to restore the outlines of the pair immediately preceding. The external margin of the anterior pair must have been parallel to that of the functional surface of the lower dental plate; and as the upper elements were probably in contact with each other in the median line, the inner margin was rectilinear, as in Mylostoma (*cf.* text-fig. 25, page 181).

The dorsomedian plate, with well developed posterior process, agrees closely in form and proportions with that of *Dinichthys intermedius*. The antero-ventro-laterals have also approximately the same form, but are nearly one-fifth smaller than the corresponding plates in the tolerably complete example of *Mylostoma variabile* figured by Dean.* In that author's restoration of the ventral armor, however, these plates have been interchanged with the postero-ventro-laterals, as is evident from an inspection of their respective centers of ossification, and direction of vascular canals.

Formation and locality. Cashaqua shale (Portage); Mt. Morris, Livingston county, New York. There is also indistinct evidence either of this or some other Mylostomid in the black Naples shale (Portage) at Sturgeon Point, on the south shore of Lake Erie near Buffalo; and an undescribed species, apparently of this genus, is thought by Dr. L. Hussakof to be indicated by dental plates from the New Albany (or Genesee) Black shale near Louisville, Kentucky.

Genus MYLOSTOMA Newberry.

Distinguishable from Dinichthys only by characters of the dentition. Oral surface of lower dental plates broad, more or less flattened, and bearing a rounded boss or V-shaped prom-

*Dean, B., Palæontological Notes: On the Characters of Mylostoma Newberry. Mem. N. Y. Acad. Sci. 1901, **2**, p. 108, pl. 7.

inence close to the inner margin, which plays into a corresponding depression of the upper pair. No positive evidence of the occurrence of vomerine teeth has yet been detected.

Our knowledge of Mylostoma is confined at present to three species, all from the Cleveland shale of Ohio. These are, *M. variabile* Newberry, which is typical of the genus; *M. terrelli* Newberry, founded upon a unique example of a lower dental plate; and *M. newberryi* Eastman, of which the complete lower dentition is known. Notwithstanding the comparatively late geological horizon of all these forms, they are not to be regarded as incipient in the Upper Devonian, but as survivals of a primitive type of Arthrodire in which the crushing type of Dipnoan dentition was a persistent feature.

One of the interesting points established by Professor Dean's study of the type species of Mylostoma is the close agreement between it and Dinichthys in all essential respects save for the dentition; and as regards this latter feature, the same difference is to be noted as exists between Rhynchodus and Palæomylus among Ptyctodonts, or between Protopterus and Neoceratodus among modern Dipnoans. Parallel modifications of this nature, occurring as they do in very diverse groups, are doubtless to be correlated with similar food habits. Among Chimaeroids, for instance, certain genera are shown by their development of tritoral dental plates to have subsisted on hard-shelled prey, such as mollusks, echinoderms and the like, thus meriting Dollo's term of "conchifrage";* whereas others, as indicated by their sharp sectorial rims, were adapted for subsistence on soft tissues, and were probably predaceous creatures ("macrophage" Dollo). Mylostoma and Dinichthys furnish examples of corresponding adaptations among Arthrodires, and an exact parallel is found in modern Lung-fishes.

The mandibles of Mylostoma would seem to have retained with great persistency typical Dipnoan conditions. The form of the dental plates strongly recalls the unmistakable Ceratodont configuration, and these elements are more sharply demarcated from the supporting splenial than in other Arthrodires. Al-

* Dollo, L., Sur quelques points d'éthologie paléontologique. Bull. Soc. Belge Géol. 1906, **20**, p. 1.

though marginal serrations have disappeared,* the divided ridge which is situated close to the inner margin is perhaps to be regarded as a relic of one of the most persistent features of Dipnoan dentition. As for the upper dental plates, had they invariably been found in the detached condition, and were we ignorant of their association with typical Arthrodiran mandibles, they would be unhestitatingly identified with the Ctenodipterine order of Dipnoans. That these plates were supported by cartilage forming the roof of the mouth is distinctly apparent from their rugose, slightly hollowed upper surface, and outwardly bevelled edges; and the contour of the hinder pair renders it extremely probable, at least, that the supporting palato-

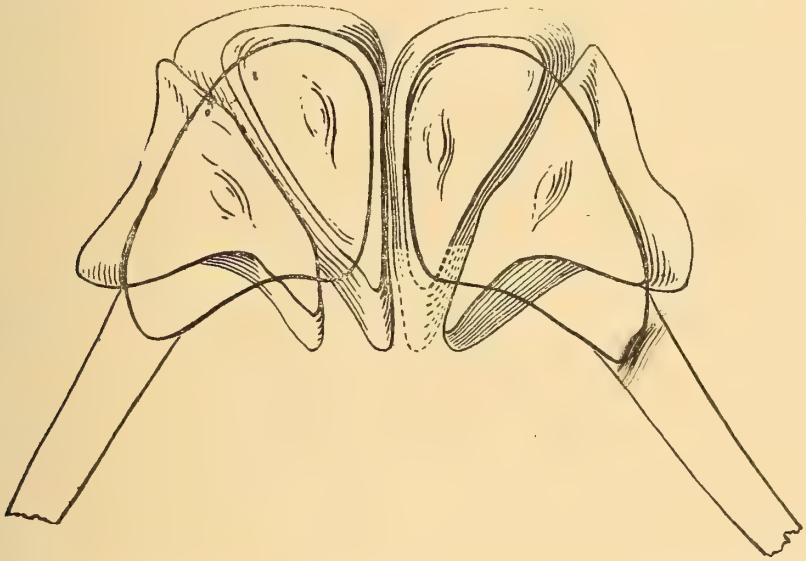


FIG. 25

Fig. 25. *Mylostoma variabile* Newb. Cleveland shale; Cleveland, Ohio. Restoration showing two pairs of palato-pterygoid dental plates arranged in their inferred normal position, and outlines of mandibular plates functioning against them, all drawn from a single, nearly complete and probably young individual.

* They are prominently retained in Diplognathus, however, a genus that belongs indubitably to the same family as Mylostoma, and are developed in the form of powerful denticles entirely around the margin of the dental plate proper. Judging from the relative proportions of plates forming the ventral armor in the imperfectly known genera Glyptaspis and Holonema, they should properly be included among Mylostomids, and it is extremely likely that they were provided with a crushing type of dentition, or modification of that type. Diplognathus is really only an extreme modification of the Mylostomid type, and, as suggested by Newberry, there is considerable reason to suppose that the mandibles known under this name, and the detached abdominal plates assigned to the provisional genus Glyptaspis, belonged in reality to the same kind of fish.

pterygoid cartilage was of the usual pattern found in all Dipnoans. This cartilage, when ossified, is commonly known as the "upper dentigerous bone"; the fact that it is unossified in Arthrodires agrees with other evidence pointing to their less highly specialized condition as compared with Ctenodipterines.

The restoration of the upper dentition of *M. variabile,* shown in the above figure, is based upon the naturally associated parts of a single individual—the same which has already been carefully described in Dean's memoir of 1901—and is consistent with the evidence obtained by fitting together of detached specimens belonging to the same species. It may be instructively compared with text-figure 23 (see page 162), which is reproduced from a photograph of the actual dental plates. The retention throughout life of two pairs of palato-pterygoid dental plates in this family, corresponding to an evanescent stage in Neoceratodus, is regarded as a primitive characteristic. Hence, in so far as the dentition is concerned, members of this family recall ancestral conditions more distinctly than either Dinichthys or Coccosteus.

In working out the above arrangement of Mylostomid dentition, upper and lower, the writer has used all available material illustrating the palatal dental plates of the type species; and in the whole number of specimens examined, absolutely no characters can be detected which point to more than individual differences between them. So close is their agreement with one another in form and relative proportions that is it quite impossible to suppose, or at least to prove, that more than a single species is represented. Their impact against the lower dentition has given rise to facets and worn surfaces which are seen to occupy a constant position in all the plates, and furthermore to coincide perfectly with similar indications of wear in the lower dental plates when the latter are applied against the pavement teeth in their inferred natural position. In this position alone is there harmonious adjustment between all mutually opposed parts, and in no other position can all of the salient points of contact and worn areas be brought together when the jaws are closed. An arrangement in which all of the parts fit thus perfectly together, and which is capable of explaining a

number of constant characteristics of all the elements thus far brought to light must be admitted to be the true arrangement; that is, the parts must have interacted according to this particular fashion in order to have produced the observed effects, for had they operated after a different fashion they would have produced different effects.

To anyone who has had the handling of the actual specimens and has experimented with them in the manner indicated, escape from the foregoing conclusion seems impossible. The evidence for it is not, however, accepted by Dean,* who believes that the normal position of palatal dental plates is indicated by two specimens lying side by side in the slab containing the single tolerably complete individual described by him in his memoir of 1901. It is assumed by Dean that the juxtaposition of these two palatal plates is natural, not fortuitous owing to post-mortem displacements, as is the case with the dissociated half of the same pavement. The reconstruction proposed by Dean rests entirely upon this unproved assumption, and his arguments in support of it lead from theoretical premises to theoretical conclusions. Some of the latter involve if not incredible, at least startlingly curious features, such as the assignment to Mylostomids of rotary and other complicated jaw movements, the like of which exists nowhere among chordates; and partly as a corollary to this inference it is suggested that the jaws themselves are not homologous with those of ordinary fishes. The inherent improbability of the conclusions depending upon Dean's reconstruction is sufficient reason for distrusting the validity of the premises upon which it is based.† A really decisive test of its efficiency may be applied, however, the same in fact as has already been applied to the restoration proposed by Eastman in 1906. This consists simply in fitting the oral surfaces of upper and lower dentition together according to what is assumed to have been their normal position, and observing the mutual correspondence of marginal contours and grinding areas, and interplay of all the parts that are shown by markings to have closed

*Science, 1907, **26**, pp. 46-50. *Ibid.*, 1908, **27**, p. 203.

†"A false conception, when the consequences from it are followed further and further, will sooner or later lead to absurdities and palpable contradictions."—Quoted by Fritz Müller, in "Facts for Darwin," chap. ii.

against one another. The result reached by the present writer after application of this test to a large series of Mylostomid dental plates, all in fact that are anywhere procurable, is that the earlier of the two rival reconstructions of Mylostomid dentition is inadequate, since it fails to explain all the observed facts, and is inconsistent with some of them. According to the newer interpretation, the upper dentition of Mylostomids and Dinichthyids is reducible to a common plan, which is in itself a comparatively slight modification of that found in typical Dipnoans; the jaw parts operate in the usual manner, that is to say without anomalous movements; and there is no reason to suppose these parts to be non-homologous with the jaws of ordinary fishes.*

Family COCCOSTEIDAE.

Cranial shield consisting of few elements, namely, a median and two external occipital plates, in front of which is a single pair of large centrals more or less in contact along the median line; these are in turn preceded by a pair of large preorbitals, which are either wholly or partially separated from each other by the azygous pineal and rostral ("ethmoid") elements; postero-lateral border of the shield formed by marginals and postorbitals. Orbits not completely enclosed within the shield, bounded inferiorly by a single suborbital plate, behind which occur one or two opercular elements. Upper dentition consisting of a pair each of vomerine and palato-pterygoid elements (commonly known, however, as "premaxillaries" and "maxillaries"), the latter with trenchant functional margin, often serrated or denticulated; lower dental plate intimately fused with the forward portion of the supporting splenial, turned more or less upright with sharp sectorial margin, often serrated or denticulated like the upper. Symphysial margin also sometimes denticulated.

The structure of the typical genus, Coccosteus, is so well known from the luminous researches of Pander, Traquair, Jaekel and

* For a further exposition of this view consult the following: Eastman, C. R., Structure and relations of Mylostoma. Bull. Mus. Comp. Zool. 1906, **50**, no. 1.—Mylostomid Dentition. *Ibid.*, 1907, **50**, no. 7.—Jaekel, O., Ueber Pholidosteus etc. Sitzungsber. Ges. naturf. Freunde, 1907, no. 6, p. 12.

other writers, that further description of it here would be superfluous. It furnishes a most valuable standard of comparison for referring the detached plates of other Arthrodires to their natural position, and for correlating the numerous minor variations observed in different members of the group. Interest centers in it also from the fact that this is commonly looked upon as the progenitor of the remarkable series of Dinichthyids that constitute perhaps the most striking feature of the late American Devonian fish fauna. That it is itself descended from a more primitive Arthrodiran ancestor having a simpler cranial pattern and a triturating type of dentition, seems to be an inevitable conclusion in the light of all the known facts. A weighty argument in favor of the Dipnoan origin of Arthrodires would lie in the confirmation of Jaekel's reported discovery of the long sought articulare in Coccostean mandibles.

Neural and haemal arches are occasionally seen in well preserved skeletons, but never any traces of axial segmentation; nor do ossified ribs occur in any member of this family. The structures which have sometimes been mistaken for ribs are in reality haemal arches.* There is one dorsal fin, the tail tapers gradually and to all appearances was diphycercal, but definite information on this point and concerning the presence of an anal fin is lacking. Indistinct traces of pelvic fins have been observed in Coccosteus, and an arch for their support seems to be represented by a pair of club-shaped internal plates, which Jaekel somewhat inappropriately calls "ilia". A pair of short, deep external plates lying immediately in front of the ventral armor in Coccosteus, but not represented in Dinichthys so far as known, has been thought by some to indicate the presence of a pectoral arch. The fact remains, however, that even the most exquisitely preserved specimens have failed thus far to reveal the slightest traces of pectoral fins, and the so-called pectoral spine or "Ruderorgan" in Coccosteus and Brachydirus, which is apparently fused in some species with one of the dermal plates protecting the sides, can in no sense be homologized with a pec-

*Jaekel, O., Ueber Coccosteus und die Beurtheilung der Placodermen. Sitzungsber. Ges. Naturforsch. Freunde, 1902, p. 107, restoration.

toral limb. As shown by Fürbringer,* the two opercular plates of Neoceratodus are sometimes fused into a single piece, and this fact acquires significance on recollecting that only a single opercular element is known to occur in most Arthrodires. Jaekel is the only investigator who has reported the presence in Coccosteus of two opercula, the normal number among Dipnoans, and it would be interesting to have this observation confirmed.

Genus COCCOSTEUS Agassiz.

Of the four American species that have been referred to this genus, only one, *C. canadensis* Woodward, is satisfactorily known, the others being represented by detached plates exclusive of the headshield. To *C. occidentalis,* described in the first instance by Newberry from the Onondaga limestone of Ohio, are possibly to be referred a few isolated fragments occurring in the Middle Devonian of New York State, and it has further been surmised by the original author that the dental plates known as *Liognathus spatulatus* belong to the same species. No illustration has been published of the form described by Cope from the Chemung of Leroy, Pennsylvania, under the name of *C. macromus,* but it is said to be distinguished from *C. occidentalis* by its coarser tuberculation. A restoration of the type species of this genus is given in the accompanying text-figure 26.

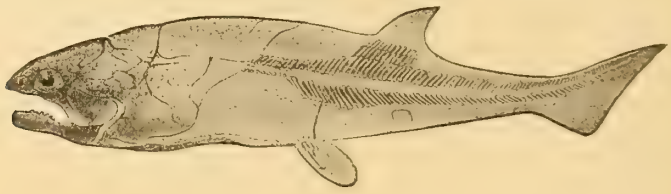


FIG. 26.

Fig. 26. *Coccosteus decipiens* Agassiz. Lower Old Red Sandstone; Scotland. Lateral aspect restored by Smith Woodward, in part after Traquair. x ¼. [The caudal fin is here conjecturally represented as heterocercal, for which there is no evidence; it may be regarded with even greater probability as having been diphycercal.]

Coccosteus macromus Cope.

1892. *Coccosteus macromus* E. D. Cope, Proc. Amer. Phil. Soc. **30,** p. 225.
1907. *Coccosteus macromus* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 116.

The only known examples of this species are those obtained by the late Professor Cope, whose original description is as follows:

*Fürbringer, K., Beiträge zur Morphologie des Skeletes der Dipnoer, etc. Semon's Zool. Forsch. in Australien. Jena Denkschr. 1904, **4,** p. 493.

Fragments of this species are abundant in the Chemung rocks at Leroy [Pennsylvania], and I select as typical of it a pair of supraclavicular and adjacent pieces, which display its characters best. The supraclavicle has lost the condylar articulation. Both extremities display the unsculptured surface, and the usual groove extends obliquely across the sculptured portion at about two-fifths the length from one of the extremities. The sculpture consists of obtuse tubercles with delicate radiate-grooved bases, which are usually separated by spaces equal to their own diameters, sometimes by narrower spaces, but never by spaces which are wider. At some points they have a linear arrangement. This sculpture is coarser than in the *C. americanus* [*i. e., C. occidentalis*] Newberry (see the Palæozoic Fishes of North America, by this author), but resembles that of *C. decipiens* Agass., of Scotland. From this species the *C. macromus* differs in the elongate form of the supraclavicle which is relatively short and wide in the *C. decipiens* (see Agassiz, in the Poissons du Vieux Grès Rouge, and Zittel, Handbuch der Paläontologie). Length of supraclavicle, 35 mm; width just above condyle, 16 mm.

Formation and locality. Chemung group (Chautauquan); Leroy, Pennsylvania.

Genus BRACHYDIRUS A. von Koenen.

(Syn. Pholidosteus Jaekel, 1907)

A genus closely resembling Coccosteus and primitive species of Dinichthys (*e. g., D. halmodeus*) in configuration of the headshield and system of abdominal armoring, but more laterally compressed, functional margin of dental plates simply trenchant, and a fixed or movable spinous appendage (the so-called "Ruderorgan" or "pectoral spine") developed in connection with the antero-lateral plates in the pectoral region. Some minor differences are also stated to exist with regard to the articulars union between the headshield and plates of the dorsal armor, and with regard to the uncovered area between the headshield and dorsomedian plate.

The earliest described species of this genus is *B. bickensis,* from the Upper Devonian of Bicken, Nassau, which should still be regarded as the genotype, although von Koenen at one time expressed himself in favor of reuniting it with Coccosteus. The cranial topography, however, as shown both by himself in 1883

and 1895, and by Gürich in 1891 (Zeitschr. deutsch. geol. Ges. 43, p. 907), differs to an extent that readily permits generic separation, and the spinous appendage in the pectoral region is always much more strongly developed than in the single species of Coccosteus where it is known to occur. In the species described by von Koenen as *B. bidorsatus,* and subsequently renamed *Pholidosteus friedelii* by Jaekel, the spiniform process is represented as being fused with the lower border of the antero-lateral plate, thus recalling the very similar conditions observed between one of the plates of the ventral armor and its lateral spine in *Phylctaenaspis acadica* (Whiteaves). Analogous conditions exist also in the singular Ostracophore described by Smith Woodward from the Lower Devonian of Spitzbergen under the name of *Acanthaspis decipiens,** which we have proposed to make the type of an independent genus. It is evident that the spinous process of this Spitzbergen form is non-homologous with the segmented spiniform projection of those plates now known to belong to Rhynchodus, such as were formerly described under the name of *Acanthaspis armata,* nor can it by any possibility be homologized with the so-called "pectoral spines" of Coccosteus and Brachydirus.

Genus DINICHTHYS Newberry.

It is difficult to frame a satisfactory diagnosis of this genus which shall enumerate its principal characters and at the same time enable one to draw a rigid distinction between its various species and those of Coccosteus. The fact is, the two genera are most intimately related, and though their terminal members are sufficiently well characterized, they are connected by insensible gradations. The typical species of Dinichthys represent unquestionably a later and more advanced stage of specialization than that with which we are familiar in *Coccosteus decipiens,* for example; but between these extremes lies a host of intermediate forms. Evidence of specialization in forms like *D. herzeri, D. terrelli,* etc., is strikingly apparent in their gigantic size, the headshield measuring nearly a meter across, and their massive and cumbersome armor being unrivaled among

* Ann. Mag. Nat. Hist. 1891, ser. 6, **8**, p. 4. See also Dr. Traquair's observations in the same magazine for 1894, **14**, p. 371.

fishes. As a necessary accompaniment of increase in size, the cranial plates become more intimately fused in the adult, the articulations between headshield and abdominal armor more complicated, and various minor modifications are to be seen in the dentition and arrangement of the body plates. Nevertheless, in spite of hypertrophic enlargement of all the parts, there is everywhere a surprising conformity to the basal type of Coccosteus. This close correspondence has not been generally recognized, yet must be obvious to those who have actually compared the different parts in well preserved specimens.

The arrangement of dental elements in Dinichthys merits special consideration. In the upper jaw there are always two pairs of dental plates, whose structure clearly reveals their dermal origin. It is denied by Dr. Bashford Dean that these plates, which are known in common parlance as "premaxillaries" and "shear-teeth", can be homologized with any structures within the mouth of other fishes, hence he proposes to call them by the non-committal names of "rostro-gnathals" and "orbito-gnathals" respectively, and employs the term "gnathal" for the mandible. The same view is reiterated, with some further changes in terminology, by Dr. L. Hussakof, in his "Studies on the Arthrodira," 1906.

According to the view adopted throughout this volume, the anterior pair of upper dental elements in Dinichthys is to be interpreted as vomerine, and the posterior as palato-pterygoid, thus recognizing actual and definite homologies between them and the like-named structures—which are also of dermal origin—in modern Lung-fishes. The vomerine pair is situated close to the median line, one on either side of the cranial plate corresponding in part to the dermal mesethmoid in Neoceratodus; and the tumid basal expansion of each of these elements is received into a slight concavity on the visceral surface of the preorbital plate of the headshield. The exposed, or functional portion of the vomerine teeth is cleft so as to form two vertical prongs or "beaks" of unequal length, the shorter of which is inwardly placed and abuts closely against its fellow of the opposite side. The extremities of the vomerine teeth protruded very slightly in advance of the mandibular beaks, which closed within

the angle formed by the prongs of the opposing elements. The best extant illustration of the manner in which the lower and upper dentition came together in front will be found in the frontispiece of Dean's work on "Fishes, Living and Fossil."*

The vomerine teeth are succeeded almost immediately behind by the cleaver-like palato-pterygoid plates called by Dean "orbito-gnathals", but popularly known as "shear-teeth", in allusion to their mode of working against the trenchant margin of the lower dental plates like the blade of a pair of shears. The manner of their operation remains the same even in those species where the opposing margins are denticulated, a condition which is regarded as more primitive than that with simply sharpened, or beveled edges. Traces of an original denticulation, which once extended along the entire functional margin, are often observed in the form of tubercles, or denticles, whose position is confined in specialized species to the extreme posterior margin of the tooth. It is to be noted that this posterior margin is usually narrower and more rounded than the anterior. Slightly in advance of the middle portion of the tooth, along its superior margin, there is given off from this upper margin a well marked, inwardly curved ascending process or "shoulder," which corresponds without question to the similarly placed process of Ceratodont dental plates. Notwithstanding the large size and evidently great efficiency of the shear-teeth, they do not appear to have been rigidly attached to the headshield, but rather to have been held in place by cartilage against the prominent inferior ridge which extends forwards as far as the orbital region from the postero-lateral angles, in a direction parallel with the sides of the headshield. Precisely similar conditions are observed in Neoceratodus, where the ridges referred to serve as a support for the upper dental plates, and relieve the strain incurred through the action of the jaws. It is interesting to note that these ridges along the under side of the headshield in Dinichthys acquire greater solidity in proportion as the dental plates become more masive and powerful.

Not more than two elements are known to take part in the formation of the mandible. These are the splenial, a long,

* See also the more recent restoration by E. B. Branson, in the Ohio Naturalist, 1908, **8**, pp. 365, 367.

slender shaft of bone, and the dental plate proper; but the presence of a third element, not distinctly differentiated, is perhaps to be inferred in case Jaekel is correct in his recognition of an articulare in the mandible of Brachydirus. In almost all species of Dinichthys the anterior extremity of the mandible is developed into a powerful piercing beak, usually much facetted by wear. At no great distance behind this the functional margin of the lower dental plate rises again into a prominent projection, shorter and less massive than the one in front, and appearing on the inner aspect as a distinct rib-like swelling, nearly vertical, and evidently in the nature of a rudimentary tooth. From this point backward along the functional margin, the lower dental plate is compressed into a thin edge, beveled somewhat on the outer face by contact against the opposing palato-pterygoid plate of the upper jaw. In the majority of species, the margins of both upper and lower dental plates are smooth and blade-like; but a few, including the type, have them denticulated as in Coccosteus. Vestigial remnants of a primitive Ceratodont-like denticulation occur in the lower dental plates along the abrupt declivity of their posterior margin; that is to say, in a position corresponding to that in which they are seen in the palato-pterygoid elements. The Middle Devonian species known as *D. lincolni* is peculiar in that a series of tubercles is present along the outer face of the vomerine teeth, thus suggesting that tubercles or denticles were formerly present in the lower dental plates as well, at least in primitive species.

Dinichthys halmodeus (Clarke).

(Fig. 27)

1894. *Coccosteus* (?) *halmodeus* J. M. Clarke, Rept. N. Y. State Geol. **1**, p. 162, pl. 1, and text-figures.
1900. *Dinichthys halmodeus* C. R. Eastman, Journ. Geol. **8**, p. 34.
1906. *Dinichthys halmodeus* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9**, p. 140, text-fig. 22, 24*a*.
1907. *Dinichthys halmodeus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 126, pl. 2, fig. 7; pl. 10, fig. 4; text-fig. 24.

A primitive species of small size, the headshield having a total length of about 11 cm, and very similar to Coccosteus in the configuration of plates, arrangement of sensory canals, and charac-

ter of the superficial ornamentation. The suture lines, however, are less undulating than in Coccosteus, the articulation with the abdominal armor is much stronger, the pineal is partly in contact with the centrals, and the dentition is characteristically Dinichthyid, with strongly developed vomerine teeth. The anterior margin of the lower dental plates is developed into a prominent beak, and the superior or functional margin is strongly denticulated; the posterior extremity of the splenial is broad and spatulate. The suborbitals are unusually wide and massive, and the rostral seems to have been laterally expanded in front. The dorsomedian bears the usual inferior keel, its terminal process being given off at a slight distance in advance of the posterior margin.

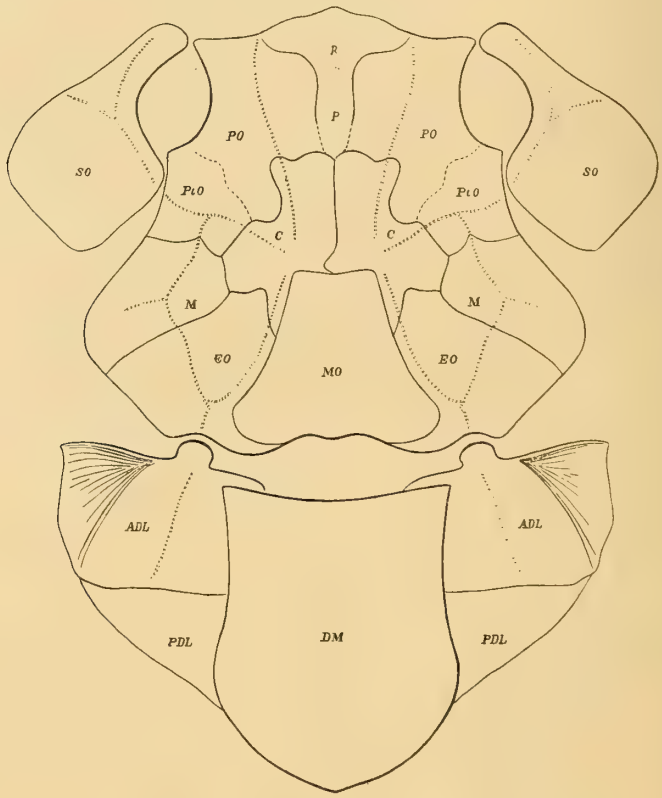


FIG. 27.

Fig. 27. *Dinichthys halmodeus* (Clarke). Marcellus shale (Erian); New York. Restoration of headshield and dorsal armoring of trunk, x $\frac{1}{8}$. *ADL*, anter-odorso-lateral; *DM*, dorso-median; *EO*, external occipital; *M*, marginal; *MO*, median occipital; *P*, pineal; *PDL*, postero-dorso-lateral; *R*, rostral; *SO*, suborbital. Original in New York State Museum.

In the detailed and in most respects very accurate description of the holotype given by the original author, it is stated that the dentition presents "an aspect highly similar" to that of Dinichthys, and comparisons are instituted between it and *D. herzeri,* which also has the functional margin of upper and lower plates denticulated. This resemblance of jaw-parts is of sufficient weight, in our opinion, to justify the transfer of the species from Coccosteus, where it was doubtfully placed by Dr. Clarke, to Dinichthys. Of special significance from a taxonomic standpoint are the vomerine teeth, which are described as follows by the same author: "Each is concave on the inner surface, convex externally, and bore a somewhat extended apophysis [or process], which in each case has been broken off. There is no evidence of denticles or a tuberculated surface; the lower edge is, however, rather sharp and would have served a cutting purpose."

Formation and locality. Marcellus Division (Erian); New York State.

Dinichthys lincolni Claypole.

(Plate II, Fig. 20)

1893. *Dinichthys lincolni* E. W. Claypole, Amer. Geol. **12,** p. 177, text-fig.
1906. *Dinichthys lincolni* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9,** p. 117, 142.
1907. *Dinichthys lincolni* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 129, pl. 7, figs. 4-6.

Known only by a single right vomerine tooth of about the size of the corresponding element in *D. intermedius* Newberry, and very similar to it in general form. The external surface, however, not only along the symphysial margin, but also over nearly all of the exposed portion, is covered with enlarged conical tubercles, or even denticles, which are arranged in more or less regular vertical series. The externo-lateral process which serves for the attachment of the tooth to the preorbital, is well developed, but distally somewhat compressed.

The unique tooth upon which this species is founded possesses a number of interesting features. In the first place, as already noted by Claypole, it is singular in having the entire outer face

strongly tuberculated; and it is noteworthy that the tubercles are most conspicuously developed, so that they become in fact denticles, along the inner or symphysial margin, thus placing the species in close relation with *D. herzeri*. The dermal origin of the different dental plates in Arthrodires could not be more distinctly indicated than by these vestigial remnants of Uronemus-like tuberculation.

Another point worthy of attention relates to the marks of contact with the lower dental plates, such as are plainly visible on the inner or posterior face of the tooth. It is evident that the larger and outer (ectad) prong has been considerably worn down by use, and its lower extremity blunted; but on examining its inner aspect, and also that of the secondary (entad) prong, one may determine the exact position occupied by the anterior beak of the mandible when the jaws were closed. Furthermore, the beveling of the inner edge is so regular, and there is such close conformity of all the parts, that it appears practically certain that the teeth were held rigidly in place against the head-shield in what is conceived to have been the usual manner in Arthrodires. Finally it is to be noted that a portion of the tooth is somewhat deformed—whether as the result of accident during life of the creature, or through post-mortem destructive agencies, it is difficult to say—but whatever the cause, it did not operate so as to crush the more slender prong, or rend it asunder.

Formation and locality. Marcellus shale; Ontario county, New York.

Dinichthys pustulosus Eastman.

(Plate I, figure 10; Plate IV; text-figure 28)

1897. *Dinichthys pustulosus* C. R. Eastman, Bull. Mus. Comp. Zool. **31**, p. 38, pl. 3, fig. 4.
1898. *Dinichthys pustulosus* C. R. Eastman, Amer. Nat. **32**, p. 748, text-figs. 1, 2.
1900. *Dinichthys pustulosus* C. R. Eastman, Journ. Geol. **8**, p. 32, text-fig. 1.
1901. *Dinichthys pustulosus* B. Dean, Mem. N. Y. Acad. Sci. **2**, p. 122.
1902. *Dinichthys pustulosus* O. H. St. John, Amer. Nat. **36**, p. 657, text-figs, 1, 2.
1906. *Dinichthys pustulosus* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9**, p. 142, text-fig. 22D.
1907. *Dinichthys pustulosus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 130, pl. 2, fig. 6; pl. 5, figs. 2, 3; pl. 12; text-fig. 25.

A primitive species seldom exceeding and usually somewhat smaller in size than *D. intermedius,* distinguished from it and its contemporariesin the Ohio Upper Devonian by its fine tuberculation, undulating suture lines, and decidedly Coccosteus-like aspect. Lower dental plates with a simple trenchant margin, terminating behind in an abrupt downward declivity bearing a series of few, regularly spaced rudimentary denticles. Palatopterygoid dental plates ("shear-teeth") with convex functional margin, simply trenchant, and not denticulated along the posterior border so far as known. Vomerine teeth resembling those of *D. intermedius.* Visceral surface of occipital region without prominent ridges, and posterior pit on under side of the median occipital scarcely divided. Pineal plate apparently in contact with the centrals, and with inconspicuous foramen.

Of this species, which appears to have been rather abundant and widely distributed in the Middle Devonian of this country, nearly the entire dermal armor is known, and the whole of the dentition. Amongst the primitive characteristics of the form in question may be reckoned its fine, Coccosteus-like tuberculation, sinuous suture lines, remnants of an original denticulation along the sloping posterior margin of the lower dental plates, and the comparatively slight development in the latter of a toothlike projection at no great distance behind the symphysial beaks. At the same time, however, it must be acknowledged that this species marks a considerable advance over typical Coccosteus-like conditions, inasmuch as the functional margin of the dental plates is no longer serrated, the dorsomedian plate has developed a strong inferior carina and posterior process, becoming also emarginate in front, and a clavicular occurs of the usual Dinichthyid type.

The occurrence of *D. pustulosus* in the New Albany Black Shale of Kentucky, a horizon corresponding approximately to the Genesee of New York State, favors the supposition that it was the immediate progenitor of forms like *D. intermedius* and *D. terrelli* of the Cleveland shale, which have retained a similar form of dentition. According to this view, *D. herzeri* and other species in which the functional margin of the dental plates is denticulated, form a separate series, descended along collateral

lines from Coccosteus, and characterized by the persistence of this distinctly Coccosteus-like feature. We should therefore be inclined to look upon *D. halmodeus* as standing in the same ancestral relations to the type species of this genus as does *D. pustulosus* to *D. terrelli*. It is noteworthy that *D. pustulosus* does not occur in rocks to the eastward of Kentucky, so far as known, until very late in the Devonian (Oneonta beds); whereas in the Mississippi Valley region it is tolerably abundant throughout the Middle Devonian. Its advent, then, in the Hamilton limestone or its equivalent in the central western states is probably to be explained on the theory of immigration from Eurasia by way of the Mackenzie Basin and Manitoba.*

The arrangement of cranial roofing plates in the headshield of this species is shown in the accompanying text-figure 28, alongside of which is placed, for sake of comparison, one showing the corresponding portion of the existing Neoceratodus. Due allowance being made for the fact that the preorbital plates remain cartilaginous and even pierced by a fontanelle in the recent form, and that the anterior median element ("dermal mesethmoid") is undivided, as it is also in Macropetalichthys, a general similarity in pattern will not fail to be observed. The significance of the various points of agreement can hardly escape notice when comparisons are made between other parts of the skeleton as well. That which is important to bear in mind is that the Arthrodiran skull, as exemplified by the best known genera, was constructed upon essentially the same model as in Neoceratodus; and the latter, accordingly, serves as a most valuable criterion for interpreting structural details of members of the extinct group we are considering.

Formation and locality. Fragmentary remains of this species are not uncommon in the Cedar Valley limestone of Bremer and Johnson counties, Iowa, and the excellently preserved headshield shown in Plate IV was obtained from the same formation near Rock Island, Illinois. The original of Plate III, fig. 12, was also derived from the latter vicinity. The typical locality for this species, where it seems to have flourished in considerable nu-

*See Professor Calvin's remarks on the Devonian System of Iowa, in Rept. Iowa Geol. Surv. 1897, **VIII**, p. 221; also Professor Schuchert's essay on the Faunal Provinces of the Middle Devonic of America, in Amer. Geol. 1903, **32**, pp. 137-162.

FIG. 28.

Fig. 28. *Dinichthys pustulosus* Eastm. Middle Devonian; Iowa. Restoration of head-shield, dorsal aspect, showing arrangement of cranial plates and course of sensory canals, x ¼. Lettering as in figure 27 (see page 192).

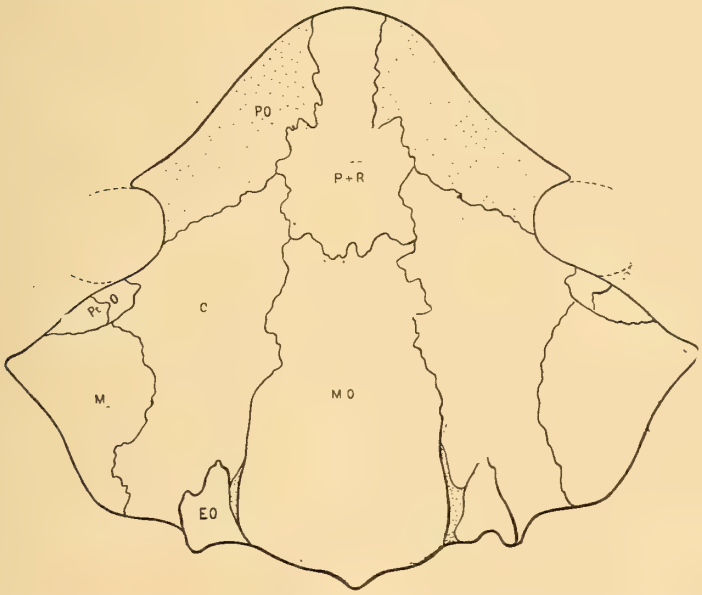


FIG. 29.

Fig. 29. *Neoceratodus forsteri* (Krefft). Dorsal aspect of cranial roof, drawn as if flattened out to same extent as in Dinichthys. Cartilaginous portions dotted, and dermal plates lettered to correspond with those in Arthrodires. The undivided anterior median plate (P + R) is commonly termed the "mesethmoid." x 1-1.

merical abundance, is the Hydraulic limestone (Hamilton) of Milwaukee, Wisconsin. Characteristic remains occur in the New Albany (=Genesee) Black Shale near Louisville, Kentucky, and also in the Oneonta beds (Senecan) near Delphi and Oxford, New York.

Dinichthys newberryi Clarke.

1885. *Dinichthys newberryi* J. M. Clarke, Bull. U. S. Geol. Surv. no. **16**, p. 17, pl. 1, fig. 1.
1889. *Dinichthys newberryi* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 153.
1897. *Dinichthys newberryi* C. R. Eastman, Bull. Mus. Comp. Zool. **31**, p. 30, pl. 1, fig. 2.
1906. *Dinichthys newberryi* L. Hussakof, Mem. Amer. Mus. Nat. Hist. **9**, p. 145.
1907. *Dinichthys newberryi* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 133, pl. 6, fig. 2.

Mandibles attaining a total length of 28⅓ cm in the type specimen, with very prominent anterior beak, simple trenchant margin, and closely resembling that of *D. pustulosus* in general outline. There are, however, no denticulations or tubercles along the downward slope immediately behind the cutting margin, and the other plates associated with the type specimen have a smooth external surface.

A single dorsomedian plate from the same horizon as the type, and considered by Dr. Clarke to be specifically identical with it, is thus described by him:

"In the same Styliola layer as it outcrops on the east side of Canandaigua like, near Genundewah, 6 miles from the Bristol locality, I had earlier discovered a dorsomedian plate belonging presumably to the same species. Its dimensions are as follows: length, 12½ cm (broken); width anteriorly, 13¾ cm; height of carinal process, 5 cm. . . . The posterior edge of this plate in *D. newberryi* is broken and has apparently lost 3 or 4 cm from its length. The smallness of the bones of *D. newberryi* does not indicate immature growth of an individual of either of the other species [*i. e., D. terrelli* or *D. herzeri*]. The discovery in outcrops of the same horizon, in localities separated by a distance of several miles, of bones of different individuals, all of which seem to agree with one another in their relative proportions, is at least presumptive evidence that these individuals had attained maturity and that the size of the bones given above is that of normal full growth."

The measurements of this element evidently indicate an immature individual, since considerably larger plates of the same kind have been found elsewhere in New York State and also in the Genesee Black Shale of Louisville, Kentucky. Some of the plates from the latter locality exceed the average proportions of *D. pustulosus,* are as a rule thicker, and differ also in the details of ornamentation. Skeletal parts belonging doubtfully to this species have also been described from the Naples shale at Sturgeon Point, near Buffalo, New York.

Formation and locality. Typically from the Genesee shale (Senecan) in the vicinity of Bristol Center and Canandaigua Lake, New York. Detached plates agreeing in proportions and ornamentation also known from the corresponding formation near Louisville, Kentucky. Doubtfully represented also in the Naples shale (Portage beds) of western New York.

Dinichthys tuberculatus Newberry.

1888. *Dinichthys tuberculatus* J. S. Newberry, Trans. N. Y. Acad. Sci. **7,** p. 179.
1889. *Dinichthys tuberculatus* J. S. Newberry, Monogr. U. S. Geol. Surv. **16,** p. 98, pl. 32, fig. 3.
1893. *Dinichthys tuberculatus* E. W. Claypole, Amer. Geol. **12,** p. 277.
1897. *Dinichthys tuberculatus* C. R. Eastman, Bull. Mus. Comp. Zool. **31,** p. 38.
1899. *Dinichthys tuberculatus* C. R. Eastman, 17th Ann. Rept. N. Y. State Geol. p. 318.
1907. *Dinichthys tuberculatus* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 137.

An imperfectly definable species, known only by detached plates which are remarkable for their relatively great thickness, and coarsely tuberculate style of ornamentation. The known portions of the abdominal armor indicate a species rather less than one-half the size of *D. intermedius.* In the present state of our knowledge, there are no reasons other than difference in geological horizon to prevent assigning to this species certain heavy and coarsely tuberculated Dinichthyid plates found in the Middle and Upper Devonian of Wisconsin and Iowa; neither is it possible, except for difference in geological age, to recognize a distinction between the plates known under this name and the so-called *D. precursor* Newberry, from the Corniferous lime-

stone of Ohio. The typical locality for *D. tuberculatus* is in the Chemung conglomerate of Warren, Pennsylvania, but according to Newberry, the same form occurs also in the Upper Devonian of Belgium.

Formation and locality. Chemung beds (Chautauquan); Warren, Pennsylvania. Also, according to Newberry, in the Psammites de Condroz, near Liège, Belgium. Either this or a very similar species is also represented in the Middle and Upper Devonian of Ohio, Wisconsin and Iowa.

Dinichthys curtus Newberry.

1888. *Dinichthys curtus* J. S. Newberry, Trans. N. Y. Acad. Sci. **7:** 179.
1889. *Dinichthys curtus* J. S. Newberry, Monogr. U. S. Geol. Sur. **16:** 156, pl. 48, fig. 3; pl. 53, fig. 1-4.
1893. *Dinichthys curtus* E. W. Claypole, Rep't Ohio Geol. Sur. **7:** 606.
1893. *Dinichthys curtus* A. A. Wright, Rep't Ohio Geol. Sur. **7:** 623.
1900. *Dinichthys curtus* C. R. Eastman, Jour. Geol. **8:** 33.
1905. *Dinichthys curtus* L. Hussakof, Bull. Am. Mus. Nat. Hist. **21:** 409, pl. 15, fig. 1; pl. 16.
1906. *Dinichthys curtus* L. Hussakof, Mem. Am. Mus. Nat. Hist. **9,** p. 112, text-fig. 5, pl. 12.
1907. *Dinichthys curtus* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 138.

Newberry's description of this species is as follows:

"Fishes of moderate or small size; head a nearly equilateral triangle, measuring about a foot on a side; cranium, maxillary and mandible similar in character to those of *Dinichthys intermedius,* but only half to two-thirds as large, and the mandible bears two subordinate prominences back of the turned up tooth-like extremity; also the posterior end of the cutting edge is set with two or three unequal denticles in place of the series of even, lancet-like points in the same position on the mandible of *D. intermedius.* The anterior ventrolateral plate is scimiter-shaped, eight inches long by two and a half inches wide, being relatively narrower than the corresponding bone in any other species known."

Occurring typically in the Cleveland shale of Ohio, this species is also reported by Newberry from the Chemung of Pennsylvania, although no precise indications as to locality are given. Investigation shows that detached plates of a species fully as large as *D. curtus,* possibly even larger, occur in the Chemung

of Warren county, Pennsylvania, but the present writer is unacquainted with any evidence which will enable one to state positively that the species is identical with any of the Ohio Upper Devonian forms. It is to be hoped that more characteristic remains from the eastern region may yet be brought to light.

Formation and locality. Cleveland shale (Upper Devonian); Ohio. Presumably also in the Chemung of Pennsylvania.

Genus **PROTITANICHTHYS** Eastman.

Primitive Coccosteans of small size, displaying synthetic characters of later forms. Arrangement of cranial roofing plates in general resembling that of Coccosteus, the centrals meeting in a sinuous longitudinal suture and not in contact with the pineal; the latter is subelliptical in outline, its major axis directed transversely, and pierced by a relatively large pineal foramen; rostral plate also very broad. External surface finely tuberculated; lateral margin of headshield apparently not much widened posteriorly; sensory canals distinct; dentition and abdominal armoring unknown.

Protitanichthys fossatus Eastman.

(Text-fig. 30)

1907. *Protitanichthys fossatus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 144, pl. 10, fig. 2, text-fig. 30.

The unique headshield which has been described under this name is of interest in two respects: first, on account of its geological antiquity, and secondly, because it displays synthetic characters. In the majority of its features, a close approximation is to be observed to typical Coccosteans, especially the more primitive species of Dinichthys, such as *D. halmodeus* for example. Of relatively small size, its superficial ornament consists of fine, closely crowded tubercles with stellate bases. The undulating suture line between the pair of central plates is a distinctly Coccosteus-like feature, and so, too, is the exclusion of the pineal from contact with this pair. The form of the headshield appears to have been long and narrow, without much lateral expansion across its posterior portion. One striking

peculiarity, however, distinguishes it from all species of Coccosteus and Dinichthys, and points to ancestral relations with Titanichthys, as implied by the generic name. We refer to the large size and transverse elongation of the pineal plate, a peculiarity that has hitherto been observed in but a single genus of late Devonian Arthrodires. It is on this account that the small Onondaga form in question is regarded as an early forerunner of the group of extremely modified Coccosteans culminating in Titanichthys.

The headshield, itself imperfectly preserved, is unaccompanied by any other bones of the skeleton. Although, as a rule, little dependence is to be placed upon theoretical association of parts, the question may properly be raised whether there are any other Coccostean remains occurring in the same horizon which correspond in general proportions and superficial ornament to the headshield under discussion. Attention rests immediately upon two forms: the lower dental plate described as *Liognathus spatulatus,* and the dorsomedian plate known as *Coccosteus occidentalis* (*ante,* p. 186). The possibility is not remote that all three of these detached parts which have received separate names may actually belong to a single species; in default of proof, however, we have no other precedure than to maintain each provisionally as an independent species, or even genus. At the same time it may not be unworthy of comment that the peculiar spiniform prolongation observed in *Coccosteus occidentalis* reappears in an abbreviated form in the triangular termination of the corresponding plate in Titanichthys. Such a coincidence certainly suggests the idea of an inherited characteristic, and confirms us in the belief that prototypes of the most highly specialized Coccosteans are to be sought as early as the Ulsterian stage in this country.

The accompanying restoration of the headshield (text-fig. 30) is intended to convey a graphic idea of the arrangement of cranial roofing plates and disposition of the sensory canals. The orbital borders are incompletely preserved, and the posterior margin, which has been broken away in the holotype, is restored in the figure after analogy with other Coccosteans. The specific title has reference, it is scarcely necessary to add, to

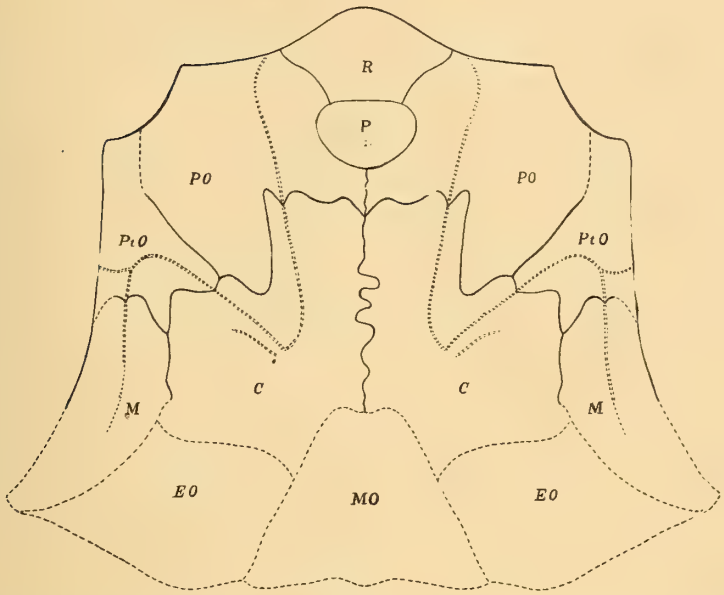


FIG. 30.

Fig. 30. *Protitanichthys fossatus* Eastm. Delaware limestone (Ulsterian); Delaware, Ohio. Restoration of headshield showing transversely elongated pineal and rostral plates, and sinuous suture-line between the centrals. Lettering as in preceding figures. x ¾. Holotype in Museum Comparative Zoology.

the very conspicuous pineal foramen, placed slightly behind the middle of the plate it pierces. Two other prominent fossae, corresponding to those in Dinichthys, occur in line with the pineal on the visceral side of the preorbitals, and these appear to have been bounded by a low transverse ridge in front. The assumption does not appear to be unreasonable that these fossae served to receive the bases of vomerine teeth.

Formation and locality. Delaware limestone (Ulsterian); Delaware, Ohio. Holotype preserved in the Museum of Comparative Zoology, Cambridge.

Genus **TITANICHTHYS** Newberry.

Plates of head and trunk resembling those of Dinichthys, but relatively thinner, and more laterally expanded. Pineal plate elliptical, broader than long, in contact with the centrals, and pierced by one or two foramina, the latter sometimes capped by a small bony operculum. Lower dental plates long and slender, without denticulations, grooved in the anterior portion of

the oral margin as if for a horny sheath, and somewhat turned upwards at the symphysis. Outer (free) portion of clavicular developed as a stout arm, rounded or semicylindrical in cross-section.

The remarkable fishes comprised by this genus represent the ultimate stage of specialization attained by Dinichthyids. Unable to maintain an existence except under peculiarly favorable conditions—their gigantic size, unwieldy organization and weak dentition presupposing an estuarine habitat and abundant food supply—they survived for a relatively short period, and within a limited area. Their remains are confined, so far as known, to the Upper Devonian of Ohio. Forerunners of the genus, however, make their appearance as early as the Ulsterian, and fragmentary plates very suggestive of Titanichthys occur in the Hamilton limestone of Milwaukee, Wisconsin.

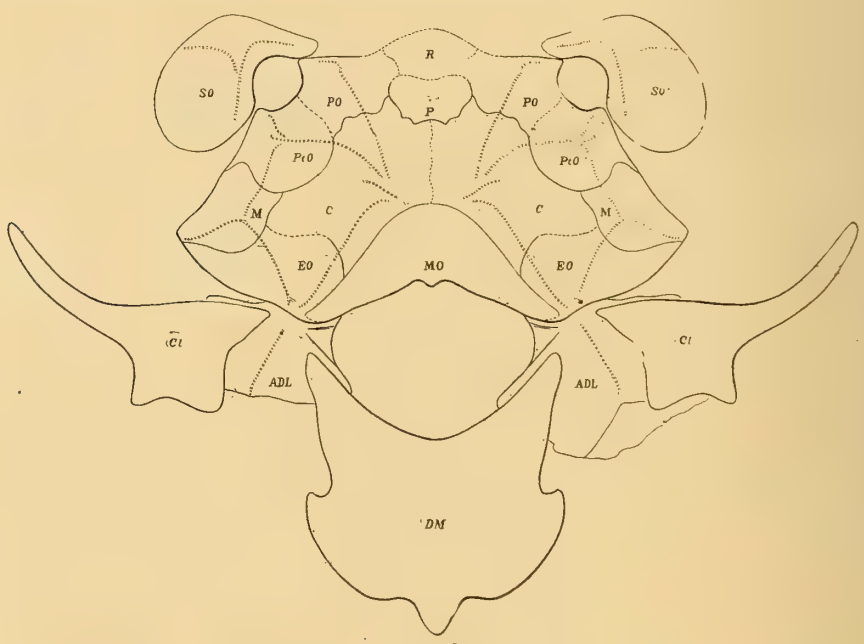


FIG. 31.

Fig. 31. *Titanichthys agassizi* Newberry. Restoration of headshield and dorsal armoring of trunk. *ADL*, antero-dorso-lateral, fused in the type specimen with the postero-dorso-lateral; *C*, central; *DM*, dorso-median restored after the outline of *T. clarki*; *EO*, external occipital; *M*, marginal; *MO*, median occipital; *P*, pineal; *R*, position of rostral; *SO*, suborbital. x 1-16.

Compare figures of body plates given in Hussakof's "Catalogue of Fossil Fishes", (Bull. Amer. Mus. Nat. Hist. 1908. **35**, p. 20).

The arrangement of cranial plates conforms closely to the pattern of typical Coccosteans. The bone substance, however, is much thinner, the sutures more intimately fused, and all of the plates are relatively broader. The long axis of the pineal, too, is transverse instead of longitudinal, as in Dinichthys and Coccosteus. The enormous width and flatness of the cranial and abdominal armor indicate a more or less depressed form of body, probably correlated with bottom-feeding and generally sluggish habits. Certainly the degenerate character of the dentition does not permit us to look upon these creatures as very formidable competitors of Dinichthys and the much more agile Cladoselache.

Interesting features are displayed by the abdominal armor. The mode of articulation between the headshield and antero-dorso-lateral plates is less complicated than in Dinichthys, the condyle and socket of the latter form being replaced by an elongated flange and groove, which probably admitted of but slight movement between the parts. In the type species at least, the antero- and postero-dorso-lateral plates are completely fused, and are overlapped to a relatively greater extent by the dorso-median than in Dinichthys.

Nothing is known of the ventral armor of Titanichthys with the exception of the postero-ventro-median, certain large thin plates of lanceolate outline, and found only in the detached condition, having been doubtfully so interpreted. One such, having a length of 29 cm, and maximum width of 12.5 cm, is preserved in the Museum of Comparative Zoology at Cambridge, and is figured in the Bulletin of that institution for 1897 (vol. *31,* pl. 5, fig. 1). It is abruptly truncated in front, and bears traces of overlap by contiguous plates, thus rendering it probable that the ventral armor of the form to which it belonged was composed of the same number of plates as in Dinichthys.

GENERA OF DOUBTFUL FAMILY POSITION.

Fragmentary remains of Arthrodires, differing from other described species as regards superficial ornament, and some of them indicating fishes of considerable size, have been described from various Devonian localities in the eastern United States and Canada. Most of the species are known only by detached

plates, none in association with the dentition or headshield, hence their precise systematic position is doubtful. Coarsely tuberculated plates, suggestive of Newberry's type of *Aspidichthys clavatus,* are reported by Professor Williams from the New York Portage.* Similar fragments occur sparsely in the New

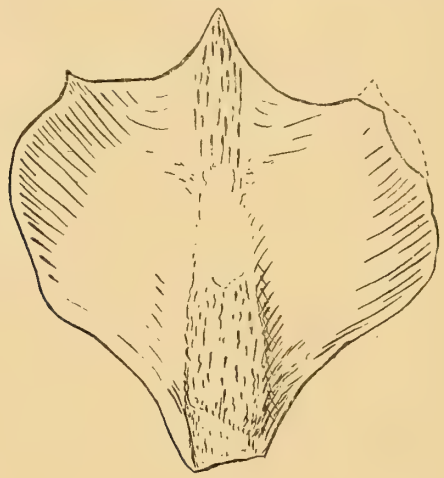


FIG. 32.

Fig. 32. Dorso-median plate of a small unknown Arthrodire surviving as late as the dawn of the Carboniferous. From nodule layer at base of the Waverly in Boyle county, Kentucky. Original in Museum Comparative Zoology. x 1-1.

Albany (= Genesee) Black Shale near Louisville, Kentucky, and Jeffersonville, Indiana. Others of equal thickness, but somewhat less coarsely tuberculated, are among the rarer fossils of the State Quarry beds (Upper Devonian) in Johnson county, Iowa.

As implied by the generic name, the ornament of Holonema consists of threadlike, radiating ridges. Two species are known, the type (*H. rugosum* Claypole) occurring in the Chemung of New York and Pennsylvania, and the other (*H. horridum* Cope), being thus far known only from rocks of the same age in Bradford county, Pennsylvania. One specimen of the typical species is interesting in that it displays the entire ventral armor, and from the relative proportion of its parts a theoretical association with Mylostomids is considered justifiable, both for this

* Williams, H. S., On the Fossil Faunas of the Upper Devonian. Bull. U. S. Geol. Surv. no. 41, 1887, p. 43.

genus and the imperfectly known Glyptaspis. Phyllolepis is distinguished from Holonema by having the superficial rugae arranged in concentric, instead of radiating lines. The only American species that has been described is *P. delicatula* Newberry, from the Chemung of Bradford county, Pennsylvania. Accompanying the latter, but of more dubious nature, are plates with arrowhead-like ornamentation, described by Newberry under the name of *Sphenophorus lilleyi.** Certain elliptical plates having a closely similar style of ornamentation are also known from the Hamilton of Milwaukee, and may be provisionally placed in the same category. An enlarged view of the surface markings of one of these plates is given in Plate III, Fig. 2. From the last-named locality and horizon are obtained a number of peculiar plates, possibly representing the dorsomedian of unknown forms, two such being illustrated in Plate I, Figs. 2 and 6. Aspidichthys, Phyllolepis, and possibly also Holonema are represented in the European Devonian, and one species from the Middle Devonian of Manitoba is doubtfully referred to Aspidichthys (*A. ? notabilis*) by Whiteaves.

Order **CTENODIPTERINI.**

Body fusiform, without dermal armor. Skeleton and chondrocranium partially ossified, skull autostylic, premaxillae and maxillae absent. Cranial roof bones small, and, like the squamation, with or without ganoine investment. Nostrils inferiorly situated; jugular plates present or not. Tail heterocercal or in some forms apparently diphycercal (gephyrocercal). Anal fin always distinct, the remaining median fins either discontinuous or becoming coalesced. Paired fins acutely lobate. Secondary pectoral arch consisting of an ossified supraclavicular and clavicle; pelvic arch present. Dentition consisting of large tritoral dental plates supported by the palato-pterygoid and splenial bones; a marginal series of teeth above and below also sometimes present, but never any vomerine teeth.

The structure of this singularly interesting order of Palæozoic fishes has been investigated in minute detail by Hugh Miller,

*The generic name being preoccupied, Oestophorus has been proposed as a substitute by S. A. Miller. The sense in which these terms are employed is in each case purely provisional.

Pander, Huxley, Traquair and others, and particularly within the last decade or so its relations to modern Lung-fishes have engaged profound attention on the part of zoologists and palæichthyologists. Recent discussion has focussed upon two rival theories, as already noted. According to the first, which has steadily gained in ascendency, the members of this order are supposed to have attained greater specialization during the Devonian and Carboniferous than all other Lung-fishes, and existing members of the subclass are regarded as decidedly more primitive in organization than Ctenodipterines. Modern Sirenoids (*i. e.,* Neoceratodus, Protopterus and Lepidosiren) would therefore be looked upon as survivals of a more generalized, more archaic Dipnoan stock than Dipterus and its allies, rather than as actual descendants of the latter.

The second and later interpretation is that of Dollo,* and the exact opposite of the first. Evidence drawn from other than cranial characters is held to confirm the belief that Dipterus itself is the most archaic of all Dipnoans, and that modern Lungfishes have been derived from it through successive stages of specialization. As a starting-point for his theory, Dollo accepts the conclusion previously reached by Balfour and Parker that the apparently diphycercal tail of recent forms is secondary, due to abortion of the termination of the vertebral axis, and coalescence of the median fins. The less ossified condition of the skull and chondrocranium in modern forms is also explained as due to secondary reversion, through degeneration, to an apparently primitive condition. The chief objection to Dollo's view is that we are unacquainted with any parallel example among vertebrates which justifies belief in the possibility of such degeneration as is here assumed.†

* Dollo, L., Sur la phylogénie des Dipneustes. Bull. Soc. Belge Géol. etc., 1895, pp. 79-128.

† For critical remarks on this point see Dr. Traquair's Vice-Presidential Address, Rept. Brit. Assoc. Adv. Sci., Bradford Meeting, 1900, p. 776 *et seq.*, and Professor Bridge's Monograph on Lepidosiren, in Trans. Zool. Soc. London, 1898, **14**, pp. 366-372. Still more recently Karl Fürbringer has remarked upon the same subject as follows (Jena Denkschr. 1904, **4**, p. 498 *et seq.*):

Ich kann dieser Ansicht [Dollo's] gegenüber, die sich namentlich auf die zeitliche Verbreitung der Dipnoer stützt, nur betonen, dass am Schädel der recenten Dipnoer kein Anhalt dafür besteht, dass hier Knochen verloren gegangen seien. Wir sehen im Gegentheil solche in Bildung und im Wachsen begriffen. . . .

Yet another view of Dipnoan interrelationships, or perhaps rather to be considered as a modification of the first, is that already outlined in the foregoing discussion of Arthrodires. The organization of the existing Neoceratodus is regarded as decidedly more primitive than that represented by Dipterus and its allies; hence the modern structural type or its immediate prototype is assumed to have been in existence at least as early as the lowermost Devonian, to have given rise to the more highly specialized orders of Ctenodipterini and Arthrodira, and to have persisted practically unchanged ever since. The modern genus therefore falls within the same category as scorpions, king-crabs, Lingula, Cestracion, Polypterus, Sphenodon and other archaic survivals of far-distant faunas which have manifested extraordinary persistence and conservatism throughout the march of untold geological ages.

This view may be said to rest almost entirely upon the evidence of comparative anatomy, and has received as yet no confirmation from the discovery of actual remains which fulfil the requirements of a common ancestor to the three recognized orders of Lung-fishes—Arthrodires, Ctenodipterines and Sirenoids. It may be that confirmation of this sort will never be forthcoming, owing to the imperfection of the palæontological record. Nevertheless, relying upon the infallible clue of structural resemblances, one may project the divergent lines of descent backward until they meet in a common point; and at this point is to be sought the ancestry of the three orders with whose history palæontology acquaints us.

The following passage, which occurs at page 500 of the same memoir, may be contrasted with the views expressed by Bashford Dean in *Science* for July 12, 1907 (**26**, pp. 46-50), and February 7, 1908 (**27**, p. 203):

Nachdem in jeder Beziehung *Ceratodus* als der primitivere erkannt ist, muss auch die Annahme Dollo's, dass die Heterocerkie bei *Dipterus* etwas Primitives bedeute, fallen. Der Schwanz von *Ceratodus* zeigt zwar gewiss Rückbildungen; für eine ehemalige Heterocerkie bei ihm ist aber kein Beweis erbracht. Ich kann nach alledem, falls überhaupt eine Verwandtschaft zwischen *Dipterus* und den recenten Dipnoern besteht, diese im Gegensatz zu Dollo nur im Sinne von Woodward und Bridge auffassen.

Family CTENODONTIDAE.*

Cranial roof bones numerous; no secondary upper jaw, and no marginal series of teeth above or below; jugular plates present or absent. Dentition consisting of an upper and lower pair of triangular "ctenodont" dental plates, whose outwardly radiating ridges usually terminate in rows of conical denticles or tubercles, rarely smooth or nearly so; no vomerine teeth so far as known. Tail heterocercal or apparently diphycercal. Excluding the anal, which is always distinct, the remaining median fins are either distinct or continuous (two dorsals in all genera but Phaneropleuron).

Genus DIPTERUS Sedgwick and Murchison.

Body elongate, not much laterally compressed, covered with enamelled cycloid scales; head depressed, snout obtuse. Dental plates, above and below, triangular in shape, with outwardly radiating ridges, tuberculated or strongly crenulated, sometimes becoming obsolescent. Paired fins acutely lobate, two remote dorsal fins opposed to the pelvic and anal fins, separated from the caudal.

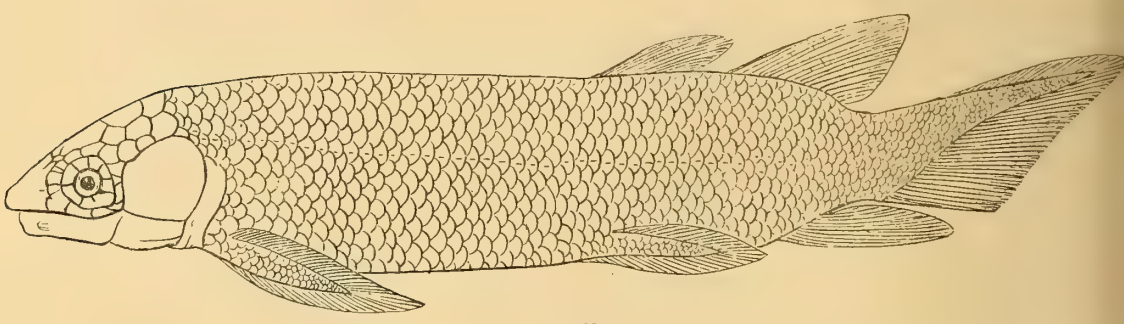


FIG. 33.

Fig. 33. *Dipterus valenciennesi* Sedgw. & Murch. Lower Old Red Sandstone; Scotland. Left lateral aspect as restored by Dr. R. H. Traquair. x ⅓. (after Traquair.)

Our knowledge of the complete form of this genus, shown in text-figure 33, is dependent entirely upon the small, well-preserved skeletons found in the Scottish Lower Old Red Sandstone. These remains were originally described in successive

* On the propriety of using this term instead of Dipteridæ, see Traquair in Geol. Mag. 1893, dec. 3, **10**, p. 264.

notices by Hugh Miller,* whose pioneer work in this field was exceedingly accurate and painstaking, and worthy of being held in grateful remembrance. In fact, nearly all of the more salient characters of the typical genera were ably described by this observer. He called attention to the peculiar dentition of Dipterus, and pointed out that the two dorsal fins are placed far back, that the paired fins are acutely lobate, that jugular plates occur in place of branchiostegal rays, besides mentioning other details that were afterwards fully confirmed by Pander and others.† His restoration of the head-roof is also more satisfactory in some respects than any that has since been published. In our own time, the most complete account of the skeletal anatomy of Dipterus is that of Traquair, whose researches have also enlightened us regarding various related genera.‡

In the New World Devonian, remains of Dipterus proper are confined exclusively to detached hard parts, such as dental plates, scales, ceratohyals, and calcified labial cartilage. Under these circumstances it is difficult to determine whether teeth of a given form should be retained in the typical genus or referred to Sagenodus, Ctenodus or others having a similar form of dentition. Newberry was well aware of this fact, and even declared that it was impossible to insist upon rigid generic distinctions in the case of Palæozoic detached teeth. "By convention," he says, "those found in the Jurassic, Triassic and Permian have been called *Ceratodus,* those in the Carboniferous *Ctenodus,* and those from the Devonian *Dipterus.* The experienced eye will easily discover differences in the groups which are arranged stratigraphically, a predominating type of form or markings associating those of the Devonian with each other, and separat-

* In the "Old Red Sandstone", "Footprints of the Creator", and "Sketch Book of Popular Geology".

† Huxley has to say of Miller's observations: "It is much to be regretted that Professor Pander should have been wholly unacquainted with these works [of Hugh Miller] when he wrote his Monograph on the Ctenodipterini, and that he has consequently inadvertently failed to do justice to the great merits of Hugh Miller, who made known almost the whole organization of Dipterus, and anticipated the most important part of Prof. Pander's labours in this field."—Mem. Geol. Surv. United Kingdom, 1861, Decade X, p. 14.

‡ Traquair, R. H., On the Genera Dipterus, Palædaphus, Holodus, etc. Ann. Mag. Nat. Hist. 1878, ser. 5, **2**, pp. 1-12, pl. 3.—Notes on the Devonian Fishes of Campbelltown and Scaumenac Bay in Canada, nos. 1-3. 1890-93.—The extinct Vertebrata of the Moray Firth Area. 1896.

ing them in a rough way from those of the Carboniferous age. Still, the type which is predominant in the Carboniferous occurs in the Devonian, where may be also found as exceptions the smooth-ridged species of the Mesozoic." He accordingly adopts the arbitrary method of classifying "all the older Dipterines as belonging to the genus *Dipterus,* the Middle and Upper Carboniferous species as *Ctenodus,* the Triassic as *Ceratodus;* but it would be quite impossible to give any satisfactory generic definitions to these different groups." *

In all, six species of Ctenodipterines were established by Newberry upon the evidence of detached teeth occurring in the Chemung of Warren, Pennsylvania, and four upon similar remains from the Catskill of Tioga and Bradford counties, in the same State. Still earlier than any of these, the undefined name of *Dipterus ithacensis* had been proposed by H. S. Williams† for certain doubtful remains discovered by him in the New York Portage, making a total of eleven species that have been recognized in the Appalachian Upper Devonian. Besides these, a solitary species (*Ctenodus wagneri* Newb.) has been described from the Cleveland Shale of Ohio, and four from the Iowa Devonian, two from the middle, and two from the upper members of the series. The names of the various Ctenodipterine species that have been proposed or described from the Devonian rocks of this continent up to the present time may be tabulated in order of stratigraphic succession as follows:

NORTH AMERICAN SPECIES OF DEVONIAN CTENODIPTERINES

Catskill Group.

Dipterus contraversus Hay (=*D. radiatus* Newb.). Tioga county, Pennsylvania.

Dipterus fleischeri Newb. Bradford county, Pennsylvania, and Delaware county, New York.

Dipterus sherwoodi Newb. Tioga county, Pennsylvania.

Sagenodus angustus (Newb.). Near Leroy, Bradford county, Pennsylvania.

---

*Monogr. U. S. Geol. Surv. 1889, **16**, p. 88.

†Proc. Amer. Assoc. Adv. Sci., 30th meeting, 1882, p. 192.

Chemung Group.

Dipterus nelsoni Newb. (including also *D. flabelliformis, levis, minutus,* and *quadratus*). Warren, Pennsylvania.

Ganorhynchus beecheri Newb.* Warren, Pennsylvania.

Heliodus lesleyi Newb.† Northern Pennsylvania.

Portage Group.

Dipterus ithacensis Williams. Ithaca beds; Ithaca, New York.

Upper Devonian of Canada.

Scaumenacia curta (Whiteaves). Scaumenac Bay, Province of Quebec.

Cleveland Shale of Ohio (Upper Devonian).

Ctenodus wagneri Newb. Near Cleveland, Ohio.

State Quarry Beds of Iowa (Upper Devonian).

Dipterus costatus Eastman. Near North Liberty, Iowa.

Dipterus digitatus, sp. nov.‡ Near North Liberty, Iowa.

Dipterus mordax Eastm. Near North Liberty, Iowa.

Dipterus pectinatus, sp. nov.§ Near North Liberty, Iowa.

Conchodus variabilis, sp. nov.|| Near North Liberty, Iowa.

Synthetodus trisulcatus Eastm. Near North Liberty, also Sweetland creek, Iowa.

Synthetodus calvini, sp. nov.¶ Near North Liberty, Iowa.

Cedar Valley Limestone (Middle Devonian).

Dipterus calvini Eastm. Near Fairport, Muscatine county, Iowa.

Dipterus uddeni Eastm. Near Buffalo, Scott county, Iowa.

Ganorhynchus sp.** Near Waverly, Bremer county, Iowa.

---

*Founded on calcified labial cartilage which accompanies dental plates of *Dipterus nelsoni*, and may possibly belong to the same species.

†Regarded by Smith Woodward as belonging to the palatal dentition of Palædaphus.

‡*Cf. infra*, p. 221. §*Cf. infra*, p. 222. ||*Cf. infra*, p. 230. ¶*Cf. infra*, p. 233.

**Represented by calcified labial cartilage very similar to that of the type species of Ganorhynchus, and much larger than that of *G. beecheri*.

Some years ago the writer had occasion to examine Newberry's types of Chemung Ctenodipterines, and became convinced that the five species of Dipterus proper made known by that author from Pennsylvania were in reality manifestations of but two tolerably distinct types, the one represented by *D. nelsoni,* the other by *D. flabelliformis.* The so-called *D. levis* of Newberry was shown to have been founded upon worn specimens of *D. nelsoni,* and the small teeth described as *D. minutus* and *D. quadratus* were regarded as probably immature examples of the same species. This latter interpretation was held to be substantiated by close intergradations between the smaller forms and the altogether similar but larger teeth of the prevailing type. More recently the writer has been fortunate in having at his command an excellent assortment of Dipterine remains from the Chemung of Pennsylvania, collected by Mr. F. A. Randall, and a review of this material has suggested a still further reduction in the number of species. In the light of well preserved specimens which reveal the complete characters of the dentition, it is impossible to doubt that the thin, flat, usually more or less crushed and broken plates known as *D. flabelliformis* are the palatine components of the same dental apparatus whose mandibular elements have received the name of *D. nelsoni.* The five species that have been recognized from the eastern Chemung rocks thus become resolved into one,* and it is probable that the detached scales, ceratohyal bones, and labial cartilage (the latter known as *Ganorhynchus beecheri*) which accompany the teeth of *D. nelsoni* belong likewise to one and the same species.

Now it is of interest to recall that a species corresponding in some respects rather closely to *D. nelsoni* occurs in the Upper Devonian of Iowa, and like its eastern associate, is of protean habit. That is to say, it assumes a multitudinous variety of shapes, due to age, wear, and various sorts of mechanical and even chemical deformation after death. In addition, there are the usual distinctions of outline and surface contour which, after analogy with *D. nelsoni* and *D. flabelliformis,* are to be under-

*Or at least not more than two, in case the small teeth of the *D. minutus* type are regarded as constituting a distinct species, instead of being the young of *D. nelsoni.* The only conspicuous difference is that of size.

stood as correlated with difference in position in the mouth; the thin, flat, multicostate plates belonging to the upper, and the heavier, more convex, fewer ridged plates to the inferior dentition. The species referred to is *D. mordax,* which appears to be numerically the most abundant of all Dipterines represented in the State Quarry beds, though seldom perfectly preserved. Even fragmentary plates, however, are as a rule easily recognized by their exceedingly coarse tuberculation, paucity of costae in the adult, and subtriangular form—flattened, or even plane or concave in the upper, more or less arched in the lower. Owing to their tenuity, and consequent liability to destruction, the upper or "flabelliform" type of plates are less numerous than the lower, and their attenuated external margins are often imperfect or broken away.

As regards general manifestation and relative profusion, *D. mordax* occupies much the same position in the Iowa Upper Devonian as does *D. nelsoni* in the Chemung of the Appalachian district. The inference is not far to seek that not only the Chemung species, but also those from the eastern Catskill—which are alike coarsely tuberculated—are derivatives or modifications of an immigrant western type, which existed plentifully in the Upper Devonian of Iowa, and whose advent in the Middle Devonian of the same State is heralded by *D. uddeni* at the base of the Cedar Valley limestone. Noteworthy is the fact that no indications of Ctenodipterines have been discovered in the Middle Devonian east of the Mississippi Valley region. The significance of this dearth of remains is twofold. First, it proves that no immigrants entered the Appalachian basin from the eastward during the early or middle part of the Devonian, and probably not at all, as the Chemung invasion (witness the resemblance between *D. nelsoni* and *D. mordax*) in all likelihood came in from the west. Secondly, the evidence furnished by the facts of Dipterine distribution is consonant with the prevailing theory that intercommunication between the Dakotan and Ohioan seas was not effected until towards the close of Hamilton time (*cf.* Plate XV).

In the course of the foregoing remarks we have confined our attention purposely to the two leading species of Upper De-

vonian Dipterines in the eastern and western provinces respectively. A critical examination of the accompanying species in the latter area would no doubt be profitable, for the reason that they all present a multitudinous range of variation, and in so far defy a precise analysis of characters. It was formerly the opinion of the present writer, and in this Professor Calvin and others who have examined the material concurred, that at least several genera and numerous species of Ctenodipterines were represented in the State Quarry deposits of Johnson county, where a most singular assemblage occurs.* That opinion now requires to be modified in the light of experience gained through a study of the varied expressions of the *D. nelsoni-flabelliformis* type in the eastern area, and the counter-series exemplified by *D. mordax* in the State Quarry beds. It is evident that a very wide latitude must be assigned to the possible limits of variation and deformation and mutilation produced by well ascertained causes. Besides those aforementioned, there remains to be considered one other, which we have reserved for the conclusion of these general remarks. One perceives, therefore, that the consequences of this synthetic mode of treatment is to merge conventional distinctions as far as possible, and reduce the number of provisional genera and species to basic terms. In the following systematic descriptions the closely intergrading series of State Quarry Dipterine teeth are grouped into four specific categories, those of the smooth Synthetodus type into two only. The great mass of worn, effete, imperfect or seemingly abnormal teeth which differ in minor details from the composite or average expression of the standard species is to be regarded merely as the débris of the latter, and interesting chiefly because of the eloquent commentary it offers as to physical, chemical and perhaps even organic destructive agencies.

A word is necessary to explain the meaning of this last statement. Briefly, the appearance of a considerable number of State Quarry Dipterine teeth suggests a mildly corrosive or solvent action that is difficult to explain by the ordinary process of mineral replacement, but finds a ready interpretation by assuming

*First described by Professor S. Calvin in Proc. Iowa Acad. Sci. 1896, **4**, pp. 16-21. Also in Rept. Iowa Geol. Surv. 1896, **VII**, pp. 72-79, and 108-116.

that the teeth in question have been exposed to the action of digestive fluids within the intestinal tract of other creatures which swallowed them. Although the agency invoked is purely conjectural, it accords well with the partial, very gradual, in some cases uniform effacement of tubercles over the functional surface of the tooth, when marks of wear are localized and very distinct, and when the obliteration of tubercles is clearly of a different order from mere mechanical abrasion. Moreover, nothing is more likely than that the large numbers of Dipterine fishes frequenting this particular locality, and whose remains, together with those of Ptyctodonts, constitute a veritable 'fish-bed,' afforded a tempting prey for whatever creatures of carniverous habit chanced to share the same environment. The identity of the predatory foe we have imagined is of course a matter of mere speculation, yet the inference is not improbable that Ptyctodonts and Dipterines, in this locality at least, were natural enemies. At all events the commingling of their remains in such astonishing abundance over a limited area might be held to signify something more than a fortuitous coincidence.

It may be objected that Ptyctodonts and Dipterines were not mutually predatory, nor did one group subsist upon the other, because both have a similar type of dentition, adapted for the comminution of hard-shelled prey, such as mollusks, brachiopods, echinoderms and the like ("conchifrage" Dollo). In view of the known habits of Lung-fishes, the objection probably holds in so far as it may be questioned whether Dipterines actually preyed upon Ptyctodonts; but in the inverse sense the objection does not hold if we may depend upon analogy with the habits of modern Chimaeroids, which are singularly omnivorous, and able to injest objects of large size. Thus, in speaking of the food-habits of the existing *Chimaera colliei,* Professor Dean has the following note:*

"In *C. colliei* observations on about a score of individuals showed a singular mixture of food. Most numerous were vertebral columns of small isospondylous fishes, a few mollusk shells, usually greatly crushed, a quantity of sand and fine gravel, squid, nudibranchs and opisthobranchs, bits of cases,

*Dean, B., Chimaeroid Fishes and their Development. Carnegie Inst. Wash Pub. no. 32, 1906, p. 20.

jaws and setae of annelids, and occasionally a fragment of crustacean. In one instance the gut was filled with seaweed. . . . Another curious feature connected with feeding is that Chimaera, in spite of the small size of its mouth, can injest objects of large size. Thus it was found that a specimen of *C. colliei* of moderate size, one whose mouth appeared too small to admit a finger-tip, had injested a fish 6 or 7 inches in length."

Finally, by way of recalling the ravages that a single voracious species is able to inflict on creatures not distantly related to its own kind, it will suffice to mention the example of the recent hammerhead shark (*Sphyrna zygaena*). An interesting note on the food habits of this selachian is contributed by Mr. E. W. Gudger in a recent number of Science,* from whose article we quote the following paragraph:

"The stomach contained an almost perfect skeleton of a fair-sized sting-ray together with many cartilaginous fragments plainly having the same origin. However, the most interesting thing found in the beast was the great number of sting-ray (*Dasyatis say?*) stings present in the body and mouth. . . . I found the mouth parts to be a perfect mine of stings. In all fifty were extracted, more than forty of which were imbedded in the flesh adherent to the jaw cartilages. These stings varied in size from perfect specimens four or five inches in length to broken-off tips hardly more than one inch long. . . . As many as three or four tips were frequently found in a cube (*sic*) of flesh one inch square and two inches long."

Dipterus uddeni Eastman.

(Plate II, Figs. 3, 3*a*)

1899. *Dipterus uddeni* J. A. Udden, Journ. Geol. **7**, p. 494 (name only).
1900. *Dipterus uddeni* C. R. Eastman, Journ. Geol. **8**, p. 37, text-fig. 5.
1907. *Dipterus uddeni* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 160, pl. 4, figs. 3, 4.

This species, which is proemial for the genus in the Devonian rocks of the western hemisphere, is founded upon a unique lower dental plate obtained by Professor Udden, in whose honor it is named, from the base of the Cedar Valley limestone (corresponding to the Hamilton stage of the Erian) near Buffalo, in Scott county, Iowa. Characterized especially by its

† June 28, 1907 (n. s. **25**, p. 1005).

coarse tuberculation and small number of radiating costae, the type is a persistent one, reappearing with slight modifications in *D. mordax* of the Upper Devonian. In the same way, the laterally ridged Upper Devonian species, hereinafter described under the names of *D. costatus* and *D. digitatus,* are probably to be regarded as the lineal descendants of *D. calvini,* which occurs near the summit of the Cedar Valley limestone.

The holotype of *D. uddeni* has a total length of 36 mm, is subtriangular in form, moderately convex, and remarkable for the paucity of its denticulated ridges. These are but four in number, and radiate outwards from the postero-internal angle, which is worn smooth by use. The anterior row of denticles, and inner moiety of the remaining rows are also considerably worn; but in the outer moiety of these rows the denticles are acutely conical, of large size, and well separated. There is a gradual increase in size of all the denticles from the inner margin outwards. The coronal surface is finely punctate.

Formation and locality. Base of the Cedar Valley limestone; Buffalo, Scott county, Iowa.

Dipterus calvini Eastman.

(Plate II, Fig. 1)

1899. *Dipterus calvini* J. A. Udden, Ann. Rept. Iowa Geol. Surv. **IX,** p. 283, (name only).
1900. *Dipterus calvini* C. R. Eastman, Journ. Geol. **8,** p. 38, text-fig. 7.
1907. *Dipterus calvini* C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 160, pl. 4, fig. 1.

Lower dental plate elliptical in outline, and moderately convex in an antero-posterior direction. Eight tuberculated ridges extend from the outer margin to about the middle of the plate, the two anterior ones larger than the rest and elevated into a slight fold. Coronal surface considerably worn in the holotype, and external margin partially broken. Tubercles conical and well separated, except those of the two anterior ridges, which are coalesced and worn on their summits. Total length of plate 3 cm.

This species, like the preceding, is founded upon a unique dental plate from the Cedar Valley limestone of Iowa. It comes, however, from a higher level, locally known as the "Euom-

phalus'' bed, which lies about eight feet below the summit of the Middle Devonian in Muscatine county.

Formation and locality. Cedar Valley limestone; Fairport, Muscatine county, Iowa. A description of the local section whence the holotype was obtained is given by Professor Udden in the Annual Report of the Iowa Geological Survey for 1898 (IX, p. 283).

Dipterus costatus Eastman.

(Plate II, Fig. 8)

1900. *Dipterus costatus* C. R. Eastman, Journ. Geol. **8**, p. 39, text-fig. 4.
1907. *Dipterus costatus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 161, pl. 4, fig. 9.

Dental plates agreeing in size and general outline with *D. calvini,* but having fewer and more widely separated coronal ridges, which disappear before reaching the middle of the plate. The distinguishing feature of this species consists in the elevated acute ridge extending along the entire length of the inner border and separated from the remaining tuberculated ridges by a broad longitudinal furrow. This ridge appears to be made up of three coalesced costae, of which the third counting from the inner margin is the largest. The two innermost costae are so faint as to be almost imperceptible against the steep face of the main ridge. The latter shows no evidence of having been tuberculated, although faint and partially coalesced tubercles occur on the five remaining costae. A number of examples of this species, including the type, are preserved in the Museum of Comparative Zoology at Cambridge, Mass.

Formation and locality. State Quarry beds (Upper Devonian); near North Liberty, Johnson county, Iowa.

Dipterus mordax Eastman.

(Plate II, Figs. 4, 5; Plate VII, Figs. 5-9)

1900. *Dipterus mordax* C. R. Eastman, Journ. Geol. **8**, p. 39, text-figs. 6, 8.
1907. *Dipterus mordax* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 161, pl. 4, figs. 5, 6.

Lower dental plates attaining a length of over 3 cm, coronal surface gently convex, with six rows of very large, discrete, conical or rounded tubercles which extend from the outer mar-

gin for a variable distance toward the posterior angle; the two posterior rows often rudimentary. Some of the tubercles, when worn by use or by post-mortem abrasion, become elongated in the direction of the ridges to which they belong, others in an oblique direction. The coarseness of tuberculation, in proportion to the size of the plates, is greater than in any other described species. Apparently some diminution in number of tubercles, coincident with increase in size, takes place in the teeth of adult or old individuals.

Upper dental plates of the *D. flabelliformis* type do not differ materially from the lower as regards outline, or size and number of tuberculated ridges, but their substance is usually much thinner, the functional surface is nearly or quite plane or in some cases even concave, and in the effete condition it becomes worn down almost perfectly smooth. In well preserved specimens the marginal contour is seen to be ovoid or subtriangular, like that of the lower dental plates, but the majority of examples have the external margin deficient, owing to wear, injury or poor preservation, and accordingly in that respect present deceptive appearances. Precisely the same faulty condition is also true of the majority of "flabelliform" upper dental plates belonging to *D. nelsoni,* as witness Newberry's figured specimens (Monogr. U. S. Geol. Survey, vol. *16*, pl. 27, figs. 21, 21*a*). With the aid of an extensive suite of material illustrating the accidental variations of this nature common to both species, one is justified in assigning a commensurate range of diversity to other Dipterine species that are affected by the same causes. This principle has been adopted in preparing the following descriptions.

Formation and locality. State Quarry beds (Upper Devonian); near North Liberty, Johnson county, Iowa.

Dipterus digitatus, sp. nov.

(Plate II, Fig. 6; Plate VII, Figs. 16-25)

1907. Palatal dental plate of undescribed Dipterine species, C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 202, pl. 4, fig. 8.

Lower dental plates very similar to those of *D. costatus,* but with more elevated and convex functional surface, and more numerous nearly rectilinear, tuberculated costae, which extend

only about midway between the external margin and the postero-internal angle. As in *D. costatus,* the inner longitudinal margin is formed by a strong tumid ridge which apparently owes its origin to the fusion of several costae, one of which is more prominent than the others, sometimes bifid, and usually very distinct even in worn specimens. By means of the ridged condition of the internal (ental) margin, both the present species and the closely similar *D. costatus* are readily distinguished from worn examples of *D. mordax.* The character just mentioned is common to both upper and lower dental plates, and is if anything more conspicuously developed in the former. Plates of the upper dentition are not to be distinguished from their opposites in the lower jaw except by the extreme flatness of their functional surface. They are, however, easily separated from the corresponding plates of *D. mordax* by their relatively greater length, shorter costae or rows of tubercles, whose appearance has suggested the specific title, and the prominent inner longitudinal ridge already indicated.

A typical example of an upper dental plate belonging to this species has been figured in another place (Memoir 10 of the New York State Museum), unaccompanied, however, by any descriptions; and the same specimen is re-figured in the present volume together with a series of teeth illustrating the upper and lower dentition. Figures 20-23 of Plate VII are examples of the former, and Figures 16-19 and 25 of the same plate are examples of the latter. The present species, and alike *D. costatus,* are regarded as lineal descendants of forms like *D. calvini,* and a similar relation is postulated between the more strongly tuberculated State Quarry Dipterines and the Middle Devonian *D. uddeni.*

Dipterus pectinatus, sp. nov.

(Plate II, Figs. 2, 7; Plate VII, Figs. 10-15)

1907. Mandibular and palatal dental plates of undescribed species of Dipterus. C. R. Eastman, Mem. N. Y. State Museum, **10**, p. 202, pl. 4, figs. 2, 7.

Dental plates of small size, relatively shorter in an antero-posterior direction than any of the foregoing species, and resembling *D. mordax* in the comparative coarseness of its tuber-

culated ridges, whose course may be either radiating or slightly curved. Lower dental plates moderately convex; upper plane or slightly concave, with usually about eight costae extending nearly or quite to the postero-internal angle, often radiating from it in fan-shaped fashion (as in the original of Plate VII, fig. 12).

The dental plates here assembled under the head of a distinct species are among the rarer examples of Dipterine teeth found at the old State Quarry workings in Johnson county, and are seldom perfectly preserved. Two that are rather better than the average have already been figured, but not described, in a memoir on the Devonic Fishes of the New York Formations, and are again illustrated in the present Report (Plate II, figs. 2, 7). The originals of these figures may be regarded as typical of the mandibular and palatal dental series respectively, of the species now definitely established. The same specimens occupy the center of the third row in Plate VII, and adjoining them on either side are other examples of the upper and lower dentition, which may be instructively compared with the types of accompanying species. The approximate uniformity in size and constancy of expression exhibited by all the specimens at our disposal do not permit us to envisage them merely as the young of some other form. Nevertheless, a not remote similarity to the type of *D. mordax* is not to be denied.

Formation and locality. State Quarry beds (Upper Devonian); near North Liberty, Johnson county, Iowa.

Dipterus nelsoni Newberry.

(Plate II, Figs. 11, 11*a*; Plate VII, Figs. 1-4)

1887. *Dipterus nelsoni* H. S. Williams, Bull. U. S. Geol. Surv. no. 41, p. 62, pl. 3, fig. 1 (*ex* Newberry MS.).

1887. *Dipterus ? laevis* or *D. alleghaniensis* H. S. Williams, *Ibid.*, pp. 63, 91, pl. 3, fig. 2.

1889. *Dipterus nelsoni* J. S. Newberry, Monogr. U. S. Geol. Surv. **16**, p. 89, pl. 27, figs. 19-20.

1889. *Dipterus flabelliformis, laevis, minutus* and *quadratus*, *Ibid.*, pp. 90, 91, 284, pl. 27, figs. 21-26.

1900. *Dipterus nelsoni* and *D. flabelliformis*, C. R. Eastman, Journ. Geol. **8**. p. 37.

1907. *Dipterus nelsoni* and *D. flabelliformis*, C. R. Eastman, Mem. N. Y. State Museum, **10**, p. 163, pl. 4, figs. 13, 14.

Lower dental plates subtriangular in outline, functional surface more or less transversely arched and marked by eight very strong subacute ridges, rather coarsely tuberculated or denticulated in the unworn condition, but becoming smooth in the effete. The antero-internal margin is formed by the most prominent of these ridges, which is at the same time more produced in front and more sinuous than the others, and sometimes more coarsely tuberculated. Slightly worn specimens often have the denticles bordering the external margin of large size, conically pointed and well separated.

Upper dental plates agreeing in outline with the lower, and having an equal number of tuberculated costae which radiate outwardly in gently sweeping curves from the postero-internal angle (*D. flabelliformis* type). Triturating surface nearly or quite flat, sometimes even slightly concave. Owing to the tenuity of the upper plates, their delicate external margin is very liable to injury, and for that reason is seldom preserved entire. The best examples known to Newberry, those figured in Plate 27, figures 21 and 21*a* of his *Monograph on Palæozoic Fishes*, are defective in this respect, hence it is scarcely to be wondered that their association in the same mouth with the type of *D. nelsoni* was entirely unsuspected by him. The teeth designated as *D. flabelliformis* by this author are merely imperfect specimens of the same form as is shown in Plate VII, fig. 1 of the present work; and the latter clearly reveals itself as a palatal dental plate agreeing in all essential respects with the mandibular elements figured alongside it in the same row (Plate VII, figs. 2-4). One of the latter, the original of figure 2, is the actual type serving for Newberry's figure and description of *D. nelsoni*. Collected in the first instance by the late Professor Beecher, it is now the property of the Peabody Museum at Yale University, and has been generously loaned for study by Professor Charles Schuchert, of that institution. The remaining examples of this species figured in Plate VII belong to the collections of the Museum of Comparative Zoology. All are from the Chemung group of Warren county, Pennsylvania. In the same beds with these teeth are found numerous punctate scales, ceratohyal bones and other detached hard parts, including the calcified

labial cartilage known as *Ganorhynchus beecheri,* all of which very possibly pertain to one and the same species. Somewhat similar calcified bodies of the "Ganorhynchus" type occur in the Cedar Valley limestone near Waverly, Iowa, in the Middle Devonian of the Eifel District, and in the Murrumbidgee Devonian limestone of New South Wales. One excellent example from the Australian locality has been described by R. Etheridge, Jr., in natural position with the head shield, the plates of which are arranged in much the same fashion as in the Canadian genus Scaumenacia.*

Formation and locality. Chemung beds; Warren county, Pennsylvania, and Alleghany county, New York. Probably an immigrant from the Upper Devonian "Dakotan Sea".

Dipterus fleischeri (Newberry).

(Plate II, Fig. 16)

1897. *Ctenodus fleischeri* J. S. Newberry, Trans. N. Y. Acad. Sci. **16,** p. 302, pl. 24, fig. 25.
1907. *Dipterus fleischeri* C. R. Eastman, Mem. N. Y. State Museum, **10,** p. 162, pl. 7, fig. 2.
1908. *Dipterus fleischeri* L. Hussakof, Bull. Amer. Mus. Nat. Hist. **25,** p. 52.

Upper dental plates thin, slightly concave, triangular in outline; coronal surface traversed by six rows of rounded obtuse tubercles increasing in size from the posterior angle outwards. At least the anterior or innermost rows of tubercles are continuous almost to the postero-internal angle.

Besides the type, only one other example of this species has yet been brought to light. This is a large upper dental plate, preserved in counterpart, now the property of the New York State Museum. It is from the Catskill of Delaware county, New York, and being more complete than Newberry's original, we present a figure of it herewith. Its relations are evidently with *D. uddeni* and *D. mordax,* as shown by the small number of coarsely tuberculated costae; but in size it is much larger, the length of the inner margin being fully 5 cm.

*Etheridge, Jr., R., The cranial buckler of a Dipnoan fish, probably Ganorhynchus, from the Devonian beds of the Murrumbidgee River, New South Wales. Rec. Austral. Museum, 1906, **6,** no. pp. 129-132, pl. 28.

Formation and locality. Catskill sandstone (Chautauquan); Tioga county, Pennsylvania, and Delaware county, New York.

Dipterus sherwoodi Newberry.

1875. *Dipterus sherwoodi* J. S. Newberry. Rept. Ohio Geol. Surv., Palæont. **2**, pt. 2, p. 61, pl. 58, fig. 17.
1889. *Dipterus* (*Ctenodus*) *sherwoodi* J. S. Newberry. Monogr. U. S. Geol. Surv. **16**, p. 118, pl. 27, fig. 32.
1907. *Dipterus sherwoodi* C. R. Eastman, Mem. N. Y. State Museum, **10**, p. 162.
1908. *Dipterus sherwoodi* L. Hussakof, Bull. Amer. Mus. Nat. Hist. **25**, p. 52.

Of this species no other examples are known but the type specimen, which is imperfect. In the text of Newberry's monograph, this is determined as "apparently one of the upper palate teeth of a species of Dipterus," but in the explanation of figures it is identified as a mandibular dental plate. It agrees with the preceding species in having a coarse tuberculation and very few ridges, some of them indistinct. The tubercles themselves are stated to be "somewhat compressed laterally, rounded, smooth, and blunt at the summit."

Formation and locality. Catskill sandstone (Chautauquan); Tioga county, Pennsylvania.

Dipterus murchisoni Pander.

(Plate II, Fig. 10)

1858. *Dipterus murchisoni* C. H. Pander, Ctenodipt. devon. Systems, p. 23, pl. 7, figs. 2-4.
1900. *Dipterus murchisoni* C. R. Eastman, Centralbl. für Mineral. 1900, p. 177.

It is of interest to note the present species in this connection on account of its geographical distribution and undoubted marine habitat, in which latter respect it agrees with State Quarry Dipterines, and differs from American Chemung and Scottish Old Red Sandstone species. Apparently indigenous in the Russian Middle Devonian, where it is accompanied by Ptyctodus, Arthrodires and Crossopterygian ganoids, it takes part also in the somewhat similar and nearly contemporaneous assemblage found in the Eifel District, in Rhenish Prussia. The single mandibular plate represented in Plate II, Fig. 10 of the present work was derived from the Middle Devonian of Bern-

dorf, in Rhenish Prussia, and belongs to the Schulze collection in the Museum of Comparative Zoology at Cambridge.

Other fragmentary Dipterine remains are found in the same locality, in particular those examples of calcified labial cartilage which were recognized by Traquair as belonging to some unknown genus allied to Dipterus, Ctenodus, etc., and upon the evidence of which he framed the provisional genus Ganorhynchus. It may be that several genera possessed labial cartilage of this nature, although it does not occur in Dipterus proper, and has not hitherto been observed in Scaumenacia. Certain it is, however, that the arrangement of cranial roofing plates in the Australian species described as *Ganorhynchus suessmilchi,** is remarkably suggestive of Scaumenacia, so much so in fact that one is obliged to assume that a form of lip cartilage not unlike that of Ganorhynchus was actually present in the Canadian genus, but has failed as yet of recognition. A single tooth of Dipterus, doubtfully determined as *D. valenciennesi,* is recorded by Jaekel† from the marine Middle Devonian of Rhineland, and another, said to be distinct from any described species, is reported by Fourmaier‡ from the Upper Devonian of Bilstein, in Belgium.

Formation and locality. Middle Devonian; Berndorf, Eifel District.

Genus CONCHODUS M'Coy.
(Syn. Cheirodus Pander *non* M'Coy)

A genus known only by detached dental plates which exhibit intermediate characters between Dipterus and Synthetodus. The plates agree in general form with those of Dipterus, and were apparently arranged in the mouth after the same fashion; but their functional surface is almost or quite smooth, and with but few short and obsolescent radiating ridges at the outer border. In some species the vestigial plicae are represented by two or three short rows of coarse tubercles. Mandibular dental

* R. Etheridge, Jr., Cranial buckler of a Dipnoan fish from the Devonian of New South Wales. Records Australian Museum 1906, **6**, pp. 129-132, pl. 28.

† Jaekel, O., Abstract in Zeitschr. deutsch. geol. Ges. 1899, **51**, pp. 37, 38 Protokoll.

‡ Fourmaier. P., Decouverte de Dipterus à Bilstein. Ann. Soc. Géol. Belge. etc. 1899, **26**, p. cxiii.

plates with convex, upper dental plates with concave or flattened functional surface. As shown by the slope and contour of their inner margin, the two lower dental plates (which correspond to the fused lateral elements in Synthetodus) were not in contact with each other along the median line, the resemblance being with Dipterus in this respect.

The type species of this genus, *C. ostraeformis* M'Coy, is founded upon a single upper dental plate from the Old Red Sandstone conglomerate of Scat Craig, Elgin, described by M'Coy in 1848, and stated by him to "resemble the inside of a plicated oyster."* In the same year the genus "Chirodus" was also established by M'Coy upon the evidence of a mandibular dental plate with rudimentary plications of the oral surface, from the Lower Carboniferous limestone of Derbyshire. There is no valid reason for supposing with Pander that these two forms of Ctenodipterine dentition, separated as they are by a considerable geological interval, are generically identical. The relations, therefore, of the smooth dental plates described by Pander† under the name of *Cheirodus jerofejewi,* from the Devonian of Northwestern Russia, are best expressed by transferring this species to Conchodus, as was first proposed by Smith Woodward. M'Coy's term is accordingly to be understood as a convenient provisional designation for Dipterus-like dental plates in which the usual radiating plications have become atrophied or greatly reduced.

Now it is interesting to note that the Russian species described by Pander in his monograph on Ctenodipterines, and further illustrated by Eichwald, in his *Lethæa Rossica,* offers sufficient points of resemblance with the smooth dental plates shown in Plate VIII of the present volume as to suggest the propriety of including them all in the same genus, for which it is proper to retain M'Coy's provisional designation of Conchodus. This procedure is accordingly adopted, and the new specific title of *C. variabilis* is proposed for the originals of Plate VIII, with the exception of those represented in Figures 16, 20, 29 and 34, which are probably worn examples of Synthetodus. Other exam-

* Ann. Mag. Nat. Hist. 1848, ser. 2, **2**, p. 311.

† Ctenodipterinen des devonischen Systems. St. Petersb. 1858, p. 33, pl. 6, figs. 15-22.

ples of the same species have been figured but not described in Volume VII of the Survey Reports (1896), pl. iv. figs. 27-32, and after pointing out their resemblance to the forms described by M'Coy and Pander it was remarked that these teeth "are seen to pass by gradual transitions into true Dipterid forms." (*tom. cit.*, p. 113.)

A comparison of the dental structures shown in Plates VIII and IX of the present work may suggest the query whether or not these may be the upper and lower dental plates of one and the same species, the paired lateral elements being fused in the upper pavement to form a single compound plate, but remaining discrete and separated from each other in the lower jaw. This interpretation was at one time adopted by the writer as perhaps the most plausible working hypothesis, and at the same time the simplest. The inclusion of all these smooth dental plates under a single species seemed to be further sanctioned by the fact that no differences in microscopic structure could be observed upon comparison of a large number of thin sections.

Professor Calvin, however, who possesses a magnificent collection of State Quarry fish-teeth, remained consistently opposed to the theoretical association of parts just indicated, and preferred to regard the originals of Plates VIII and IX as belonging to two distinct categories which required generic separation. A recent critical review of the arguments in favor of a separation has convinced the present writer of the entire reasonableness of Professor Calvin's view, and it is accordingly adopted as the one most likely to be correct. There are in fact, two difficulties which effectually prevent us from identifying the originals of Plate VIII (apart from Figs. 16, 20, 29 and 34) as the mandibular dental plates of Synthetodus, and these may be stated as follows:

(1) Although the majority of Dipnoan teeth shown in Plates VIII and IX have a convex functional surface, and are thus, after analogy with Dipterus, theoretically assignable to the lower jaw, yet there are numerous other teeth agreeing with the types represented in each plate referable to each of the categories here represented, yet differing from the originals of these plates in that their functional surface is flattened or even slight-

ly concave. Assuming, therefore, that the convex teeth of each type represent the mandibular dental plates, corresponding to these are two other types of flat or concave teeth, which must be supposed to represent the upper or palatal dentition.

(2) In the Synthetodus type of Dipnoan dentition radiating plications of the functional surface are absent, nor are any vestiges to be observed of rows of tubercles along the ectal margin. On the other hand in the Conchodus type of dentition plications of this nature occur, although often indistinct, and both upper and lower dental plates frequently display obsolescent rows of tubercles. Owing to these constant differences it appears more prudent to maintain the distinctness of the two types, at the same time admitting the probability that they are serially related, one having been derived as a modification of the other. None of the examples of *Conchodus variabilis* chosen for illustration in Plate VIII show the external plications very distinctly along the external margin, but a few still preserve traces of the obsolescent rows of tubercles. For instance, the terminal projection to be seen in the originals of Figures 4 (inverted), 13, 15, 26, 28, 33, etc., is plainly a remnant of a tuberculated ridge, and other specimens might have been selected for displaying this character more perfectly.

Conchodus variabilis, sp. nov.

(Plate VIII, with the exception of Figs. 16, 20, 29, 34)

Founded upon Dipterus-like dental plates of small or moderate size, with smooth or nearly smooth functional surface and only vestigial remnants of tuberculated ridges along the outer margin; the number of these plications or short rows of indistinct tubercles rarely exceeds one or two. Functional surface of mandibular dental plates strongly convex, that of palatal dental plates flat or slightly concave.

Hundreds of specimens of smooth, elongate-ovoidal, more or less strongly convex dental plates agreeing in form with the majority of those shown in Plate VIII, but displaying, nevertheless, a wide range of variation, have been collected from the "fish-bed" stratum at the famous State Quarry locality near North Liberty, Iowa. At one time thought to represent the lower

dentition of Synthetodus, they are now regarded with much greater likelihood, for the reasons stated above, as belonging to a distinct genus, Conchodus, in which the characteristic features of Dipterus have become well-nigh obliterated. The arrangement of dental plates in the mouth may be presumed to have been the same as in Dipterus, and the same means are available for distinguishing between upper and lower dentition. A position may be assigned to this form intermediate between Dipterus and Synthetodus.

Formation and locality. Upper Devonian, Johnson county, Iowa.

Genus SYNTHETODUS.

An imperfectly definable genus, known only by remains of the dentition. Apparently the upper and lower dental organs consisted each of three coalesced plates—a pair of ovoid lateral, and a smaller azygous symphysial element. The paired elements are evidently homologous with the single pair normally occurring in Ctenodipterines, agreeing as they do with the latter in microscopic structure, but differing from them in that the functional surface is entirely smooth, without even vestigial tubercles or costae. The azygous element is not known to occur elsewhere among Palæozoic Lung-fishes, and may possibly be indicative of the Sirenoid order of Dipnoans.*

Synthetodus trisulcatus Eastman.

(Plates IX and XI, *pars*)

1896. *Synthetodus trisulcatus* C. R. Eastman, Ann. Rept. Iowa Geol. Surv. **VII,** p. 112, pl. IV, figs. 1-26.

---

* As to the possibility of this order being represented in the Palæozoic, compare the following suggestive hint of Newberry, found at page 88 of his Monograph of 1889:

"The group designated by the name of *Dipterus* is so abundant and so well preserved in the Devonian rocks of Scotland that its entire structure has been fully made out, and we find that it was a fish having a tesselated cranium, the palate teeth already described, and a fusiform body covered with strong, enameled, punctate scales. In the Carboniferous and still higher strata, on the contrary, the fishes which carried the fan-shaped dental plates must have been somewhat differently constituted, for neither in the Old nor in the New World has anything like the complete form of the fish been made out. In the lagoons of the coal-marshes of England and Ohio, where the circumstances were favorable for the preservation of even delicate structures, the teeth, usually dismembered, but occasionally attached to the palato-pterygoid and the splenial bones, and portions of the tesselated cranium, were the only parts preserved; while, as yet, in the higher strata nothing but the teeth have been found."

Complete dentition in upper and lower jaws consisting apparently of a single compound plate, each composed of one median and two laterally disposed pieces, the sutures between them deeply insunken in the form of a trifid sulcus in immature and unworn examples, but becoming more or less obliterated in worn and effete specimens. Functional surface as a whole moderately convex, apart from the sulci referred to, and perfectly smooth and polished throughout, without even vestigial traces of denticulate ridges.

Great numbers of the fused dental plates belonging to this species have been obtained from a comparatively thin cherty layer at the old State Quarry near North Liberty, Iowa, where they rival the detached tritors of Ptyctodus in abundance. Like the latter, too, they exhibit a highly diversified aspect attributable to the effects of wear during life, post-mortem abrasion, chemical corrosion, and other familiar deforming agencies. In young stages, sutures between the component parts are tolerably distinct; but as the triturating surface becomes worn with use, and is replaced by fresh secretion from below, the sulci become shallower, fainter, and finally all but obliterated in effete examples. An endless series of individual variations is occasioned by slight differences in the hardness of the several parts of the functional surface, and the interaction of upper and lower dentition accentuates these irregularities. In this way are to be explained the circular or elongate median concavities seen in worn teeth where the longitudinal sulcus has been broadened. Very often these shallow depressions are bounded along the sides, sometimes also in front, by obtuse ridges; and not infrequently the forward part of the central excavations referred to is marked by two well separated small circular pits (as seen in Plate IX, Figs. 31, 34, 36, 38, etc.).

Means are lacking for satisfactorily distinguishing between upper and lower dental pavements, hence it is safe to affirm that the compound plates of opposite jaws were constructed after essentially the same pattern. A glance at the accompanying illustrations will satisfy one as to the extremely diversified appearance presented by the general run of specimens found at the typical locality.

Formation and locality. State Quarry beds (Upper Devonian); Johnson county, Iowa. Sweetland Creek beds (Upper Devonian); Muscatine county, Iowa. The occurrence of fish-remains at the latter locality is reported by Professor J. A. Udden in volume IX, page 302, of the Iowa Survey Reports (1898).

Synthetodus calvini, sp. nov.

(Plate II, fig. 19; Plate X; Plate XI *pars;* Plate XII)

1907. Undescribed Dipnoan dental plate, C. R. Eastman, Mem. N. Y. Mus. **10,** p. 203, pl. 4, fig. 15.

Dental pavement attaining a somewhat larger size than in the preceding species, and differing in that the three constituent pieces of upper and lower dental plates respectively are more intimately fused and non-sulcate, or with only indistinct sulci. The functional surface above and below is quite smooth, gently arched in a transverse direction, but becoming more or less tabular in the worn condition, and sometimes developing a low rounded eminence in the median portion anteriorly.

Under this species are included the larger, more squarish, flattened and tabular dental pavements of the same general pattern as in the type species, but whose tripartite division is obscured, owing to the more complete fusion of the median azygous and paired lateral elements, with consequent effacement of sutural depressions. Well preserved specimens are of tolerably uniform appearance, but amid the inexhaustible series of worn, corroded and water-rolled fragments obtained at the State Quarry fish-bed, the tabular plates display equal diversity with the rest. Such close intergradations exist among them as to render it impossible to recognize more than a single species besides the type, although until one has examined them closely and attempted to define their limits it is difficult to believe that there are not several. The writer himself was of the latter opinion when the remains were first brought to light by Professor Calvin and his students. The microscopic structure of the two species of Synthetodus here recognized is identical in all respects with that of Dipterus.

In view of the abundance of *S. calvini* and *S. trisulcatus* within a limited area of the Iowa Upper Devonian, it is indeed surprising that similar dental plates have not been brought to light in other regions of the globe, either from the same, or from earlier or later horizons. With the possible exception of the genera Conchodus and Cheirodus as defined by M'Coy, the latter occurring in the Lower Carboniferous,* it does not appear

FIG. 34.

Fig. 34. *Dipterus valenciennesi* Sedgw. & Murch. Lower Old Red Sandstone; Orkney. Well preserved headshield showing cranial roofing plates and sensory canals. x 1-1. Original in Yale Museum.

* The so-called *Conchodus plicatus*, described by Dawson from the Coal Measures of Nova Scotia, is regarded by Smith Woodward as having been founded upon an abraded dental plate of Ctenodus.

that any other variations of smooth Dipterine dental plates have been discovered. Moreover, the only known occurrence of the Synthetodus type is at two limited localities, the State Quarry and Sweetland Creek "fish-beds", near what was formerly the south-eastern terminus of the Dakotan Sea (*cf.* Plates XV, XVI, after Schuchert).

Formation and locality. State Quarry and Sweetland Creek beds (Upper Devonian); Johnson and Muscatine counties, Iowa.

Genus SCAUMENACIA Traquair.

Body laterally compressed, covered with very thin scales of moderate size. Dermal cranial roof-plates fewer than in Dipterus, those in the occipital region traversed by an Arthrodiran-like sensory canal system. Anterior margin of headshield evenly rounded, possibly terminating in front in Ganorhynchus-like labial cartilage. Dentition "ctenodont", the dental plates marked by ridges of well-separated conical tubercles. Paired fins acutely lobate; anterior dorsal arising far forwards, and separated from the long posterior dorsal by a distinct interval. Caudal fin heterocercal; anal small, separate.

This genus, represented by the solitary species, *S. curta* (Whiteaves), and known only from a single locality in the Upper Devonian of Canada, is especially interesting on account of the information it affords in regard to cranial and body characters.* The median series of cranial roof-plates bears comparison with primitive Arthrodires. The lateral series are less numerous than in Dipterus, those in the orbital region are symmetrically arranged and correspond collectively to not more than two plates in typical Arthrodires. In text-figures 34 and 35 are presented for comparison illustrations showing the arrangement of cranial roof-plates in Dipterus and Scaumenacia respectively. Their not too remote correspondence with the patterns shown in text-figures 28 and 29 (*ante,* p. 197) is not only suggestive, but regarded as very significant from the point of view of interrelationships.

* It should be noted, however, that very similar cranial characters are presented by the Australian form described as *Ganorhynchus suessmilchi* Etheridge, which is undoubtedly very closely related to Scaumenacia, if indeed not identical with it. See the foregoing description of *Dipterus murchisoni* (p. 226).

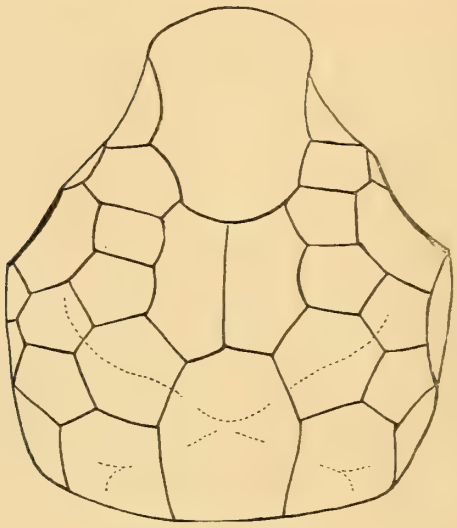


FIG. 35.

Fig. 35. *Scaumenacia curta* (Whiteaves). Upper Devonian; Scaumenac Bay, Province of Quebec. Restoration of headshield based upon a nearly complete individual belonging to the Yale Museum. Compare sensory canals with those of Dipterus, as shown in headshield figured in preceding illustration. x 1-1.

Subclass **TELEOSTOMI.**

The great group of fishes commonly known under the designations of Ganoids and Teleosts and first recognized by Owen as a single subclass, Teleostomi, makes its appearance in the Lower Devonian, but does not really become significant until the Carboniferous. The Crossopterygian order, which predominates during the Devonian, is somewhat abundantly represented toward the close of that system in this country; but except in Canada, all the remains are extremely fragmentary, consisting of detached scales, teeth, plates, and in two or three instances of imperfectly preserved skeletons. The most important American genera are Holoptychius, Sauripterus, Onychodus and Eusthenopteron, but of these the last-named alone has been found in a state bordering upon completeness. Nevertheless, it is possible to frame a tolerably accurate conception of the remaining genera through comparison of their characteristic parts with the admirably preserved skeletons of their foreign representatives, especially those from the Scottish Old Red Sandstone. In this way the detached head plates and bones of the shoulder girdle belonging to Onychodus, for instance, acquire

much greater significance than would otherwise be possible. The osteology of various typical members of the Crossopterygian order is now quite satisfactorily known, as the result especially of the researches of Pander,* Huxley† and Traquair. To the last named author‡ also, we owe our principal knowledge of the structure of Palæoniscid fishes, these being the only Devonian representatives of the next higher order of Teleostomes, or Actinopterygii.

Order **CROSSOPTERYGII.**

Pectoral fins lobate, with a large basal portion covered with scales, more or less fringed with dermal rays; the ventrals usually much like the pectorals, always abdominal in position; caudal fin diphycercal or heterocercal. Skeleton more or less ossified, body covered with rhombic or circular ganoid scales. A pair of large jugular plates developed in place of branchiostegals; no fulcra. Dorsal fins two, or a single one divided into many finlets.

Attention has frequently been called to the fact that the earliest members of this order, especially those with acutely lobate paired fins, bear a considerable resemblance to Dipnoans, and the descent of the latter has even been traced by Dollo and others to the Crossopterygii. These fishes are further interesting in that they are commonly looked upon as ancestral to amphibians and higher vertebrates. During the evolutionary history of the order, the following structural modifications are observable, as noted by Smith Woodward: (1) The paired fins become abbreviated; (2) the supports of the median fins tend towards reduction to a single series; (3) these supports sometimes become correlated in part with the dermal fin rays; and (4) there is sometimes degeneration in the external armor of the head and opercular region, some plates being fused together, others becoming lost. The reduction in the complexity of the mandibular ramus is also especially noteworthy.

* Pander, C. H. Ueber die Saurodipterinen, Dendrodonten, Glyptolepiden, und Cheirolepiden des devonischen Systems. St. Petersburg, 1860.

† Huxley, T. H. Illustrations of the Structure of the Crossopterygian Ganoids. Mem. Geol. Sur. United Kingdom, 1866. Reprinted also in the Scientific Memoirs of T. H. Huxley, Suppl. volume, 1903.

‡ Traquair, R. H., Ganoid Fishes of the British Carboniferous Formations. Monogr. Palæontogr. Soc. 1877, 1901, and 1907.

Family **HOLOPTYCHIIDAE.**

Body fusiform, with cycloidal, deeply overlapping scales, more or less enamelled. Head and opercular apparatus with well developed membrane bones; parietals large and separate; frontals separate, not fused into a continuous plate with adjoining elements; no parietal or frontal foramen; interoperculum absent; jugular plates comprising one large pair, flanked on either side by a lateral series. Dentary bone of mandible thin and deep, bearing a series of small teeth, and with well developed infradentaries, much bent inwards below; an inner series of few, large, broad shuttle-shaped bones, each supporting a "laniary" tooth; a pair of similar teeth on the roof of the mouth, but the marginal upper dentition feeble. Teeth conical, with a very small pulp cavity, of which the walls exhibit complex infoldings, appearing closely intertwined when viewed in transverse section, these producing superficial vertical flutings. Pectoral fins acutely lobate, pelvic fins either acutely or obtusely lobate; two remote dorsal fins; anal fin single; caudal fin diphycercal or heterocercal. (Woodward.)

The foregoing family definition, which we have extracted from Smith Woodward, is based chiefly upon the structural characteristics of the typical genus Holoptychius, well preserved specimens of which occur plentifully in the Scottish Old Red Sandstone, and have been obtained also from Belgium and Russia. With the exception of the closely related *Glyptolepis quebecensis* Whiteaves,* by some writers included with Holoptychius, no member of this family is represented in the North American Devonian by completely preserved remains, and by far the greater number of species is founded upon detached scales. The teeth described by Leidy under the name of *Apedodus priscus*,† from the Catskill of northern Pennsylvania, do not appear to differ from those of Holoptychius by any recognizable characters. On the other hand the accompanying *Saurip-*

* Whiteaves, J. F., Trans. Roy. Soc. Canada, 1889, vol. **6**, 4, p. 77, pl. 5, fig. 4.

† Leidy, J., Journ. Acad. Nat. Sci. Philad. 1856, ser. 2, vol. **3**, p. 164, pl. 17, figs. 5, 6.

terus taylori Hall,* founded on portions of a fish closely similar to Holoptychius, is proved by the less complicated structure of the teeth and obtusely lobate condition of the pectoral fins to agree more closely with Rhizodonts, and is definitely assigned to that family by Smith Woodward.

The most commonly occurring scales of Holoptychius in the Devonian of this country, and at the same time the most widely distributed, are those of *H. giganteus* Agassiz, and *H. americanus* Newberry. They are found not only in the Catskill of the Appalachian region (the last-named form occurs in the Chemung as well), but also in the Upper Devonian of southwestern Colorado. The scales of *H. giganteus* are very large, those of the abdominal region externally ornamented with closely set, thick, irregularly tortuous longitudinal ridges, often branching and interrupted, more or less broken up into rounded tubercles posteriorly. In *H. americanus* the ridges are subparallel, strong, flexuous and sometimes inosculating, but not disintegrating into tubercles nor interrupted to any appreciable extent. *H. halli* Newberry, from the Catskill of Delhi, New York, is known by a unique example which displays a portion of the trunk, and is covered with smaller and thinner scales than those of the foregoing species. Other scales have been described from the Catskill of Pennsylvania under the names of *H. flabellatus, latus* and *serrulatus* Cope; and from the Chemung of the same State are known *H. filosus* Cope, and *H. granulatus, pustulosus* and *tuberculatus* Newberry. A single scale belonging to an undetermined member of the genus is also reported by H. S. Williams from the Chemung of Wellsville, New York.† Very interesting from a distributional standpoint is the occurrence of Holoptychian scales in the Upper Devonian rocks of East

*Hall, J., Nat. Hist. New York, pt. iv. Geology, 1843, p. 282, text-fig. 130. The type specimen is further noticed by Newberry in his Monograph of 1889, p. 112, and portions of the skeleton are refigured by Dr. L. Hussakof in his "Catalogue of the type and figured specimens of fossil vertebrates in the American Museum of Natural History" (Bull. Amer. Mus. Nat. Hist. 1908, **25**, p. 58, 59).

†Williams, H. S., On the fossil faunas of the Upper Devonian. Bull. U. S. Geol. Surv. no. 4, 1887, p. 78.

Greenland and Spitzbergen, for our knowledge of which we are indebted to Smith Woodward.*

Family **ONYCHODONTIDAE.**

Scales cycloidal, deeply overlapping. Head and opercular apparatus with well developed membrane bones. Dentary bone of mandible thin and deep, bearing a single close series of large conical teeth, flanked by an outer series of very minute teeth; an azygous series of large, more or less recurved teeth attached in front of the symphysis. Teeth plicated only at the base, with a central cavity; dentary teeth tipped only, presymphysial teeth completely enveloped with enamel.

This family is at present known to be represented in the Devonian of Europe and North America by but a solitary genus, Onychodus, whose remains invariably occur in a fragmentary condition. The various bones of the cranial roof and pectoral girdle that have been found suggest a certain resemblance to Holoptychians and Rhizodonts. The tooth structure, however, is simple, and a conspicuous difference exists in the presence of a dentigerous presymphysial bone. The external bones and scales of the type species, *O. sigmoides* Newberry, are ornamented with fine tuberculations, more or less conical and radially grooved. The clavicle is triangular in shape, with relatively large inferior limb; the infraclavicle is without an elongated ascending process. In this species, also, the presymphysial bone is very prominent, its teeth being much larger than those of the dentary. Remains of *O. sigmoides* are not uncommon in the Columbus and Delaware limestones of Ohio, and probably occur also in the Onondaga limestone of LeRoy, New York. A few detached presymphysial teeth not readily distinguishable from this form are also known from the Hamilton of Milwaukee, Wisconsin, an imperfect one of this nature being shown in Plate I, fig. 4; others, with less pronounced curvature and elliptical cross-section are present in the Middle Devonian of the Eifel District. As an example of the latter, a single tooth be-

*Woodward, A. S., Notes on fossil fish-remains collected in Spitzbergen by the Swedish Arctic Expedition, 1898. Bihang till Svenska Vet.-Akad. Handl. 1900, vol. **25**, no. 5, pp. 1-7.—*Idem*, Notes on some Upper Devonian Fish-remains discovered by Prof. Nathorst in East Greenland. *Ibid.* 1900, vol. **26**, no. 10, pp. 1-10.

longing to the Museum of Comparative Zoology at Cambridge is figured for comparison in the same plate (fig. 12).

By far the most abundant of any species of this genus is that which Newberry described under the name of *O. hopkinsi,* occurring typically in the Chemung of Delaware county, New York, but being also represented in enormous quantities in the basal bituminous layer of the Marcellus shale in the same State. The average length is stated by Newberry to be about 2.5 cm. This, together with the considerable stratigraphic interval separating the smaller teeth from *O. sigmoides,* probably furnishes sufficient reason for maintaining them as distinct species. A series of five well preserved presymphysial teeth belonging to *O. hopkinsi,* from the Chemung of Franklin, New York, is shown in Plate I, fig. 3.

An undetermined species of Onychodus seems to be indicated by a few detached plates, teeth and jaw-fragments from the Cedar Valley limestone of Bremer county, Iowa, and the Hamilton of Oran, Onondaga county, New York. A single detached scale from the latter locality, closely resembling those of the type species, is shown in Plate I, fig. 11. Supposed Crossopterygian scales with longitudinally striate ornamentation occur also in the Portage beds of Livingston county, New York. It is possible that some of these may be of Coelacanthid nature, but until other parts of the skeleton are known, their precise determination is impossible.

Suborder **ACTINISTIA.**

The extremely specialized Crossopterygians embraced by this suborder have frequently been cited as furnishing perhaps the most remarkable example of a persistent type that we are acquainted with among fishes, continuing as they do practically unchanged from the Upper Devonian to the close of the Cretaceous. As noted by Smith Woodward, the group has become specialized chiefly by degeneration, one of its characteristic features being "the large symmetrical caudal fin, which exhibits a series of supports directly apposed to the neural and haemal arches, equalling in number both these and the overlapping dermal rays."

The same author remarks further, in his "Outlines of Vertebrate Palæontology," that the group "is also specialized in (i.) the fusion of the bones of the pterygo-quadrate arcade, (ii.) the reduction of the infradentaries to one, (iii.) the reduction of the opercular apparatus to the operculum on each side and a pair of gular plates, (iv.) the loss of the baseosts in the anterior dorsal fin, and (v.) the ossification of the air-bladder." The typical genus Coelacanthus ranges from the Devonian to the Permian inclusive; Undina is the best-known Jurassic genus; Diplurus, with greatly elongated caudal pedicle, is limited to the Trias of this country; and Macropoma occurs in the English and Bohemian Upper Cretaceous.

Family COELACANTHIDAE.

The principal diagnostic features of this family are thus summarized by Professor Bridge in the volume on *Fishes* in the Cambridge Natural History:

"Scales cycloid. Paired fins obtusely lobate. Tail symmetrical but apparently gephyrocercal, usually with a protruding axial vestige of the disappearing terminal part of the tail and of the proper caudal fin. Radialia of the functional caudal lobes agree in number with the contiguous neural and haemal arches and dermal fin-rays (the diagnostic feature of Smith Woodward's *Actinistia*). Proximal radials of the dorsal and anal fins fused into a single, internally forked basipterygium in each fin. Teeth simple. Vertebral column acentrous. The skull presents several interesting features. The hyomandibular and the palato-quadrate bar, for example, are fused on each side into a continuous triangular bone, articulating with the cranium above and with the lower jaw below. The opercular skeleton is reduced to an operculum and two jugular plates. A very singular modification in these fishes is the ossification of the walls of the air-bladder, a structural modification which has no parallel in Fishes except in certain Teleosts (Siluridae and Cyprinidae) in which the organ becomes encapsuled by bone owing to the partial ossification of its walls."

This family, first proposed by Agassiz in the second volume of his *Poissons Fossiles,* (p. 168, 1844), and afterwards greatly restricted by Huxley in two important memoirs of the British Geological Survey (Decades X and XII, 1861 and 1866), is at present understood as comprising not more than six well recog-

nized genera, among which the most satisfactorily known are Coelacanthus proper, Macropoma and Undina. The typical genus enjoys the truly remarkable range from the Upper Devonian to the close of the Palæozoic, and if the evidence of one or two doubtful forms be accepted, possibly even higher; the remaining genera extend throughout the Mesozoic, and exhibit such constancy of structural characters that the family has been frequently cited as one of the most distinct and well defined in the animal kingdom. Huxley, for instance, drew attention to its singular compactness in the following paragraph:*

"The Coelacanthini, as thus understood, are no less distinctly separated from other fishes than they are closely united to one another. In the form and arrangement of their fins; the structure of the tail and that of the cranium; the form and number of the jugular plates; the dentition; the dorsal interspinous bones; the pelvic bones; the ossified air-bladder; the Coelacanthini differ widely from either the Saurodipterini, the Glyptodipterini, or the Ctenodipterini; but, on the other hand, they agree with these families and differ from almost all other fishes, in the same respects as those in which the several families just mentioned have been shown to agree with one another; viz., the number of the dorsal fins, the location of the paired fins, the absence of branchiostegal rays and their replacement by jugular bones."

It will be instructive in this connection to compare the views of the elder Agassiz in regard to the family as originally defined by him, and also regarding Coelacanthus itself, the following passage being taken from Huxley's translation of a portion of pages 168 and 170 of the second part of the second volume of the "*Recherches sur les Poissons Fossiles*":

Agassiz on the "Family of the Coelacanths".

"I unite in this family many genera of an altogether peculiar physiognomy, but with whose true affinities I am, as yet, only very imperfectly acquainted. A remarkable peculiarity which has struck me in most of these fishes is the circumstance that their bones, and notably their fin rays, are all hollow internally, a peculiarity which is not met with in other ganoids, and which

* Huxley, T. H., Preliminary essay upon the systematic arrangement of the fishes of the Devonian Epoch, prefixed to the tenth decade of the "Figures and Descriptions illustrating British Organic Remains" (1861), p. 20.

is the origin of the name "Coelacanth" which has been conferred on the family. This character is especially striking in the typical genus Coelacanthus. To this singular structure of the bones is added another more apparent and more external character, viz., the form and disposition of the fins, and the mode of articulation of the rays; and in the first place, most of the rays are stiff, or only articulated at their ends. Their combination with the apophyses [neural arches and spines] and inter-apophysial [interspinous] bones is very singular, especially in the caudal fin, the rays of which are supported by interspinous bones; an arrangement which in other fishes is found ordinarily only in the anal and the dorsal [*caudale* in the text]. Lastly, the vertebral column is prolonged more or less distinctly between the principal lobes of the caudal fin, so as to form a median tapering process. . . ."

Of the genus Coelacanthus proper, Professor Agassiz remarks (p. 170):

"This genus, which I regard as the type of the family, was long known to me only by fragments; but these were so different from most other ichthyolites that I did not hesitate to incorporate them into a distinct genus. What especially struck me was the form and the structure of the fins, their relation with the interspinous bones, and the manner in which the apophyses [vertebral arches and spines] are united on the one hand with the bodies of the vertebrae, and on the other with the inter-apophysial [interspinous] bones. The apophyses divide at their bases into two branches, forming a fork, which embraces the body of the vertebra; to this apophysis succeeds an ossicle which, instead of being interposed between two apophyses, is fitted on to the end of one, so as to form its direct prolongation. The ray properly so called, the longest of the three pieces, is also forked at its base; its extremity alone is jointed, but never bifurcated. These three pieces, the apophysis, the inter-apophysial bone and the ray, are of subequal length and all three are hollow. . . .

"This singular structure characterizes most of the rays which lie at the posterior part of the trunk; now, as usually only the anal and the dorsal have inter-apophysial bones, I at first concluded that these two fins must be excessively developed; and what helped to strengthen this idea was the fact that the vertebral column appeared to be continued beyond the two azygous fins, to form further on a bundle of very small articulated rays, attached directly to the vertebrae. But Lord Enniskillen's

discovery of an entire specimen has completely modified my views. It now appears that besides the fins of so exceptional a structure, which I regarded as anal and dorsal, this fish has a very distinct normal anal and two dorsals. Now, unless the existence of three dorsal and two anal fins of very different structure—an arrangement which occurs in no known genus of fishes—be admitted, it is necessary to regard the terminal fin of the body as a caudal. For the rest, this is not the only known example of a caudal supported by inter-apophysial bones, the caudal of *Polypterus bichir* being supported by similar bones, at least in its upper lobe. What is truly exceptional is the prolongation of the tail beyond these rays, and the little fascicle of articulated rays surrounding its extremity. . . .

"The most important difference [as compared with other Coelacanths] is presented by the dentition. The genus Undina has, according to Münster, pavement-like teeth very similar to those of certain Pycnodonts. Coelacanthus, on the other hand, has conical teeth like the Sauroids, and everything leads to the belief that it is a carniverous fish, so that, far from belonging to the same genus, it is doubtful whether it belongs to the same family. Leaving the caudal aside, the other fins of the genus Coelacanthus present a very simple structure, composed of slender but not dichotomous rays. The first dorsal corresponds to [*i. e.,* arises opposite] the extremity of the pectorals. The second is opposite the space between the ventrals and the anal. The anal itself is very closely approximated to the caudal. This last fin (comprising in it the bundle of articulated rays which fringes the extremity of the vertebral column) nearly equals one-third of the total length of the fish. The vertebrae are much higher than they are long towards the anterior part of the trunk, but they become sensibly elongated posteriorly. The same is true of the apophyses, which, very slender in the abdominal region, take on a much greater development in the caudal region. The scales, to judge from the fragment of *C. granulosus,* are large, elongated, and have their posterior margin rounded. I have not been able to ascertain whether they are enamelled or not, but the fact that they are found in strata older than the Jura leads me to suppose that, as in all the fishes of that age, they were invested with a layer of enamel. Their extreme thinness, no doubt, has made them too fragile to be commonly preserved. I conclude from this description that the genus Coelacanthus, although near the genus Undina of Count Münster, is nevertheless distinct from it, and that the latter should therefore form a separate type of the Coelacanth family."

Finally, concerning the extraordinary conservatism and persistency manifested by the family ever since its introduction, the illustrious English biologist whom we have already quoted expresses himself in following terms:*

"Bearing in mind the range of the Coelacanths from the Carboniferous [since ascertained to extend from the Devonian] to the Chalk formations inclusive, the uniformity of organization of the group appears to be something wonderful. I have no evidence as to the structure of the base and side walls of the skull in Coelacanthus, but the data collected together in the present Decade shows that, in every other particular save the ornamentation of the fin-rays and scales, the organization of the Coelacanths has remained stationary from their first recorded appearance to their exit. They are remarkable examples of what I have elsewhere termed "persistent types", and, like the Labyrinthodonts, assist in bridging over the gap between the Palæozoic and the Mesozoic faunae."

Genus **COELACANTHUS** Agassiz.

Supplementary caudal fin prominent; the rays of all the fins long and slender, without denticles or tuberculations, unjointed for a considerable length proximally, but closely articulated distally without being expanded. Superficial ornament of external bones and scales consisting of more or less discontinuous fine ridges of ganoine, sometimes broken up into a series of tubercles.

The earliest known representative of this genus is a small form occurring in the lower part of the Upper Devonian near Gerolstein, in the Eifel District, first described by von Koenen† in 1895, and referred by him with some hesitation to Holoptychius, but afterwards recognized by Smith Woodward‡ as a typical Coelacanth. On the basis of that interpretation the form is to be recorded as *C. kayseri* (von Koenen). Prior to its discovery the opinion had been generally entertained that, owing to the sudden appearance of Coelacanth fishes in a complete state of development in the Calciferous sandstones of Scotland,

*Memoirs of the Geological Survey of the United Kingdom, Decade XII. 1866. Reprinted in the supplementary volume of the "Scientific Memoirs of Thomas Henry Huxley" (1903), p. 65.

†Von Koenen, A., Ueber einige Fischreste des norddeutschen und böhmischen Devons. Abhandl. k. Ges. Wiss. Göttingen, phys. Cl. (1895), **40**, p. 28.

‡Woodward, A. S., Note on a Devonian Coelacanth Fish. Geol. Mag. (1898), Dec. 4, vol. **5**, p. 529.

it was necessary to postulate the existence of their ancestors during the Devonian, although their remains had escaped notice both in Europe and North America. Frequently it happens in natural as well as in physical science that, through the exercise of trained imagination, predictions can be made with such confidence that our faith in them amounts almost to a certainty, even though there appear to be little chance of ultimate demonstration of the truth;* but in all such cases it is gratifying when well-founded forecasts happen to become verified by fresh discoveries. Smith Woodward's recognition of a Devonian Coelacanth in the new form brought to light by von Koenen is a good instance in point. Another instance, even more striking than the first, is found in the fortunate discovery by Dr. Stuart Weller of a completely developed Coelacanth, immediately to be described under the name of *C. welleri,* at the base of the Kinderhook limestone near Burlington, Iowa. These discoveries compel us to project the origin of the family backward in point of time to an earlier period than was at first thought necessary.

Coelacanthus welleri, Eastman.

(Plate III, Fig. 7; Text-fig. 36)

1908. *Coelacanthus welleri* C. R. Eastman, Journ. Geol. **16,** p. 358, text-fig. 1.

Holotype a somewhat imperfect fish, the total length of which to the base of the caudal fin is about 19 cm, or a little more than three times the length of the head with opercular appar-

* The necessity for postulates of this nature in palæontology is too obvious, and the practice of making them too common, for illustrations not to suggest themselves readily to all well informed persons. We may, however, be allowed to cite an excellent recent example of this art of visualizing undiscovered prototypes of fossil forms, which is to be found in Dr. Bashford Dean's recently published "Notes on Acanthodian Sharks" (Amer. Journ. Anat. 1907, **7,** p. 220). Having reached the conclusion that Acanthodian sharks "have passed through a stage which is best represented by the Cladoselachian," the author seeks to answer the inquiry why it is that the more specialized group of Acanthodians is known from an earlier horizon than the less specialized? The situation is met by framing the following hypothesis:

"This is in truth a question which can be answered only by the time-worn appeal to the defectiveness of the palæontological record, noting especially in this regard that the soft structures of the Cladoselachians would be less apt to be preserved than the hard structures of the Acanthodians. We may, however, safely predict that from the earliest Acanthodian horizon there will be discovered forms which will represent the ancestors of all the early groups of sharks. And we may predict with the same degree of security that these forms will be found to picture the Cladoselachian in essential characters. For the Acanthodians, as we at present know them, are obviously too specialized to have represented the ancestors of the line of Cladoselachians." (*cf. supra, pp. 61, 99.*)

atus. Trunk robust, its maximum depth twice as great as that of the caudal pedicle. Anal and paired fins situated as in the typical species (*C. granulatus* Ag.), the greater part of the caudal and both dorsals not preserved. Operculum and cheek-plates ornamented with numerous fine antero-posteriorly directed spiniform ridges, their position being indicated in the worn condition by faint tubercles. Scales ornamented with numerous fine raised lines of ganoine, more or less continuous and rectilinear, but when worn assuming the appearance of elongated tubercles. Scales along the lateral line with prominent raised tubules directed parallel with the body axis.

The unique and in many respects remarkable specimen answering to the above description, and shown in the accompanying half-tone figure (Fig. 36), was discovered a few years ago by Dr. Stuart Weller, of the University of Chicago, in the course of his investigation of the Kinderhook fauna of Iowa and adjoining states. In recognition of his important work, and for the rest, as *hommage d'esprit,* we have pleasure in dedicating the specific title of the new form brought to light by him in his honor. The exact horizon whence the specimen was obtained is the blue shale bed at the base of the Kinderhook limestone near Burlington, Iowa. An analysis of the fauna occurring in this bed, designated as No. 1 in the local section, is given by Dr. Weller in volume X (1899) of the Iowa Geological Survey Reports, p. 69 *seq.* The peculiar relations of this assemblage are thus noticed by the author in the course of his general remarks (p. 70):

"The fauna of this bed is a most interesting one, it probably being the oldest of the Kinderhook faunas of the Mississippi Valley. The presence of typical forms of the genus Productus gives to the fauna a strong Carboniferous aspect, the undetermined species of Productella and Gomphoceras being the only members which are suggestive of the Devonian, unless the fish-remains should show some such alliance. The fauna is really more strongly Carboniferous in aspect than is that of bed No. 2, whose large number of pelecypods are for the most part allied to Devonian species in New York. For the satisfactory study of this fauna, however, larger collections than are now available must be secured, and as soon as the necessary material

FIG. 36.

Fig. 36. *Coelacanthus welleri* Eastman. Kinderhook limestone; near Burlington, Iowa. Lateral aspect of holotype, x 5-6. Original in Walker Museum of the University of Chicago.

is at hand, this fauna will be made the basis of one number of 'Kinderhook Faunal Studies'."*

Bearing in mind the remote geological antiquity of the new Coelacanth we have just described, it is suggestive to note that its totality of characters by no means indicates a primitive member of the group, but on the contrary bespeaks a typical species as completely developed as any subsequent form with which we are acquainted. In this respect it resembles the only well known British Coelacanth of an age anterior to the Coal Measures, this being *C. huxleyi,* from the Calciferous sandstones of southern Scotland. Palæontologists are well aware that the oldest known Coelacanths from the western hemisphere are of Coal Measure age, and are represented by poorly or indifferently preserved material. In all, but four species of Coelacanthus† proper, and three of Cope's genus Peplorhina, are recorded from a few localities in Ohio and Illinois.

It is now in order to present a more detailed description of the new Kinderhook form. The characters of specific value which it displays may be enumerated as follows: (1) The delicate spiniform ornamentation of the operculum and cheek plates, together with the form and disposition of the latter; (2) the peculiar form of the mandibular ramus; and (3) details of scale ornament; and (4) prominence of the lateral line canal. Owing to the decidedly imperfect preservation of most of the fin structures, it is impossible to say in what respect, if any, these differ from the normal type. The cranial structure, however, offers a number of interesting points of comparison with other forms, as will be immediately pointed out.

The roofing-bones of the skull are missing in the type specimen, and that portion of the head in advance of the orbits has been fractured in such manner as to strip off the maxillary and other external facial elements, exposing at the same time the anterior spatulate portion of the parasphenoid, together with

*Earlier numbers of these Studies, the second one dealing with the fauna of the Chonopectus sandstone at Burlington (immediately overlying the fish-bearing bed No. 1), are published in vols. 9 and 10 of the Transactions of the St. Louis Academy of Science.

†Certain of these types are now preserved in the American Museum of Natural History in New York. *Cf.* Hussakof's "Catalogue of Fossil Fishes," etc., published in vol. **25**, of the Bull. Amer. Mus. Nat. Hist., June, 1908.

the steeply inclined triangular palatine plates that abut against it on either side. The inferior border of the palatines, parasphenoid and vomer appears to have suffered somewhat from chemical corrosion, in consequence of which no indications of teeth are anywhere visible. Possibly for the same reason no teeth are to be observed along the margin of the lower jaw, nor lying free in the matrix, in case any had been broken off.

The mandibular ramus of the right side is well displayed, and the dentary is seen to be still in union with its fellow of the left side at the symphysis. The articulo-angular element is long, narrow in front, its superior border rising into a small median and a large posterior elevation, between which is a deep concavity; and its inferior border is nearly rectilinear. The superficial ornament of this piece has become well-nigh obliterated by weathering or abrasion, and of the two gular plates immediately underneath, nothing remains but an impression of their inner surfaces.

A notable peculiarity of the type specimen, one that possibly bears witness to primitive traits, consists in the arrangement of cheek-plates immediately in advance of the operculum. In all other Coelacanths so far as known, two postorbital plates of subequal size are placed one above the other in the space between the orbit and operculum, in such fashion that the small triangular plate called "postmaxillary" by Huxley is excluded from contact with the operculum. The new Kinderhook species, however, has all three of these cheek-plates situated in vertical series, one overlapping the other from above downward, and each overlapping the anterior border of the operculum. The lowermost cheek-plate, that corresponding to the so-called "postmaxillary" of Huxley, terminates below in line with the inferior border of the operculum, and covers the space immediately behind the inflected portion of the articulo-angular element of the lower jaw. Its antero-superior margin is apposed to the strongly arched, probably semicircular suborbital element, of which only a small segment is preserved in the type example. In this latter respect the plate in question is seen to occupy the same relation as the "postmaxillary" of other Coelacanths. Owing to the fact, however, that in later species this plate is

displaced far forwards, and has to accommodate itself to the contours of the suborbital and lower postorbital, it suffers considerable reduction in size, whereas in the form under discussion it is fully as large as either of the superjacent postorbitals, and is ornamented in similar manner.

No indications are to be observed in the specimen before us of a sclerotic ring, although one may be inferred to have been present as in other known Coelacanths. Neither is there any external indication of the presence of an ossified air-bladder, for which members of this family are remarkable. The caudal, anal and pelvic fins are too imperfectly preserved for description, and the pectoral pair is altogether wanting. The squamation is admirably shown, especially in the posterior part of the trunk, where the fine longitudinal ridges of ganoine and concentric growth-lines are pyritized. The lateral line is rendered conspicuous by a single large raised tubule of ganoine extending for nearly the entire length of each scale in this row. An enlarged view of the superficial ornament of scales lying a little above the anal fin is given in Plate III, Fig. 7.

Formation and locality. Basal member of Kinderhook limestone, near Burlington, Iowa, beneath a bed carrying an invertebrate assemblage of markedly Devonian aspect. Holotype preserved in the Walker Museum of the University of Chicago.

Genus **PALAEOPHICHTHYS**, novum.

An aberrant Crossopterygian genus provisionally referred to the Coelacanthidae, and distinguished from all other members of the family by its elongate, anguilliform body, and continuous median fins. Scales very delicate with exceedingly fine antero-posterior striations. Neural and haemal spines long and delicate, almost filiform.

Although the scope of this Report is limited in a strict sense to forms of fish life of Devonian age, yet on account of the great rarity and peculiar organization of the older Coelacanths in this country, it has been deemed advisable to include a notice here of a remarkable specimen from the famous Mazon Creek locality of Illinois, which differs notably from all other genera and species thus far described. We propose to recognize it, therefore, under the following caption:

Palæophichthys parvulus, sp. nov.

(Text-fig. 37)

A very small species, attaining a total length of 4 or 5 cm, with very slender, elongated, eel-shaped form of body. Length of head contained nearly six times in the total length. Arrangement of cranial plates indistinguishable, and extremity of tail deficient in the solitary known specimen. Paired fins not observed. Median fins continuous, the dorsal arising behind the occiput at a distance equal to about one and one-half times the length of the head itself, and the origin of the anal not far behind that of the dorsal.

The original specimen serving for the holotype of the above defined genus and species is preserved in counterpart, as is usually the case when organic nuclei are exposed within ironstone nodules at the Mazon Creek locality in Grundy county, Illinois. It at one time formed part of the S. S. Strong collection, and is now the property, along with the type of *Coelacanthus exiguus* from the same locality and horizon, of the Museum of Comparative Zoology at Cambridge, Massachusetts. Interesting as the specimen is on account of its relations and general features, it is to be regretted that it is defective as regards preservation of certain parts, the head region being encrusted with a whitish film of silicious matter, the extreme tip of the tail wanting, and no trace remaining of the paired fins.

The most salient and at the same time truly surprising characteristics of the new form are two: first, the anguilliform proportions of body; and secondly, the continuity of the median fins.

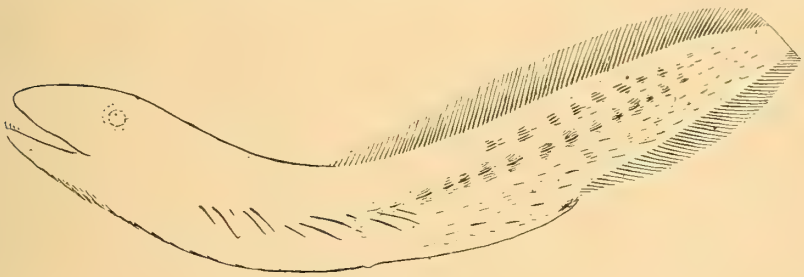


FIG. 37.

Fig. 37.—*Palæophichthys parvulus*, sp. nov. Coal Measures; Mazon creek, Illinois. Lateral aspect of holotype showing elongate form of body, degenerate squamation, and continuous median fins, x 2-1.

We are justified in expressing surprise at these features, for not only is their occurrence singular for the family of Coelacanths in general, but they have not hitherto been known to be combined in any Palæozoic fish. Eel-shaped forms occur in a few groups, mostly sharks, during the Palæozoic, as has already been noted in treating of Cladoselache and Acanthodians; and it will be remembered that this form of body has been interpreted as a symptom of decadence.* These forms do not, however, develop continuous median fins. Contrariwise, Phaneropleuron and Uronemus furnish examples among Palæozoic Dipnoans where the unpaired fins are confluent, but the form of body is massive and cylindrical, and hence can hardly be described as eel-shaped. Typical eels, as every one knows, do not occur until the Upper Cretaceous.

In so far as the specimen before us is remarkable for exhibiting the combination of characters just described, precisely on that account is it difficult to affiliate it with other contemporary forms of fish life with which we are familiar. Its reference to Coelacanths is admittedly provisional. Yet at the same time we cannot deny that its affinities are more readily to be sought in the vicinity of this group than any other. Grounds for this belief are to be found in the delicately striated scales of the new form, the posterior prolongation of the body axis, and its ossified neural and haemal spines, features which offer suggestive points of comparison with typical Coelacanths. One will recall also, that at least one undoubted member of the family, *C. exiguus*,† is of about the same size, has degenerate squamation, and accompanies the present form in the same fauna. On the whole, the most plausible interpretation of Palæophichthys seems to be to regard it as an aberrant and extremely degenerate offshoot of fringe-finned ganoids adapted to a mud-grovelling mode of existence.

Formation and locality. Coal Measures; Mazon creek, Grundy county, Illinois.

* *Cf. ante*, p. 61.

† Described in Journal of Geology (1902), vol. **10**, p. 538, text-fig. 3.

Order **ACTINOPTERYGII.**

Paired fins nonlobate, having an extremely abbreviated endoskeletal portion, and the dermal rays prominent. Caudal fin abbreviate-diphycercal, heterocercal, or homocercal. A single paired series of transversely elongated rays, with or without an anterior azygous element, developed in the branchiostegal membrane between the mandibular rami.

Suborder **CHONDROSTEI** (Sturgeons).

In these fishes, the oldest and most primitive of the Actinopterygii, the notochord is more or less persistent, the supports of the dorsal and anal fins are less numerous than the dermal rays opposed to them, the paired fins more abbreviate than in the Crossopterygian order, and the tail completely heterocercal. Primitive Sturgeons differ also from fringe-finned ganoids in the development of a paired series of transversely elongated branchiostegal rays to replace the pair of jugular plates between the mandibular rami; infraclavicular plates, however, are retained in both groups. Nearly all the older forms have a well developed rhombic and ganoid squamation. So far as known the chondrocranium is but little ossified, and the cranial bones are mainly dermal.

The evolutionary history of the Sturgeon tribe, and the leading characters of the family Palæoniscidae, are thus indicated by Professor Bridge in the Cambridge Natural History volume on *Fishes* (1904), p. 485:

"The Chondrostei are first represented in the Lower Devonian by the solitary Palæoniscid genus Cheirolepis, a contemporary of the earliest Crossopterygii. They occur throughout the Mesozoic period, except in the Cretaceous, and also in the Eocene, and while steadily diminishing in number and variety, they gradually approximate to their degenerate and in some respects highly specialized descendants, the sturgeons and paddlefishes of the existing fish-fauna. Of the seven families included in the group, the Palæoniscidae are the oldest and most generalized. The Platysomidae are a specialized offshoot from the Palæoniscidae, and, if they are rightly to be considered as Chondrostei, perhaps the same may be said of the problematic

Belonorhynchidae. On the other hand, there are certain features which indicate an approach to Fishes of an altogether more modern type. Finally, the Chondrostei represent a stage in a career of degeneration, the climax of which is reached by the modern Polyodontidae and Acipensideridae."

Family PALAEONISCIDAE.

Primitive Chondrostei with fusiform bodies, short dorsal and anal fins, and usually with a complete investment of articulating rhombic, rarely cycloid, ganoid scales. Fulcra generally present at the bases of the median fins, and especially along the dorsal border of the upper caudal lobe. Ribs are not known to be present. Skull invested by a very complete series of paired dermal bones, which in number and disposition conform to the normal Teleostome type. The secondary upper jaw includes both premaxillæ and large maxillæ; and, as a rule, both the dentary and splenial bones of the lower jaw are dentigerous. Except for the absence of an interoperculum, the opercular series of bones is complete, including numerous branchiostegal rays. There is a single small median jugular plate.

The earliest representative of this family, and of primitive sturgeons generally, is the genus Cheirolepis, which is remarkable for the very small size of its scales. Long associated with Acanthodian fishes, even by experienced observers, its Palæoniscid nature was first completely demonstrated by Dr. Ramsay H. Traquair* in 1875, who was also the first to point out the presence of a median jugular plate in typical genera. The type and best known species of Cheirolepis, *C. trailli* Agassiz, occurs in the Old Red Sandstone of northern Scotland; and another well preserved form, described by Whiteaves as *C. canadensis,* is known from the Upper Devonian of Scaumenac Bay, in the Province of Quebec.

Aside from examples of the Canadian form just mentioned, no completely preserved representatives of this family are known from the Devonian rocks of North America, although

*Traquair, R. H., On the structure and systematic position of the genus Cheirolepis. Ann. Mag. Nat. Hist. (1875), ser. 4, vol. **15**, pp. 237-249. A similar suggestion had been made tentatively two years earlier by Dr. Karl Martin (Zeitschr. deutsch. Geol. Ges. 1873, **25**, p. 699).

three species have been founded upon portions of the squamation. These have been doubtfully referred to the genus Palæoniscus under the names of *P. antiquus* and *P. reticulatus* Williams, * and *P. devonicus* Clarke,† but are more properly assignable to Rhadinichthys. The two first-named are from the Portage beds near Buffalo, New York, and the last-named, much more complete than the others, is from the Naples beds of Sparta, in the same State. A re-investigation of the type of the Naples species enables us to add a few details to the extant knowledge of its characters, which are recorded below. In addition, one new species showing very remarkable features is described, and the characters of several imperfectly known and hitherto unillustrated forms belonging to the same genus are set forth as the result of recent study of the type specimens, whose whereabouts had for many years been lost sight of. The types referred to are the originals of two or three species of Rhadinichthys and Elonichthys described by Dr. C. T. Jackson in 1851 from the Albert coal mine of New Brunswick. There is no record of their early history, but ten of them became the property of the Boston Society of Natural History, and several were afterwards acquired by the Harvard Museum. Their identification was made possible quite recently through the discovery in the Redfield collection at Yale of two unpublished lithograph plates by Sonrel which had been struck off subsequent to the issue of Jackson's Report, but appear never to have been regularly distributed. Through the kindness of Professor Charles Schuchert it has been possible to provide photographic copies of these proofs for the use of students in different museums.

Genus RHADINICHTHYS Traquair.

Trunk elegantly fusiform, more or less elongated. Mandibular suspensorium very oblique; teeth in two series, a small outer row and larger incurved conical laniaries, well-spaced,

*Williams, H. U., Bull. Buffalo Soc. Nat. Sci. (1886), **5**, p. 84, fig. 2.

†Clarke, J. M., Bull. U. S. Geol. Surv. no. **16** (1885), pp. 20, 41, pl. 1, figs. 2, 6.

within. Fins of moderate size, consisting of delicate rays, distally bifurcated, with an anterior series of slender fulcra; principal rays of pectoral fin unarticulated except near their distal extremity. Dorsal and anal fins triangular, partly or completely opposed; upper caudal lobe slender, and caudal fin deeply forked, unsymmetrical. Scales large or of moderate size, more or less delicately sculptured; ridge-scales in advance of dorsal fin much enlarged.

This genus was established by Dr. Traquair in 1877 to include several earlier described Palæoniscid species, typified by *P. ornatissimus* Agassiz, from the Scottish Lower Carboniferous. The characters of generic importance displayed by this species and by the closely related *P. carinatus* Agassiz, and the form designated (but not described) by Professor J. Young as "*P. wardi*", are stated by the original author to be as follows:

"The body is comparatively slender; the suspensorium is very oblique; the jaws are armed with a row of incurved conical laniaries, outside of which there is a series of smaller teeth; the principal rays of the pectoral fin are, as in Pygopterus and Oxygnathus, unarticulated till towards their terminations; the caudal body-prolongation is comparatively delicate. There are, besides these, several other new species from British Carboniferous strata referable to this type, the description of which I hope soon to be able to overtake; in some of these the scales are nearly smooth, as in *R. carinatus*, in others elaborately ornamented."*

Rhadinichthys devonicus (Clarke).

(Text-figure 38)

1885. *Palæoniscus devonicus* J. M. Clarke, Bull. U. S. Geol. Surv. no. **16**, pp. 20, 41, pl. 1, figs. 2-6.

1889. *Palæoniscus devonicus* J. P. Lesley, Dictionary of the fossils of Penn., etc. Geol. Surv. Penn., Rept. *P4*, vol. **1**, p. 585, figures.

1907. *Rhadinichthys devonicus* C. R. Eastman, Mem. N. Y. State Mus. **10**, p. 171.

1907. *Rhadinichthys devonicus* D. D. Luther, 59th Ann. Rept. N. Y. State Mus. **2**, p. 46.

A gracefully formed species with slender trunk, attaining a length of at least 12 cm and possibly longer. Headbones deli-

*Traquair, R. H., On the Agassizian Genera Amblypterus, Palæoniscus, etc. Quar. Journ. Geol. Soc. (1877), **33**, p. 559.

cately striated, lower border of maxilla with long anterior projection. Scales of flank somewhat broader than deep, not much overlapping, ornamented with from five to seven oblique or sometimes sigmoidally flexed striae which terminate at the posterior border in a corresponding number of sharp serrations. A series of greatly enlarged ridge-scales extending to the base of the caudal fin, pointed posteriorly, ornamented with wavy striae, and presenting a punctate appearance in the worn or weathered condition. Some of the ridge-scales behind the dorsal fin have a length of about 5 mm and breadth of 3.5 mm. Fins imperfectly preserved in all specimens thus far examined. Fulcra along dorsal lobe of the caudal moderate.

The original description of this species is accompanied by figures of worn flank-scales which do not show the posterior

FIG. 38.

Fig. 38. *Rhadinichthys devonicus* (Clarke.) Naples shale (Portage beds); Sparta, New York. Holotype, now the property of the United States National Museum at Washington. x 1-1.

serrations, a pair of imperfectly preserved frontal bones (pl. 1, fig. 6, U. S. G. S. Bull. No. 16) found in natural juxtaposition, and two delicately striated plates, one of which is evidently the maxilla stripped of its teeth, (*ibid,* fig. 4), and the other may perhaps be regarded as the operculum (*ibid,* fig. 5). The type specimen is preserved in the United States National Museum, and bears the catalogue number 30,842.

Formation and locality. This species is stated by Dr. Clarke to occur abundantly in bituminous layers of the Naples shale (lower black band of the Portage group) in the town of Sparta, Livingston county, New York. A single scale displaying the same ornamentation is also reported by him from the Genesee shales of Glenville, Hemlock Lake, a few feet above the Styliola layer. Similar scales have been noticed by Dr. G. J. Hinde from the Genesee of Erie county in the same State, and others are reported from the corresponding horizon in Kentucky. No examples from the last-named region, however, have come under the present writer's observation, nor is record to be found of their detailed description. On the other hand the fact deserves mention that patches* showing a considerable portion of the squamation of Eurylepis have been obtained from the Waverly black shale at Vanceburgh, Kentucky. Several specimens of this nature are to be seen in the State College collection at Lexington.

Rhadinichthys sp.

1907. *Rhadinichthys* sp. indes. C. R. Eastman, Mem. N. Y. State Mus. **10,** p. 172, pl. 4, fig. 11, and pl. 9, fig. 4.

A single small thick-scaled Palæoniscid fish, too imperfect for accurate determination, was obtained some years ago by Mr. F. A. Randall from the Chemung rocks of Warren, Pennsylvania, and is now preserved in the Museum of Harvard University. The specimen is chiefly interesting on account of its excellent display of median and paired fin characters. These, together with the general form of the body and scale characters have suggested a position for it in the vicinity of *R. elegantulus*

* Remains of this nature are by no means uncommon, and are perhaps to be explained as voided contents of the intestinal tract of predatory fishes.

Traquair, from the Calciferous sandstone series of Eskdale, Scotland. The fragmentary specimen affords the only indication thus far obtained of the presence of Palæoniscid fishes in the Chemung of the eastern Appalachian area.

Rhadinichthys alberti (Jackson).

1851. *Palæoniscus alberti* C. T. Jackson, Rept. Albert Coal Mine,* p. 22, pl. 1, fig. 1, pl. 2, figs. 2-8 (? *non* 7).
1852. *Palæoniscus alberti* C. T. Jackson, Proc. Boston Soc. Nat. Hist. **4**, p. 138.
1853. *Palæoniscus alberti* P. G. Egerton, Quart. Journ. Geol. Soc. **9**, p. 115.
1868. *Palæoniscus alberti* J. W. Dawson, Acadian Geology, p. 131, fig. 62.
1877. *Rhadinichthys alberti* R. H. Traquair, Quart. Journ. Geol. Soc. **33**, p. 559.
1877. *Palæoniscus alberti* J. W. Dawson, Canadian Nat. n. s., **8**, p. 338.
1878. *Palæoniscus alberti* J. W. Dawson, Acadian Geology, 3d Ed., p. 231, and Suppl., p. 100.
1889. *Rhadinichthys alberti* S. A. Miller, North American Geol. and Pal., p. 611, fig. 1172 (after Dawson).
1889. *Palæoniscus alberti* J. P. Lesley, Dictionary of Fossils, etc. Geol. Surv. Penna., Rept. *P4*, p. 584, figure.

A small robust species, attaining a length of about 8 cm. Maximum depth of trunk contained about four times in the total length. Head relatively small, and external bones ornamented with coarse waved ridges, sometimes interrupted. Dorsal fin arising slightly in advance of the anal, and the latter much elongated. A continuous series of enlarged ridge-scales along the back from the occiput to the upper lobe of the caudal fin; flank-scales as broad as deep; scale-ornament consisting of irregular fine longitudinal striae, more or less oblique, terminating in a number of coarse serrations (5-8) along the posterior border.

Formation and locality. Lower Carboniferous; Albert county, New Brunswick.

Rhadinichthys cairnsi (Jackson).

1851. *Palæoniscus cairnsii* C. T. Jackson, Rept. Albert Coal Mine, p. 23, pl. 1, fig. 3. (Plates not issued with text).
1852. *Palæoniscus cairnsii* C. T. Jackson, Proc. Boston Soc. Nat. Hist. **4**, p. 139.

*Plates not issued with text, and missing in all copies examined. Apparently a few proof impressions were distributed privately, one set being preserved with the Redfield collection of fossil fishes at Yale. The original specimens represented in Pl. 1, figs. 1-3, 5, and Pl. 2, figs. 2, 3, 7, are now the property of the Museum of Comparative Zoology at Cambridge.

1877. *Palæoniscus cairnsii* J. W. Dawson, Canadian Nat. n. s. **8**, p. 339.
1878. *Palæoniscus cairnsii* J. W. Dawson, Acadian Geology, Suppl., p. 100.
1891. *Rhadinichthys cairnsi* A. S. Woodward, Cat. Foss. Fishes Brit. Mus. pt. 2, p. 465.
1904. *Rhadinichthys cairnsi* A. Tornquist, Zeitschr. deutsch. geol. Ges. **56**, p. 350.

Trunk robust, with slender caudal pedicle, the maximum depth somewhat greater than the length of the head with opercular apparatus, and contained about four and one-half times in the total length. Dorsal fin shorter than the anal, arising slightly in advance of the latter. Scales of flank scarcely deeper than broad; scale-ornament consisting of delicate longitudinal striae, parallel with the inferior border, and terminating in very fine serrations of the posterior border (A. S. Woodward).

From a comparison of Jackson's type specimens it is apparent that the dorsal fin in this species is relatively somewhat smaller and more remote than the corresponding structure in *R. alberti.*

Formation and locality. Same as preceding.

Rhadinichthys modulus (Dawson).

(Text-fig. 39)

1877. *Palæoniscus modulus* J. W. Dawson, Canadian Nat. n. s. **8**, p. 337, woodcut fig. 1.
1878. *Palæoniscus* (*Rhadinichthys*) *modulus* J. W. Dawson, Acadian Geology, 3d Ed., Suppl., p. 100, woodcut fig. 18.
1891. *Rhadinichthys modulus* A. S. Woodward, Cat. Foss. Fishes Brit. Mus. pt. 2, p. 466.

A small species attaining a length of about 6 cm, in general resembling *R. alberti,* but described as distinguished by its relatively shorter anal fin, the coarseness of the scale-ornament, and ovate form of the dorsal ridge-scales. The ridge-scales between the occiput and dorsal fin are stated by Dawson to be ten in number, of large size, oval in form, and sculptured with wavy lines running subparallel with the lateral borders. The head is elaborately ornamented with fine waving lines.

The original description of this species is in reality composite, being founded upon two individuals preserved in close proximity on the same slab of shale, one shown mostly in impression,

the other, which Dawson figures, displaying the entire outline. This latter exhibits no trace of dorsal ridge scales; impressions of five or six such, however, occur in advance of the dorsal fin in the more poorly preserved specimen. Examination shows that these ridge-scales are distinctly not truncated behind, as Dawson supposed, but on the contrary are obtusely pointed. Consequently the outline sketch given in Fig. 18 *d* of his Notes and Addenda to the "Geology of Canada" (3d edition, 1878, p. 100) requires to be emended in this particular.

FIG. 39.

Fig. 39. *Rhadinichthys modulus* Dawson. Lower Carboniferous; Beliveau, Albert county, New Brunswick. Cotypes, x 1-1.

The ornamentation of the flank scales as represented in Fig. 18*b* of the same work is also imperfectly shown. The posterior margin of the scales is indeed strongly serrate, and the exposed surface is covered by from five to six relatively coarse plica-

tions which extend obliquely downward and backward, or are sometimes sigmoidally curved. The coarseness of the scale ornament and that of the external bones of the head are remarkable for so small sized a species. It is to be observed further that the anal fin, with twenty-one rays, arises opposite the middle of the short dorsal.

For an opportunity to study the type specimens, now the property of the Peter Redpath Museum of McGill University, the writer is indebted to the kindness of Professor F. D. Adams, who collected them near Beliveau, New Brunswick, many years ago.

Formation and locality. Lower Carboniferous; Albert county, New Brunswick.

Rhadinichthys deani, sp. nov.

(Plate XIII; text-figs. 40, 41 *a-c*)

A moderate-sized, elaborately ornamented species, of which the head has a length of from 1.4 to 1.8 cm, and is estimated to have been contained from four to five times in the total length. Cranial, opercular and maxillary plates ornamented with delicate, wavy and sometimes branching and anastomosing raised lines of ganoine; ornament of flank-scales consisting of fine gently curved or oblique striae terminating in very delicate serrations along the posterior border; a series of enlarged ridge-scales extending along the middle of the back, ornamented with rather coarse, wavy enamelled ridges. Flank-scales with strong articular spines and sockets on inner surface. Suspensorium very oblique, gape of mouth wide, maxillae deep and strongly excavated anteriorly in the orbital region; dentition in both jaws consisting of several series of different sized teeth, all erect and slender-conical in shape, the larger teeth somewhat widely spaced and irregularly interspersed with the smaller ones. Form of body and fin-characters, with the exception of the pectorals, not observed. Sensory canals of the head prominently developed, and correlating with large size of the internal auditory organs, as revealed by a number of exceptionally perfect specimens showing the brain-structure.

Remains of this small and highly ornamented species occur rather abundantly in a well marked horizon in central Kentucky, being embedded in phosphatic nodules, vast quantities of which are carried by a continuous layer less than two feet thick and distributed over a wide area. This horizon marks the very base of the Waverly series, and rests conformably upon the evenly bedded Devonian Black Shale, whose age corresponds with the Genesee shales of New York State.* The phosphatic nodules near Junction City and elsewhere in Boyle and Marion counties carry an extensive fish and invertebrate fauna, besides a considerable quantity of fossil wood. As a result of systematic collection made at the principal localities during the last two or three years, chiefly by Mr. Moritz Fischer, a large supply of material has been brought together, the greater part of which is now owned by the Museum of Comparative Zoology at Cambridge, and the American Museum of Natural History in New York. Cordial thanks are here rendered to Dr. Bashford Dean, in whose honor the new species under discussion is named, for the generous loan of all the most valuable and instructive specimens in his custody.

It is to be regretted that no completely preserved individual of the new species has yet been brought to light, although from amongst a large series of nodules it is possible to reconstitute nearly all the different parts and to restore the general outline. The part most commonly preserved, and that, too, with a perfection and fidelity of detail that extends even to soft tissues and hence may be compared to the process of embalming, is the head portion. And by this is to be understood the complete head, since the combined lot of specimens presents for study the cranial roof, facial plates, branchiostegals, jaw-parts, brain structure, internal ear, nerve endings and arterial blood vessels. A complete head exposed so as to be visible from both sides and from below, and remaining in natural association with the pectoral fins and a portion of the trunk, is preserved in the Ameri-

*Knott, W. T., Report on the Geology of Marion County. Reports of Progress, Geol. Surv. Kentucky (1885), p. 21. —— Girty, G. H., Description of faunas in the Devonian Black Shale of Eastern Kentucky. Amer. Journ. Sci. 1898, ser. 4, **6**, p. 384. —— Foerste, Aug. F., The Silurian, Devonian and Irvine Formations of East-Central Kentucky. Bull. no. 7, Kentucky Geol. Surv. (1906), p. 110.

can Museum of Natural History. Other specimens of the head with associated squamation and fin structures are the property of the Cambridge Museum, one such being shown in counterpart at the lower corners of Plate XIII.

From the great wealth of material that has been laid under contribution it is easy to perceive that the complete fish must have been one of those elaborately ornamented Palæoniscids such as are embraced within the genus Rhadinichthys, and the species that most readily suggest themselves for comparison are those which have been described from the Lower Carboniferous of New Brunswick—*R. alberti, cairnsi* and *modulus*. The average size of the new form would appear to be somewhat less or at least not exceeding that of *R. alberti,* and the ornamentation of similar nature, but finer and more extensive. In the case of some specimens, however, allowance must be made for an apparent coarseness of striation or thickening of raised ridges, which is plainly due to mineral incrustation. The same agency is likewise responsible for an occasional enlargement of some of the internal soft parts.

Without doubt the most remarkable feature which engages attention in connection with this species is the unrivalled preservation of soft parts. From the nature of things a state of affairs of this kind is most unusual among fossils, vertebrate or invertebrate. Dawson has described for us what he regards as "the crystalline lens of the eye" of *Elonichthys browni,** and Traquair has remarked upon the "eye spots" of Thelodus and Lanarkia.† Bashford Dean, too, has recently found vestiges of the membranous labyrinth in the Permian *Acanthodes bronni,* after having previously made known the delicately preserved musculature of Cladoselache from the Cleveland shale.‡ An

*Dawson, J. W., Acadian Geology. 3d edition, supplement, p. 101. London, 1878.

†Traquair, R. H., Supplementary Report on Fossil Fishes, etc. Trans. Roy. Soc. Edinb. (1905), **40**, pt. 4, pp. 880, 882.

‡Dean, B., The Preservation of Muscle-fibres in Sharks of the Cleveland Shale. Amer. Geol. (1904), **30**, pp. 273-8. This article contains a critical discussion of Otto Reis's views concerning the conditions of fossilization. See also by the same author, Notes on Acanthodian Sharks, in Amer. Journ. Anat. (1907), **7**, p. 218.

It will be convenient to refer here to a suggestive paper by L. Cayeux on the origin of phosphatic nodules, and two others by MM. Paul Combes fils and Stanislas Meunier, all contained in Bull. Soc. Géol. France (1906), ser. 4, **5**, fasc. 6. Important also is Joh. Lehder's article on phosphatic concretions from the lowermost Culm of Thuringia, published in Supplementary Vol. **22** (1906) of the Neues Jahrbuch für Mineralogie, pp. 48-113.

entirely new chapter, however, in the anatomy of extinct animals is opened by the discovery of the actual phosphatized brain, internal ear and blood vessels of a Palæozoic vertebrate, such as are clearly revealed by the contents of these fish-bearing nodules from the base of the Waverly in Kentucky.

Perhaps the best single specimen thus far examined which displays the actual brain itself *in situ,* with parts of the auditory sense organ on either side, is that shown in the accompanying text-figure (Fig. 40 *A*, A^1). In the middle figure of the

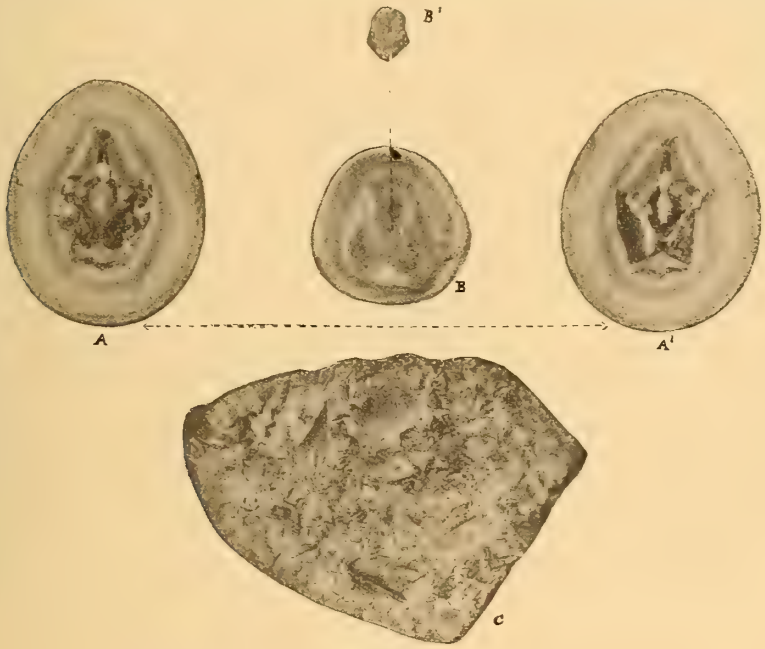


FIG. 40.

Fig. 40. *Rhadinichthys deani*, sp. nov. Base of the Waverly in Boyle county, Kentucky. In this photograph are shown detached heads forming the central mass of phosphatic nodules. The latter are split open in such manner as to cleave through the head longitudinally immediately below the cranial roof, and exposing the fossilized organs of the brain:—the olfactory lobe, cerebral hemispheres (covered in the central figure by a choroid plexus), optic lobes, and cerebellum, on either side of which are to be seen the well preserved semicircular canals with their sacculæ and ampullae. Very nearly natural size.

same illustration is seen the interior of the head of another example which allows of the removal of the brain from its proper cavity, thus facilitating its inspection from all sides. For the purpose of photographing the organ more distinctly, it has been placed in a right line above the head to which it belongs, and is

here viewed from the dorsal aspect (Fig. 40 B^1). The brain, to be seen in its natural position within the interior of the head, Fig. 40 *A*, is oriented in a corresponding fashion, and the nodule containing it is fractured in such manner as to cleave off the cranial roof, which latter is seen from the cerebral aspect in A^1. Both specimens, *A* and *B*, show a relatively large-sized fish brain, as completely formed as in any modern teleost, and segmented in the usual manner.

In the median line posteriorly is to be observed the funnel-shaped expansion of the spinal cord known as the medulla, which merges forwardly into a quadripartite organ well represented at the base of Fig. 40 B^1, which can scarcely be interpreted other than the cerebellum or hindbrain. This organ is moderately large, probably correlating with the activity of the animal, just as the large size of the optic lobes is correlated with a keen visual sense, and the auditory ampullae with a well developed faculty of equilibration. The two anteriorly situated lobes of the cerebellum are larger than the posterior pair, and diverge laterally so as to embrace the bilobed midbrain or mesencephalon, whose dorsal wall is constricted into two lateral portions known as the optic lobes. That the eyes were of importance for this creature is betokened by the large size of the optic lobes, and also by the relatively wide orbital openings. The section of the brain lying immediately in advance of the optic lobes is that formed by the cerebral hemispheres, still covered in one of the specimens (Fig. 40 B^1) by a choroid plexus.

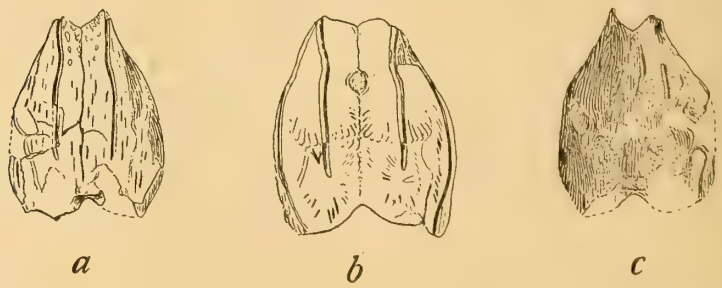


FIG. 41.

Fig. 41. *Rhadinichthys deani*, sp. nov. Base of the Waverly; near Junction City, Boyle county, Kentucky. *a*, *b* Cranial shields with partly denuded surface ornamentation, showing course of sensory canals and parieto-frontal sutures. *c* Impression of internal surface of cranial roof showing detail of superficial ornament. Photographic reproductions of the same specimens are given in Plate XIII, figs. 5, 7, and 11. Slightly enlarged.

Most anteriorly of all is the region known as the prosencephalon or forebrain, represented in Fig. 40 *A* by a slender elongated process which may perhaps be regarded as identical with the olfactory lobes, although its details are not entirely clear.

From the description of parts just given, as well as from the appearance of the surface of the organ when examined under the lens, it is evident that we have here to deal with a veritable brain-structure the substance of which became transformed into calcium phosphate before decomposition could set in, and whose walls in consequence are scarcely shrunken. This view is further confirmed by the presence of nerve fibres and blood vessels, slightly enlarged in some cases, it is true, by the segregation of mineral matter, but coinciding in position with altogether similar nervous and vascular structures in modern ganoids and bony fishes. The case, therefore, is entirely different from the state of affairs which arises from infiltration of the brain cavity, thus producing a natural cast of the interior, and so far as the present writer is aware the phenomenon is unparalleled in the annals of palæontology. We may be permitted to refer in passing to an interesting dissertation on fossil brain casts, to be found in chapter 7 of Professor Albert Gaudry's "Essai de paléontologie philosophique" (Paris, 1896), wherein are considered examples of all the higher classes of vertebrates.

We pass now to an examination of the most interesting of all the internal structures revealed by the heads of those specimens which have been fractured in such manner as to disclose the contents of that long-sealed abode, which, eloquent of 'silence and slow time,' recalls Keats' apostrophe of a Grecian urn:

> Thou still unravish'd bride of quietness,
> Thou foster-child of silence and slow time, ...
> Thou, silent form, dost tease us out of thought
> As doth eternity: cold Pastoral!

The structures referred to are the internal ear and its associated parts; and, as in the case of the brain itself, their like has never before been found in the fossil condition. As will presently appear, they are nearly as well suited for purpose of investigation as alcoholic preparations, and naturally are of surpassing interest on account of their antiquity. Concerning the origin of the auditory sense organ, embryology teaches

that it was primarily derived from a modified integumentary sense organ, such as the lateral line system; that it gradually became more deeply seated within the skull, at the same time dividing into two parts, utriculus and sacculus, the former of which gave rise to the semicircular canals, and the latter to the tube-like ductus endolymphaticus and the lagena (=cochlea). In some cases, however, as in certain sharks and rays, the separation between the utricular and saccular chambers remains incomplete, and their common cavity is known as the utriculo-saccular organ. Other primitive features retained among Elasmobranchs are the simpler relations of the semicircular canals to the utriculo-sacculus, and the opening of the endolymphatic duct (closed in higher fishes) upon the dorsal surface of the head, where it connects with the lateral line canals.*

In view of the great antiquity and lowly systematic position of the Palæoniscid species we are considering, one might expect that the auditory sense organs would betray signs of a primitive condition approximating to that observed among sharks and rays, or would at least manifest simpler relations than those we are familiar with among modern bony fishes. In this expectation, however, we are disappointed. The type of membranous labyrinth which is preserved for us with utmost nicety of detail in these ancient Palæoniscids is to all intents and purposes identical with that in existing teleosts. No really essential differences can be detected, and we are obliged to affirm that these early ganoids were provided with as efficient auditory sense organs as any fishes now living. The faculty of equilibration must have been perfectly developed among them, and for aught that can be inferred to the contrary, they may even have possessed the power of hearing, a sense that some authors regard as the most delicate and most recently acquired in point of evolutionary sequence among the various means of receiving sense impressions from the external world.

From these general observations we may pass on to a more particular description of the internal ear, as displayed by a

* References to the principal literature of this subject are brought together by J. B. Johnston, in his manual on "The Nervous System of Vertebrates" (1906), by G. Schwalbe, in his "Lehrbuch der Anatomie der Sinnesorgane" (1887), and with still greater fulness by the authors of special monographs on the vertebrate ear, foremost among whom is the Swedish anatomist, Retzius.

number of exquisitely preserved specimens. One of these is shown in text-figure 40 *A*, and others which fortunately supplement it in important details are now the property of the American Museum of Natural History. The entire suite of material exhibiting the soft parts within the interior of the head in this species has been submitted to several experts for examination, among whom should be mentioned Professors Dean, Patten and Parker, and to these three friends in particular the writer is indebted for valuable hints and suggestions. The liberality of the first-named in committing all the specimens in his keeping to the writer's hands for study and report testifies to his extreme interest in furthering so promising an investigation, and the writer is mindful of his instructions to section or otherwise manipulate the precious material in order to gain all possible information. Sectioning has not been resorted to, however, because the structure of the phosphatic matter into which the organic tissue was transformed immediately after death is seen to be amorphous, except for a thin superficial layer which faithfully preserves the outline of the different organs. Furthermore, it seemed advantageous to request Dr. Parker, of the Harvard Zoological Department, to draw up a succinct account of his lection of the membranous labyrinth in order that students may have the benefit of his views. This suggestion met with a ready response, and we accordingly have pleasure in presenting the following statement on the part of a skilful investigator of the sense organs of vertebrates. It will be profitable to consult in this connection the same author's papers on hearing and allied senses in fishes.*

* Parker, G. H., Hearing and Allied Senses in Fishes. Bull. U. S. Fish Comm. (1902), **22**, pp. 44-64.—The Sense of Hearing in Fishes. Amer. Nat. (1903), **37**, pp. 185-204. See also in volume **38** of the same journal a paper by H. B. Bigelow on The Sense of Hearing in the Goldfish, *Carassius auratus* Linn.

SPECIAL DESCRIPTION OF THE AUDITORY ORGAN AND OTHER SOFT PARTS.

BY DR. G. H. PARKER.

The preservation of soft parts in fossils is so unusual that the specimens submitted to me for examination are worthy of special attention. Some of these show what seem to be indubitable remains of the actual brain, internal ears, nerve endings and blood vessels. In the specimen shown in Fig. 40 *A* the remains of the ears are especially perfect. On the right-hand side the anterior vertical canal is well preserved throughout its whole extent from the apex of the superior sinus of the utriculus to the anterior ampulla. This ampulla is somewhat embedded in the matrix, but is sufficiently exposed to be clearly recognizable. The posterior horizontal canal is also observable throughout its extent, though its ampulla is not, being probably concealed by matrix. Immediately behind the anterior ampulla is a spherical body, distinctly shown in Fig. 40 *A*, which represents the ampulla of the horizontal (external) canal. This canal is not visible in the particular specimen here figured, but in another that is not figured the horizontal canal is shown with perfect clearness and is seen to connect with the spherical body just mentioned, thus proving it to be the ampulla. The unfigured specimen referred to (it is the property of the American Museum of Natural History) also shows near the posterior end of the horizontal canal a rounded body which without doubt is the posterior ampulla.

The left-hand side of the specimen shown in Fig. 40 *A* is almost identical with the right-hand side, except that the anterior vertical canal has been partly fractured near its junction with the anterior ampulla. In the ears of each side of this specimen the apex of the superior sinus where the two vertical canals unite shows a well marked depression as though the walls of the membranous labyrinth were slightly invaginated. It is possible that this depression marks the spot from which a well developed apex has been broken away, but the depression has the appearance of a slight superficial involution rather than a ruptured membranous wall. These two specimens together show with remarkable clearness all the essential parts of the semicircular apparatus of a fish, and conform to precisely the same plan as is exemplified in modern forms.

Arteries.—Among other soft parts preserved in these specimens may be mentioned a body to be seen on the inner surface of the ventral wall of the cranium, and well toward the posterior end of that structure. It is *Y*-shaped with the stem of the *Y* median and directed posteriorly. The two arms of the *Y* extend forwardly, and near their anterior ends they seem to divide into two unequal branches. The smaller branch is directed anteriorly and probably was contained within the cranial cavity, but the larger one is flexed ventrally and laterally, and apparently pierced the cranial wall. At first sight this structure might be taken for the remains of nerves, but its position and the relation of its parts are much more suggestive of arteries. The posterior median stem corresponds to the basilar artery, the large ventro-lateral branches to the carotid arteries, and the smaller branches to those vessels which in fishes are distributed to the ventral and lateral surfaces of the brain. It seems, therefore, that vascular as well as nervous organs are preserved in these highly remarkable specimens.

Formation and locality. Base of the Waverly series; Boyle county, Kentucky.

Genus **ELONICHTHYS** Giebel.

Trunk more or less deeply fusiform. Mandibular suspensorium very oblique; jaws stout and teeth acutely conical, arranged in two series—an inner row of well-spaced laniaries and an outer row of numerous, closely arranged small teeth; bones of head and opercular apparatus ornamented with tuberculations and striae. Fins large, with fulcra, the rays branching distally, covered with ganoine, and the more robust sculptured. Pectoral, pelvic, dorsal and anal fins with short base-line: dorsal opposed to space between pelvic and anal fins: upper caudal lobe much produced, the fin deeply forked and inequilobate. Scales of moderate thickness, very slightly imbricating, covered with ganoine, more or less sculptured; ridge-scales immediately in advance of median fins much enlarged.

The American species of this genus are few in number, and confined to the Lower Carboniferous and Coal Measures of New Brunswick and the United States respectively. European species are numerous and locally very abundant, especially in the Lower Carboniferous of Scotland. The Scottish forms have been exhaustively treated by Dr. Traquair in several important monographs, the most recent of which are included among the publications of the Palæontographical Society and of the Royal Society of Edinburgh. Of interest in the present connection is a small and elaborately ornamented species, first described in 1904 and afterwards more fully illustrated, known as yet by but two nearly perfect individuals, and designated as *E. striatulus*.* Concerning this rare species the author remarks that he has referred it to the genus Elonichthys "on account of its general aspect, and the form and position of the unpaired fins, though the condition of the fin-fulcra deviates considerably from that which is usual in the genus. In all its details it is strikingly different from every other known species."

* Summary of Progress of the Geol. Survey for 1903 (1904), p. 121. —— Trans. Roy. Soc. Edinb. (1907), **46**, pt. 1, p. 107. —— Ganoid Fishes of the British Carboniferous Formations, Part 1, no. 3, in Monogr. Palæontogr. Soc. for 1907.

A study of an extensive suite of material from the Lower Carboniferous of Albert county, New Brunswick, including the originals of Dr. C. T. Jackson's figures and descriptions, shows that a minute form apparently closely allied to the Scottish *E. striatulus* is present in this horizon and locality, where it accompanies *E. browni* and the several species of Rhadinichthys already noticed in the preceding pages. The new form, for which the title of *E. elegantulus* is not inappropriate, may be readily distinguished by its small size, slender and graceful proportions, and decidedly prominent, even coarse, details of scale ornament. The scales are traversed longitudinally by a number of closely crowded raised ridges, smooth, continuous, glistening, and the whole presenting an appearance not distantly recalling Ptycholepis, from a much later horizon. In addition, the lateral line is very conspicuous. The head and fin structures are not clearly revealed in any individual that has thus far come to light, but the general resemblance to the little fish made known by Traquair from Eskdale and East Lothian* necessitates its reference to the same vicinity.

---

*For complete lists of the fauna and remarks on the distribution of species in the Scottish Lower Carboniferous, see the following papers by Dr. Traquair:

On the distribution of fossil fish-remains in the Carboniferous rocks of the Edinburgh District. Trans. Roy. Soc. Edinb., 1903, **40**, pp. 687-707.—Report on fossil fishes collected by the Geological Survey of Scotland from shales exposed on the shore near Gullane, East Lothian. *Ibid.*, 1907, **46**, p. 114 *et seq.*

V. Faunal Lists*.

1. SPECIES OF FOSSIL FISHES OCCURRING IN THE LOWER DEVONIAN OF NORTH AMERICA.

OSTRACODERMS.

1. *Thelodus* scales. Oriskany sandstone; Nictaux Falls, Nova Scotia.

2. *Cephalaspis campbelltonensis* Whiteaves. Lower Devonian; Campbellton, New Brunswick.

3. *Cephalaspis dawsoni* Lankester. Lower Devonian; Gaspé, Province of Quebec.

4. *Cephalaspis* sp. Lower Devonian; Campbellton, New Brunswick.

5. *Asterolepis clarkei* Eastman. Chapman sandstone (Lowermost Devonian); Aroostook county, Maine.

ELASMOBRANCHS.

6. *Protodus jexi* Smith Woodward. Lower Devonian; Campbellton, New Brunswick.

7. *Doliodus problematicus* (Smith Woodward). Lower Devonian; Campbellton, New Brunswick.

8. *Acanthodes semistriatus* Smith Woodward. Lower Devonian; Campbellton, New Brunswick.

9. *Cheiracanthus costellatus* Traquair. Lower Devonian; Campbellton, New Brunswick.

---

*Besides the following distributional lists, one should consult tables 17-19 of Frech's Lethæa Palæozoica, vol. 2 (1897), in the first of which Devonian fishes are listed according to their occurrence in marine and brackish-water sediments in all parts of the globe. In addition, the following catalogues will be found useful:

Bigsby, J. J., Thesaurus Devonico-Carboniferous. London, 1878.

Etheridge, R., Fossils of the British Islands stratigraphically and zoologically arranged. Oxford, 1888.

Sherborn, C. D., and Woodward, A. S., Catalogue of British Fossil Vertebrata. London, 1890.

Hay, O. P., Bibliography and Catalogue of the fossil Vertebrata of North America. Bull. U. S. Geol. Surv. No. **179**, Washington, 1902.

Hussakof, L., Catalogue of Fossil Fishes. Bull. Amer. Mus. Nat. Hist., 1908, **25**, pt. 1.

10. *Climatius latispinosus* (Whiteaves). Lower Devonian; Campbellton, New Brunswick.

11. *Homacanthus gracilis* Whiteaves. Lower Devonian; Campbellton, New Brunswick.

12. *Machaeracanthus sulcatus* Newberry. Lower Devonian; Gaspé, Province of Quebec. Also at higher levels of the Gaspé series.

13. *Gyracanthus incurvus* Traquair. Lower Devonian; Campbellton, New Brunswick.

ARTHRODIRES.

14. *Phlyctaenaspis acadica* (Whiteaves). Lower Devonian; Campbellton, New Brunswick.

CROSSOPTERYGIANS.

15. *Dendrodus arisaigensis* Whiteaves. Arisaig series (? Helderbergian); Nova Scotia.

2. SPECIES OF FOSSIL FISHES OCCURRING IN THE MIDDLE DEVONIAN OF NORTH AMERICA.

OSTRACODERMS.

16. Shagreen granules of *Thelodus, Cœlolepis,* etc. Columbus limestone (="Corniferous"); Columbus, Ohio.

ELASMOBRANCHS.

17. *Cladodus prototypus* Eastman. Columbus limestone; Columbus, Ohio.

18. *Cladodus monroei* Eastman. Hamilton limestone; Milwaukee, Wisconsin.

19. Dermal tubercles, possibly of *Cladoselache.* Marcellus shale; Le Roy, New York.

20. *?Psammodus antiquus* Newberry. Columbus limestone; Ohio.

21. *Onchus* sp. Middle Devonian; Gaspé, Province of Quebec.

22. *Ctenacanthus wrighti* Newberry. Moscow shale (Upper Hamilton); Yates county, New York.

CHIMAEROIDS.

23. *Ptyctodus punctatus* Eastman. Onondaga limestone; Le Roy, New York.

24. *Ptyctodus calceolus* Newberry and Worthen. Cedar Valley limestone; Iowa and Illinois. Hamilton limestone; Wisconsin and Ontario. "Cuboides zone" of the Devonian; Manitoba. Also Genesee and Portage groups of New York, and Upper Devonian of Iowa, Kentucky and Missouri.

25. *Ptyctodus ferox* Eastman. Hamilton limestone; Milwaukee, Wisconsin. Cedar Valley limestone and State Quarry beds of Iowa.

26. *Rhynchodus excavatus* Newberry. Hamilton limestone; Milwaukee, Wisconsin, and Cedar Valley limestone of Iowa.

27. *Rhynchodus* sp. ind. "Cuboides zone" of the Devonian; Manitoba.

28. *Rhynchodus secans* Newberry. Columbus and Delaware limestones; Ohio.

29. *Palæomylus crassus* (Newberry). Columbus and Delaware limestones; Ohio.

30. *Palæomylus frangens* (Newberry). Columbus and Delaware limestones; Ohio.

31. *Palæomylus greenei* (Newberry). Hamilton limestone; Milwaukee, Wisconsin.

32. *Phlyctaenacanthus telleri* Eastman. Hamilton limestone; Milwaukee, Wisconsin.

33. *Acantholepis fragilis* Newberry. Onondaga limestone; New York. Columbus and Delaware limestones; Ohio.

34. *Acanthaspis armata* Newberry. Onondaga limestone; Le Roy, New York. Columbus and Delaware limestones; Ohio. Closely similar structures, probably dermal ossifications of Rhynchodus, occur also in the Cedar Valley limestone of Iowa.

35. *Heteracanthus politus* Newberry. Hamilton limestone; Milwaukee, Wisconsin, and Cedar Valley limestone of Iowa.

36. *Heteracanthus uddeni* Lindahl. Hamilton limestone; Milwaukee, Wisconsin, and Cedar Valley limestone of Iowa.

37. *Machaeracanthus peracutus* Newberry. Columbus and Delaware limestones; Ohio. Onondaga limestone; Le Roy and Lime Rock, New York.

38. *Machaeracanthus sulcatus* Newberry. Delaware limestone; Ohio and Canada. Onondaga limestone; New York. Gaspé series; Province of Quebec.

39. *Machaeracanthus major* Newberry. Columbus and Delaware limestones; Ohio.

40. *Machaeracanthus longaevus* Eastman. Lower Hamilton; Eighteen Mile creek, New York, and (?) Hamilton limestone of Milwaukee, Wisconsin.

41. *Cyrtacanthus dentatus* Newberry. Columbus and Delaware limestones; Ohio.

ARTHRODIRES.

42. *Macropetalichthys rapheidolabis* Norwood and Owen. Columbus and Delaware limestones; Ohio and Indiana, also from rocks of equivalent age in Ontario and James Bay region, Canada, but probably not in Kentucky and certainly not in Iowa, as has sometimes been claimed. Onondaga limestone; Le Roy, New York.

43. *Asterosteus stenocephalus* Newberry. Delaware limestone; Ohio.

44. *Coccosteus* sp. Onondaga limestone; Clifton Springs, New York.

45. *Coccosteus occidentalis* Newberry. Delaware limestone; Ohio.

46. *Coccosteus* (*Liognathus*) *spatulatus* Newberry. Delaware limestone; Ohio.

47. *Protitanichthys fossatus* Eastman. Delaware limestone; Delaware, Ohio.

48. *Dinichthys precursor* Newberry. Columbus limestone; Columbus, Ohio.

49. *Dinichthys halmodeus* (Clarke). Marcellus shale; Livonia and Manlius, New York.

50. *Dinichthys lincolni* Claypole. Marcellus shale; Geneva, New York.

51. *Dinichthys pustulosus* Eastman. Cedar Valley limestone; Iowa and Illinois. Hamilton limestone; Milwaukee, Wisconsin. Also as a recurrent form in the Oneonta beds (Portage) of New York.

52. *Dinichthys tuberculatus* Newberry. Cedar Valley limestone; Iowa. Hamilton limestone; Milwaukee, Wisconsin. Also in the New Albany or Genesee black shale near Louisville, Kentucky, and typically in the Chemung of Warren, Pennsylvania.

53. *Dinichthys canadensis* Whiteaves. "Cuboides zone" of the Devonian; Manitoba.

54. *Aspidichthys* (*?*) *notabilis* Whiteaves. Hamilton limestone; Ontario. "Cuboides zone" of the Devonian; Manitoba.

55. *Sphenophorus* (*"Oestophorus"*) sp. Hamilton limestone; Milwaukee, Wisconsin.

CTENODIPTERINES.

56. *Dipterus calvini* Eastman. Cedar Valley limestone; Fairport, Iowa.

57. *Dipterus uddeni* Eastman. Cedar Valley limestone; Buffalo, Iowa.

58. *Dipterus* sp. Labial cartilage of a large undescribed form collected by Professor W. H. Norton in the Cedar Valley limestone at Waverly, Bremer county, Iowa, and now preserved in the collection of Cornell College, Mount Vernon, Iowa.

CROSSOPTERYGIANS.

59. *Onychodus sigmoides* Newberry. Onondaga limestone; New York. Columbus and Delaware limestones; Ohio. Either this or a closely similar species occurs also in the Hamilton of Milwaukee, Wisconsin, and Cedar Valley limestone of Bremer county, Iowa.

60. *Onychodus* sp. indes. Hamilton limestone; Milwaukee, Wisconsin.

61. *Holoptychius* scales. Lower Hamilton; Oran, New York, and Cedar Valley limestone, Iowa.

Middle or Upper Devonian of Kentucky.

62. *Tamiobatis vetustus* Eastman. Powell county, Kentucky.

3. SPECIES OF FOSSIL FISHES OCCURRING IN THE UPPER DEVONIAN OF NORTH AMERICA.

Upper Devonian of the Quebec Province.

OSTRACODERMS.

63. *Cephalaspis laticeps* Traquair. Scaumenac bay, Quebec.
64. *Euphanerops longævus* Woodward. Scaumenac bay, Quebec.
65. *Bothriolepis canadensis* Whiteaves. Scaumenac bay, Quebec.

ELASMOBRANCHS.

66. *Diplacanthus striatus* Agassiz. Scaumenac bay, Quebec.
67. *Diplacanthus horridus* Woodward. Scaumenac bay, Quebec.
68. *Acanthodes affinis* Whiteaves. Scaumenac bay, Quebec.
69. *Acanthodes concinnus* Whiteaves. Scaumenac bay, Quebec.

DIPNOANS.

70. *Scaumenacia curta* (Whiteaves). Scaumenac bay, Quebec.
71. *Coccosteus canadensis* Woodward. Scaumenac bay, Quebec.

CROSSOPTERYGIANS.

72. *Holoptychius quebecensis* (Whiteaves). Scaumenac bay, Quebec.
73. *Eusthenopteron foordi* Whiteaves. Scaumenac bay, Quebec.

ACTINOPTERYGIANS.

74. *Cheirolepis canadensis* Whiteaves. Scaumenac bay, Quebec.

SENECAN STAGE OF THE UPPER DEVONIAN (TULLY LIMESTONE, GENESEE SHALE AND PORTAGE BEDS); APPALACHIAN PROVINCE.

ELASMOBRANCHS.

75. *Cladodus urbs-ludovici* Eastman. New Albany (=Genesee) Black Shale; Louisville, Kentucky.

76. *Cladoselache* sp. Naples shale (Portage); Eighteen Mile creek, New York.

77. *Acanthodes ? pristis* Clarke. Naples shale (Portage); Sparta, New York.

78. *Ptyctodus calceolus* Newb. & W. Genesee shale; Eighteen Mile creek, New York, and Louisville, Kentucky. Also Portage of Naples, New York.

79. *Ptyctodus* sp. Goniatite or Parrish limestone (Portage group); Naples, New York.

80. *Rhynchodus* sp. New Albany (=Genesee) Black Shale; Kentucky.

81. *Apateacanthus vetustus* (Clarke). Naples shale (Portage); Milo, Yates county, New York.

82. *Heteracanthus politus* Newberry. Naples shale; New York.

83. Undetermined fin-spine. Tully limestone; Cayuga lake, New York.

84. Dermal denticles of (?) *Cladoselache*. Genesee shale; Le Roy, New York.

ARTHRODIRES.

85. *Dinichthys newberryi* Clarke. Genesee shale; Bristol Center and Canandaigua lake, New York. New Albany (Genesee) Black Shale, Louisville, Kentucky.

86. *Dinichthys ringuebergi* Newberry. Naples shale (Portage); Sturgeon Point; near Buffalo, New York.

87. *Dinichthys pustulosus* Eastman. Oneonta beds; New York. Evidently a recurrent species in this horizon.

88. *Dinichthys dolichocephalus* Eastman. Naples shale (Portage); Sturgeon Point, near Buffalo, New York.

89. Dinichthyid dermal armor. Oneonta beds; Oxford, New York.

90. *Dinichthys* sp. Naples shale (Portage); Eighteen Mile creek, New York.

91. *Dinomylostoma beecheri* Eastman. Portage beds; Mt. Morris, Livingston county, New York. Fragmentary remains, doubtfully pertaining to the same genus, are known also from the New Albany (=Genesee) Black Shale near Louisville, Kentucky.

92. *Glyptaspis abbreviata* Eastman. Genesee shale of Eighteen Mile creek, New York, and New Albany (=Genesee) Black Shale of Louisville, Kentucky.

93. *Aspidichthys* sp. New Albany (=Genesee) Black Shale; Louisville, Kentucky.

94. *Callognathus serratus* Newberry. Naples shale (Portage); Eighteen Mile creek, New York. Also typically in the Huron and Cleveland shales of Ohio.

CTENODIPTERINES.

95. *Dipterus ithacensis* Williams. Ithaca beds (Portage); Ithaca, New York.

ACTINOPTERYGIANS.

96. *Rhadinichthys devonicus* (Clarke). Genesee shale; North Evans, New York, and said to occur also in the corresponding formation of Kentucky. Similar scales also obtained by J. M. Clarke from the Naples shale (Portage) of Sparta, New York.

97. *Rhadinichthys antiquus* Williams. Naples shale (Portage); Eighteen Mile creek, New York.

98. *Rhadinichthys reticulatus* Williams. Naples shale (Portage); Eighteen Mile creek, New York.

Ohio Shale (Huron, Erie and Cleveland shales); Ohio and Kentucky.

ELASMOBRANCHS.

99. *Phœbodus politus* Newberry. Cleveland shale; Lorain county, Ohio.

100. *Cladodus claypolei* Hay. Cleveland shale; Rocky river, Ohio.

101. *Cladodus concinnus* Newberry. Cleveland shale; Lorain county, Ohio.

102. *Cladodus rivi-petrosi* Claypole. Cleveland shale; Rocky river, Ohio.

103. *Cladodus subulatus* Newberry. Cleveland shale; Ohio.

104. *Cladodus terrelli* Newberry. Cleveland shale; Lorain county, Ohio.

105. *Cladodus tumidus* Newberry. Cleveland shale; Sheffield, Ohio.

106. *Monocladodus clarki* Claypole. Cleveland shale; Ohio.

107. *Monocladodus pinnatus* Claypole. Cleveland shale; Ohio.

108. *Cladoselache clarki* Claypole. Cleveland shale; Ohio.

109. *Cladoselache fyleri* Newberry. Cleveland shale; Cuyahoga county, Ohio.

110. *Cladoselache kepleri* Newberry. Cleveland shale; Cuyahoga county, Ohio.

111. *Cladoselache sinuatus* (Claypole). Cleveland shale; Ohio.

112. *Xenodus herzeri* (Newberry). Huron shale; Ohio.

113. *Hoplonchus parvulus* Newberry. Cleveland shale; Bedford, Ohio.

114. *Ctenacanthus clarki* Newberry. Cleveland shale; Berea, Ohio.

115. *Ctenacanthus compressus* Newberry. Cleveland shale; Lorain county, Ohio.

116. *Ctenacanthus vetustus* Newberry. Cleveland shale; Sheffield county, Ohio.

ARTHRODIRES.

117. *Coccosteus cuyahogae* Claypole. Cleveland shale; Cuyahoga county, Ohio.

118. *Dinichthys herzeri* Newberry. Huron shale; Delaware, Worthington and elsewhere in Ohio, also along Copperas creek near the junction of Clark and Powell counties, Kentucky. If the titles *D. kepleri* Claypole and *D. ingens* Wright (MS.) are rightly held to be synonymous with *D. herzeri,* this species is common to both the Huron and Cleveland shales of Ohio.

119. *Dinichthys terrelli* Newberry. Cleveland shale; northern Ohio.

The most recent restoration of the skeletal parts of this species is that given by Professor E. B. Branson, of Oberlin College, in volume *8* of the Ohio Naturalist (1908), pp. 365, 367, figs. 1, 2.

120. *Dinichthys intermedius* Newberry. Cleveland shale; northern Ohio.

121. *Dinichthys minor* Newberry. Cleveland shale; northern Ohio.

122. *Dinichthys curtus* Newberry. Cleveland shale; northern Ohio. Also according to Newberry's identification, from the Chemung of Warren, Pennsylvania.

123. *Dinichthys gouldi* Newberry. Cleveland shale; Berea, Ohio. The so-called *D. prentis-clarki* of Claypole is very likely identical with this species.

124. *Dinichthys clarki* Claypole. Cleveland shale; Berea, Ohio. The type of this species was originally described under the name of *"Gorgonichthys" clarki,* but is not generically distinct from Dinichthys. The obscure dental plate subsequently described as *D. clarki* is of different nature, and requires a new specific title if retained in the genus Dinichthys.*

125. *Dinichthys gracilis* Claypole. Cleveland shale; Berea, Ohio.

[*Dinichthys kepleri* and *D. prentis-clarki* Claypole. These are probably synonymous with *D. herzeri* Newberry and *D. gouldi* Newberry respectively. Both are from the Cleveland shale of the Rocky river valley, Ohio.]

126. *Brontichthys clarki* Claypole. Cleveland shale; Cuyahoga county, Ohio.

127. *Stenognathus corrugatus* (Newberry). Cleveland shale; Lorain county, Ohio.

128. *Titanichthys agassizii* Newberry. Cleveland shale; Lorain county, Ohio.

129. *Titanichthys attenuatus* Wright. Cleveland shale; Ohio.

130. *Titanichthys brevis* Claypole. Cleveland shale; Ohio.

* Journal of Geology 1900, vol. **8**, p. 35.

131. *Titanichthys clarki* Newberry. Cleveland shale; Lorain county and Berea, Ohio.

132. *Titanichthys rectus* Claypole. Cleveland shale; Ohio.

133. *Selenosteus kepleri* Dean. Cleveland shale; Ohio.

134. *Stenosteus glaber* Dean. Cleveland shale; Ohio.

135. *Callognathus serratus* Newberry. Cleveland shale; Lorain county, Ohio.

136. *Trachosteus clarki* Newberry. Cleveland shale; Berea, Ohio.

137. *Aspidichthys clavatus* Newberry. Huron shale; Delaware, Ohio.

138. *Diplognathus mirabilis* Newberry. Cleveland shale; Lorain county, Ohio. Probably referable to Mylostomatidae.

139. *Mylostoma variabile* Newberry. Cleveland shale; Cleveland and Sheffield, Ohio.

140. *Mylostoma terrelli* Newberry. Cleveland shale; valley of the Vermillion river, Erie county, Ohio.

141. *Mylostoma newberryi* Eastman. Cleveland shale; Sheffield, Ohio.

142. *Glyptaspis verrucosa* Newberry. Cleveland shale; northern Ohio.

CTENODIPTERINES.

143. *Ctenodus wagneri* Newberry. Cleveland shale; Cleveland, Ohio.

CROSSOPTERYGIANS.

144. *Onychodus ortoni* Newberry. Huron shale; Franklin county, Ohio.

ACTINOPTERYGIANS.

145. *Actinophorus clarki* Newberry. Cleveland shale; Brooklyn, Cuyahoga county, Ohio.

Upper Devonian of Iowa, Illinois and Colorado.

OSTRACODERMS.

146. *Bothriolepis coloradensis* Eastman. Elbert formation; Rockwood, Colorado.

ELASMOBRANCHS.

147. *Cladodus formosus* Hay. Ouray limestone; Needles Mountain, Colorado.

148. *Diplodus priscus* Eastman. Upper Devonian; Elmhurst, Illinois.

149. *Diplodus striatus* Eastman. Upper Devonian; Elmhurst, Illinois.

150. *Diplodus* sp. ind. Upper Devonian; Elmhurst, Illinois.

151. *Ptyctodus calceolus* Newb. & W. Upper Devonian; Elmhurst, Illinois. Also State Quarry, Lime Creek and Sweetland Creek beds, Iowa.

152. *Ptyctodus compressus* Eastman. State Quarry beds; Johnson county, Iowa.

153. *Ptyctodus ferox* Eastman. State Quarry beds; Johnson county, Iowa.

ARTHRODIRES.

154. *Dinichthys pustulosus* Eastman. State Quarry beds; Johnson county, Iowa.

155. *Dinichthys (?) tuberculatus* Newberry. State Quarry beds; Johnson county, Iowa.

156. Arthrodire fragments, mostly of dermal armor. Elbert formation; Devon Point, southwestern Colorado.

CTENODIPTERINES.

157. *Dipterus costatus* Eastman. State Quarry beds; Johnson county, Iowa.

158. *Dipterus digitatus* Eastman. State Quarry beds; Johnson county, Iowa.

159. *Dipterus mordax* Eastman. State Quarry beds; Johnson county, Iowa.

160. *Dipterus pectinatus* Eastman. State Quarry beds; Johnson county, Iowa.

160a. *Conchodus variabilis* Eastman. State Quarry beds; Johnson county, Iowa.

161. *Synthetodus trisulcatus* Eastman. State Quarry beds and Sweetland Creek beds; Johnson and Muscatine counties, Iowa.

162. *Synthetodus calvini* Eastman. State Quarry beds; Johnson county, Iowa.

CROSSOPTERYGIANS.

163. *Holoptychius giganteus* Agassiz. Elbert formation; Devon Point, southwestern Colorado.

164. *Holoptychius tuberculatus* Newberry. Elbert formation; Devon Point, southwestern Colorado.

Chemung-Catskill Group of New York and Pennsylvania.

OSTRACODERMS.

165. *Bothriolepis minor* Leidy. Chemung group; Bradford county, Pennsylvania. Also in the Catskill of Delaware county, New York.

ELASMOBRANCHS.

166. *Cladodus coniger* Hay. Chemung group; Warren, Pennsylvania, and Waverly of Meadville, Pennsylvania.

167. *Cladodus* sp. High Point sandstone; Naples, New York.

168. *Helodus gibberulus* Agassiz. Chemung group; Warren, Pennsylvania.

169. *Rhynchodus pertenuis* Eastman. Chemung group; Franklin, New York.

170. *Rhynchodus* sp. High Point sandstone; Naples, New York, and base of Waverly, Kentucky.

171. *Homacanthus acinaciformis* Eastman. Chemung group; Warren, Pennsylvania.

172. *Ctenacanthus chemungensis* Claypole. Chemung group; New York and Pennsylvania.

173. *Ctenacanthus randalli* Newberry. Olean conglomerate; Warren, Pennsylvania.

174. *Gyracanthus sherwoodi* Newberry. Chemung group; Pennsylvania, and Cattaraugus county, New York.

ARTHRODIRES.

175. *Coccosteus macromus* Cope. Chemung group; Leroy, Pennsylvania.

176. *Dinichthys curtus* Newberry. Chemung beds; Warren, Pennsylvania.

177. *Dinichthys tuberculatus* Newberry. Chemung group; Warren, Pennsylvania.

178. *Holonema rugosum* (Claypole). Franklin, Delaware county, New York; and Pennsylvania.

179. *Holonema horridum* Cope. Chemung group; Pennsylvania.

180. *Phyllolepis delicatula* Newberry. Chemung group; Bradford county, Pennsylvania.

181. *Spenophorus lilleyi* Newberry. Chemung group; Leroy, Bradford county, Pennsylvania.

CTENODIPTERINES.

182. *Dipterus nelsoni* Newberry (including *D. alleghaniensis* Williams, and the upper dental plates described as *D. flabelliformis*). Chemung group; Warren, Pennsylvania. Cuba sandstone; Alleghany county, New York.

183. *Dipterus minutus* Newberry. Chemung group; Warren, Pennsylvania.

184. *Ganorhynchus beecheri* Newberry. Chemung group; Warren, Pennsylvania.

185. *Heliodus lesleyi* Newberry. Chemung group; northern Pennsylvania.

CROSSOPTERYGIANS.

186. *Apedodus priscus* Leidy. Chemung group; Pennsylvania.

187. *Strepsodus* sp. (Detached tooth; also fragments of *Osteolepis* sp., *fide* Cope.)

188. *Holoptychius americanus* Leidy. Chemung group; Delaware county, New York; and Pennsylvania.

189. *Holoptychius filosus* Cope. Chemung group, Pennsylvania.

190. *Holoptychius giganteus* Agassiz. Pennsylvania. (Also Upper Devonian of Colorado.)

191. *Holoptychius granulatus* Newberry. Chemung group; northern Pennsylvania.

192. *Holoptychius pustulosus* Newberry. Chemung group; Warren, Pennsylvania.

193. *Holoptychius tuberculatus* Newberry. Leroy, Bradford county, Pennsylvania. Also Upper Devonian of southwestern Colorado.

Catskill Beds.

OSTRACODERMS.

194. *Bothriolepis nitida* (Leidy). Tioga county, Pennsylvania, and Delaware county, New York.

195. *Bothriolepis minor* Newberry. Leroy, Bradford county, Pennsylvania, and Delaware county, New York.

ELASMOBRANCHS.

196. *Onchus rectus* Eastman. Delaware county, New York.

197. *Gyracanthus sherwoodi* Newberry. Mansfield, Tioga county, Pennsylvania.

ARTHRODIRES.

198. *Dinichthys* sp. Franklin, Delaware county, New York.

199. *Holonema rugosum* (Claypole). Bradford county, Pennsylvania.

CTENODIPTERINES.

200. *Dipterus angustus* Newberry. Pennsylvania.

201. *Dipterus contraversus* Hay. Tioga county, Pennsylvania.

202. *Dipterus fleischeri* Newberry. Tioga county, Pennsylvania, and Franklin, Delaware county, New York.

203. *Dipterus sherwoodi* Newberry. Tioga county, Pennsylvania.

204. *Ganorhynchus beecheri* Newberry. Warren, Pennsylvania.

CROSSOPTERYGIANS.

205. *Holoptychius americanus* Leidy. Tioga county, Pennsylvania.

206. *Holoptychius giganteus* Agassiz. Tioga county, Pennsylvania.

207. *Holoptychius halli* Newberry. Delhi, New York.

208. *Holoptychius radiatus* Newberry. Blossburg, Pennsylvania.

209. *Sauripteris taylori* (Hall). Blossburg, Pennsylvania.

210. *Glyptopomus sayrei* Newberry. Susquehanna river near mouth of Mehoopany.

Acknowledgments.

The writer finds it difficult to express adequately the sense of his indebtedness to Professor Calvin, Director of the Survey, for the generous and active assistance he has rendered in the prosecution of the present Report, as well as for helpful advice and constant encouragement. To him alone is due whatever credit belongs to the inception of a work of this kind, and its publication in the present form, which marks a radical departure from the general plan and purpose of previous Survey Reports. Having first brought to light one of the most remarkable fish-faunas yet discovered in any region, namely that which characterizes the State Quarry beds of Johnson county, it is due to his appreciation of the scientific importance of the great quantity of unworked material obtained from this and other Devonian localities, both within the political boundaries of the State, and extra-limital, that an exception in favor of a volume of this character should be made in a series of principally economic reports.

In addition, sincere and cordial thanks are extended to Professor Calvin and his assistants on the Survey, notably Professors J. A. Udden and W. H. Norton, for the loan or other use of numerous valuable specimens. For similar courtesies the writer is indebted to the authorities of several large museums, the American, New York State, Yale and Harvard. For many and very special favors thanks are gratefully rendered to his friends and colleagues, Professors Bashford Dean, John M. Clarke, Charles Schuchert, Arthur M. Miller, and Dr. Stuart Weller.

To his foreign associates, Drs. Ramsay H. Traquair, A. Smith Woodward, Otto Jaekel, Louis Dollo, and others, the writer is indebted for a number of helpful suggestions received through correspondence, and above all for the wealth of information contained in the large body of publications emanating from these accomplished masters of a difficult field of research. The extent to which their published writings have been drawn upon in the preparation of the present Report will be evident to all; and the writer's sense of obligation for this aid is correspondingly great.

EXPLANATION OF PLATES

Plate I.

Fig. 1. *Diplodus striatus* Eastm. Upper Devonian; Elmhurst, Illinois. Detached tooth, anterior face. x 4-1. Page 105

Fig. 2. Detached dorso-median plate of a small undetermined Arthrodire seen from the visceral aspect. Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. x 2-1. Page.....207

Fig. 3. *Onychodus hopkinsi* Newberry. Chemung beds; Franklin, Delaware county, New York. Series of five presymphysial teeth. x 3-4. Page.....241

Fig. 4. *Onychodus* sp. (*cf. O. sigmoides* Newb.). Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. Imperfect slightly arcuate presymphysial tooth seen partly in longitudinal section and displaying central pulp-cavity. x 2-1. Page.....240

Fig. 5. *Diplodus priscus* Eastm. Upper Devonian; Elmhurst, Illinois. Detached tooth, anterior face. x 4-1. Page.....104

Fig. 6. Detached dorso-median plate comparable to that shown in Fig. 2, and belonging to an unknown Arthrodiran genus. Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. x 2-1. Page 207

Figs. 7, 8. Detached Thelodus-like scales from the "bone-bed" of the Columbus limestone, near Columbus, Ohio. x 3-1. Page 72

Fig. 9. *Phoebodus politus* Newberry. Cleveland shale (Upper Devonian); Lorain county, Ohio. Detached tooth, anterior face. x 4-1. Page.....106

Fig. 10. *Dinichthys pustulosus* Eastm. Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. Left posterior palato-pterygoid dental plate or "shear-tooth." x 1-1. Page.....194

Fig. 11. *Onychodus* sp. (*cf. O. sigmoides* Newberry). Marcellus shale (Erian division of the Middle Devonian); Oran, Onondaga county, New York. x 1-1. Page.....241

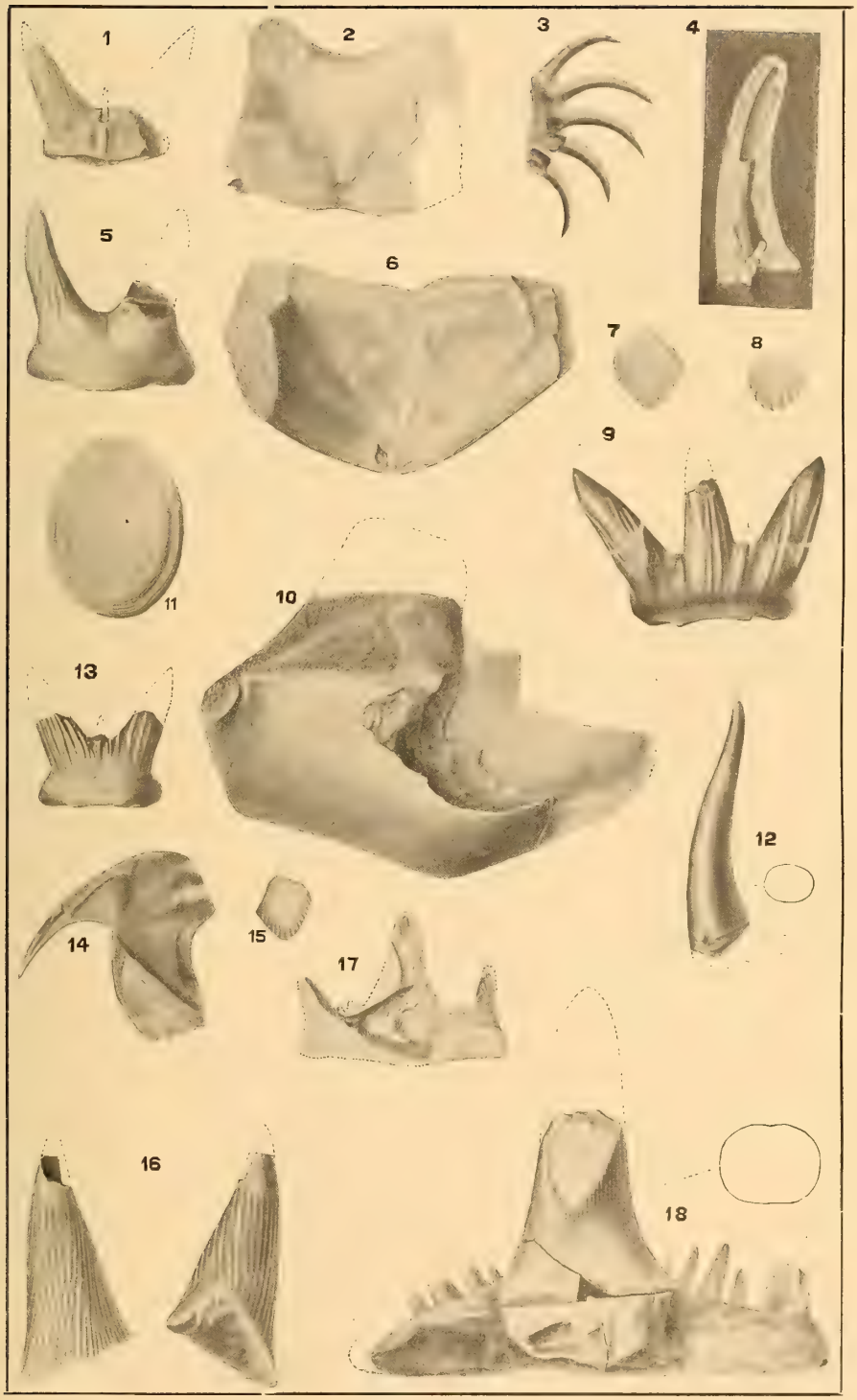

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Plate I.—Continued.

Fig. 12. *Onychodus* sp. indes. Middle Devonian; Eifel District, Rhenish Prussia. Detached presymphysial tooth differing from the typical American species in its less pronounced curvature and more slender form. Cross-section of base of crown shown at the right. Original in the Museum of Comparative Zoology, Cambridge, Mass. x 3-4. Page.....240

Fig. 13. *Diplodus priscus* Eastm. Upper Devonian; Elmhurst, Illinois. Detached tooth, anterior face. x 4-1. Page.104

Fig. 14. *Acanthaspis armata* Newberry. Columbus limestone (Middle Devonian); Sandusky, Ohio. Dermal plate with segmented spinous process, the whole strictly homologous with the so-called "shoulder-girdle of Rhamphodus," as described by O. Jaekel from the Upper Devonian of Wildungen, Waldeck. An external dermal ossification formerly supposed to be of Arthrodiran nature, but now considered, in the light of Jaekel's discovery, to belong to Rhynchodus or some similar Palæozoic Chimaeroid. x 5-7. Page.....145

Fig. 15. Detached Thelodus-like shagreen granule, of the same nature and from the same horizon and locality as those shows in Figs. 7 and 8. x 5-1. Page.....72

Fig. 16. *Diplodus striatus* Eastm. Upper Devonian; Elmhurst, Illinois. Anterior and posterior face of a single large detached cone. x 4-1. Page.....105

Fig. 17. *Cladodus monroei* Eastm. Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. Detached tooth, coronal apex and portion of the base broken away. x 3-2. Page...108

Fig. 18. *Cladodus prototypus* Eastm. Columbus limestone (Middle Devonian); Columbus, Ohio. Detached tooth serving as holotype of the species, seen from the posterior face; coronal cross-section shown at the right. Original in American Museum of Natural History, New York. x 2-1. Page.....108

Plate II.

All specimens represented four-fifths natural size unless otherwise stated.

Fig. 1. *Dipterus calvini* Eastm. Cedar Valley limestone (Middle Devonian); Fairport, Iowa. Right mandibular plate, holotype of the species. Page.....219

Fig. 2. *Dipterus pectinatus,* sp. nov. State Quarry beds (Upper Devonian); North Liberty, Johnson county, Iowa. Left mandibular plate, cotype. A photograph of the same specimen is reproduced in Plate VII, fig. 13. Page.....222

Fig. 3, 3*a*. *Dipterus uddeni* Eastm. Base of Cedar Valley limestone (Middle Devonian); Buffalo, Iowa. Left mandibular plate of holotype, shown from the oral and lateral aspects. Page.....218

Fig. 4. *Dipterus mordax* Eastm. State Quarry beds (Upper Devonian); North Liberty, Johnson county, Iowa. Right mandibular dental plate; contour not entirely complete. Cotype. Page.....220

Fig. 5. *Dipterus mordax* Eastm. A worn and somewhat fragmentary specimen from same horizon and locality as the last. Cotype. Page.....220

Fig. 6. *Dipterus digitatus,* sp. nov. Left palatal dental plate of cotype from same locality and horizon as the preceding. A photograph of the same specimen is reproduced in Plate VII, fig. 20. Page.....221

Fig. 7. *Dipterus pectinatus,* sp. nov. Palatal dental plate of cotype from same horizon and locality as the preceding. The concavity of the oral surface is in reality greater than the artist has here represented, and the lower right-hand margin is slightly deficient in the original. Other specimens illustrating the upper dentition of the same species are shown in Plate VII, figs. 11, 12 and 15. Page.....222

Fig. 8. *Dipterus costatus* Eastm. Left mandibular dental plate selected as holotype of the species, from same horizon and locality as the preceding. Page.....220

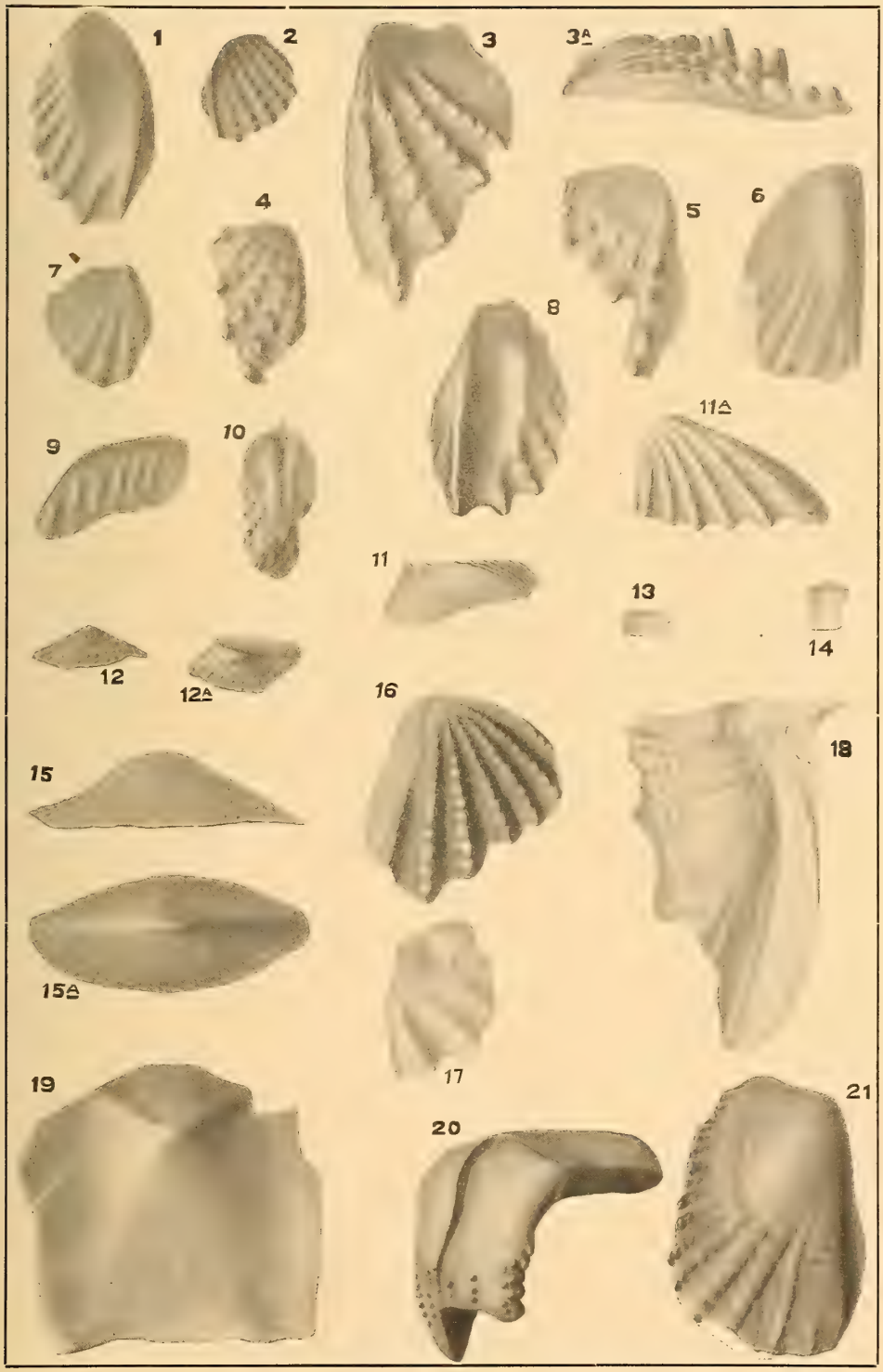

1
2
3
3A
4
5
6
7
8
9
10
11A
11
13
14
12
12A
16
18
15
15A
17
19
20
21

Plate II.—Continued.

Fig. 9. *Dipterus nelsoni* Newberry. Chemung beds; Warren, Pennsylvania. Oral surface of greatly abraded dental plate, worn so as to simulate the smooth forms usually referred to Sagenodus. Page 223

Fig. 10. *Dipterus murchisoni* Pander. Middle Devonian; Berndorf, Eifel District. Right mandibular dental plate of a Russian and Eifelian species approximating closely to the *D. mordax* series of Dakotan seas (*cf.* Plate VII, figs. 5-9). Original in Museum of Comparative Zoology. Page.....226

Figs. 11, 11*a*. *Dipterus nelsoni* Newberry. Chemung beds; Warren, Pennsylvania. Right mandibular dental plate shown from the antero-lateral and oral aspects. The same specimen is shown in natural juxtaposition with its fellow of the left side in Plate VII, fig. 3. Page.....223

Figs. 12, 12*a*. Small dermal tubercle, supposed to be of Chimaeroid nature, from the Kinderhook limestone of Burlington, Iowa. Compare with Fig. 15. Page.....149

Figs. 13, 14. Thelodus-like scales from the Columbus limestone (Middle Devonian) of Columbus, Ohio. x 3-1. Page...72

Figs. 15, 15*a*. Large-sized Chimaeroid (?) dermal plate from the Kinderhook limestone of Burlington, Iowa. Page.....149

Fig. 16. *Dipterus fleischeri* Newberry. Oneonta beds; Franklin, Delaware county, New York. Right palatal dental plate. Page 225

Fig. 17. Dipterus sp. ind. Worn example of palatal dental plate from the State Quarry beds (Upper Devonian) of Johnson county, Iowa. Page 216

Fig. 18. Scale-like dermal plate supposed to be of Chimaeroid nature, and theoretically associated with Rhynchodus. Compare with the young example of *Acanthaspis armata* shown in Plate I, fig. 14, and with the so-called "shoulder-girdle of Rhamphodus" as described by O. Jaekel. Hydraulic limestone (Hamilton); Milwaukee, Wisconsin. Page.....126

Fig. 19. *Synthetodus calvini,* sp. nov. State Quarry beds (Upper Devonian); North Liberty, Johnson county, Iowa. Holotype. Original in Museum of Comparative Zoology, Cambridge, Mass. Page 233

Plate II.—Continued.

Fig. 20. *Dinichthys lincolni* Claypole. Marcellus shale (Erian division of the Middle Devonian); Geneva, Ontario county, New York. Right vomerine tooth seen from the inner side and slightly from in front. Along the anterior face is seen a longitudinal fracture due to mechanical deformation; above and behind is the stout process serving for attachment of the tooth. Holotype in New York State Museum. Page.....193

Fig. 21. *Dipterus digitatus,* sp. nov. State Quarry beds (Upper Devonian); North Liberty, Johnson county, Iowa. Right mandibular plate of a fully grown individual. A photograph of the same specimen is reproduced in Plate VII, fig. 25. Compare with the series of palatal dental plates belonging to the same species, and shown in Plate VII, figs. 20-24. Page.....221

Plate III.

Fig. 1. *Gyracanthus sherwoodi* Newberry. Chemung beds; Ischua township, Cattaraugus county, New York. Drawn from squeeze of spine. x 3-4. Page.....114

Fig. 2. Detail of surface ornamentation of Arthrodiran (?) plates similar to those described by Newberry under the name of Sphenophorus (="Oestophorus" S. A. Miller), from the Hamilton limestone of Milwaukee, Wisconsin. x 2-1. Page.207

Fig. 3. *Cladodus urbs-ludovici,* sp. nov. Genesee shale (="New Albany black shale"); near Louisville, Kentucky. Holotype in Museum of Comparative Zoology, Cambridge, Mass. x 2-1, approximately. Page.....110

Fig. 4. *Machaeracanthus sulcatus* Newberry. Onondaga limestone; Victor, Ontario county, New York. Re-drawing of holotype figured by Hall; original in New York State Museum. x 3-4. Page 114

Fig. 5, 5*a*. Acantholepis sp. Corniferous limestone; Falls of the Ohio. A small, probably immature and fragmentary spine, showing expanded nature of the pyramidal inserted portion. The lateral and anterior faces are shown in figs. 5 and 5*a* respectively. x 3-4. Page.....142

Fig. 6. *Ptyctodus punctatus* Eastm. Onondaga limestone (Ulsterian division of the Middle Devonian); LeRoy, New York. Functional surface of the detached tritor. x 3-4. Page.....133

Fig. 7. *Coelacanthus welleri,* sp. nov. Kinderhook limestone; Burlington, Iowa. Flank scales, slightly enlarged, showing spiniform ornamentation. Holotype in Walker Museum of University of Chicago. Page.....247

Fig. 8. *Rhynchodus major* Eastm. Upper Devonian; Wildungen, Waldeck. Left upper and lower dental plates (inner aspect) arranged in natural position. The outlines of these plates are copied from Jaekel, who figures them, however, in inverted position, and renames the species "*R*[*h*]*amphodus tetrodon.*" x 3-4. Page.....127

Plate III.—Continued.

Fig. 9. *Onchus rectus* Eastm. Chemung group; Delaware county, New York. Dorsal fin-spine, lateral face. x 6-5. Page 150

Fig. 10. *Homacanthus acinaciformis* Eastm. Chemung group; Warren, Pennsylvania. Dorsal fin-spine, lateral face. x 4-3. Page 151

Fig. 11. *Dinichthys pustulosus* Eastm. Oneonta sandstone (Portage group); Delhi, New York. External aspect of left mandibular ramus, partly restored. x 1-2, approximately. Page 194

Fig. 12. *Dinichthys pustulosus* Eastm. Cedar Valley limestone; near Rock Island, Illinois. Incomplete mandible collected and drawn by Orestes H. St. John, and described in the American Naturalist for 1902, p. 657. x 3-4. Page.....194

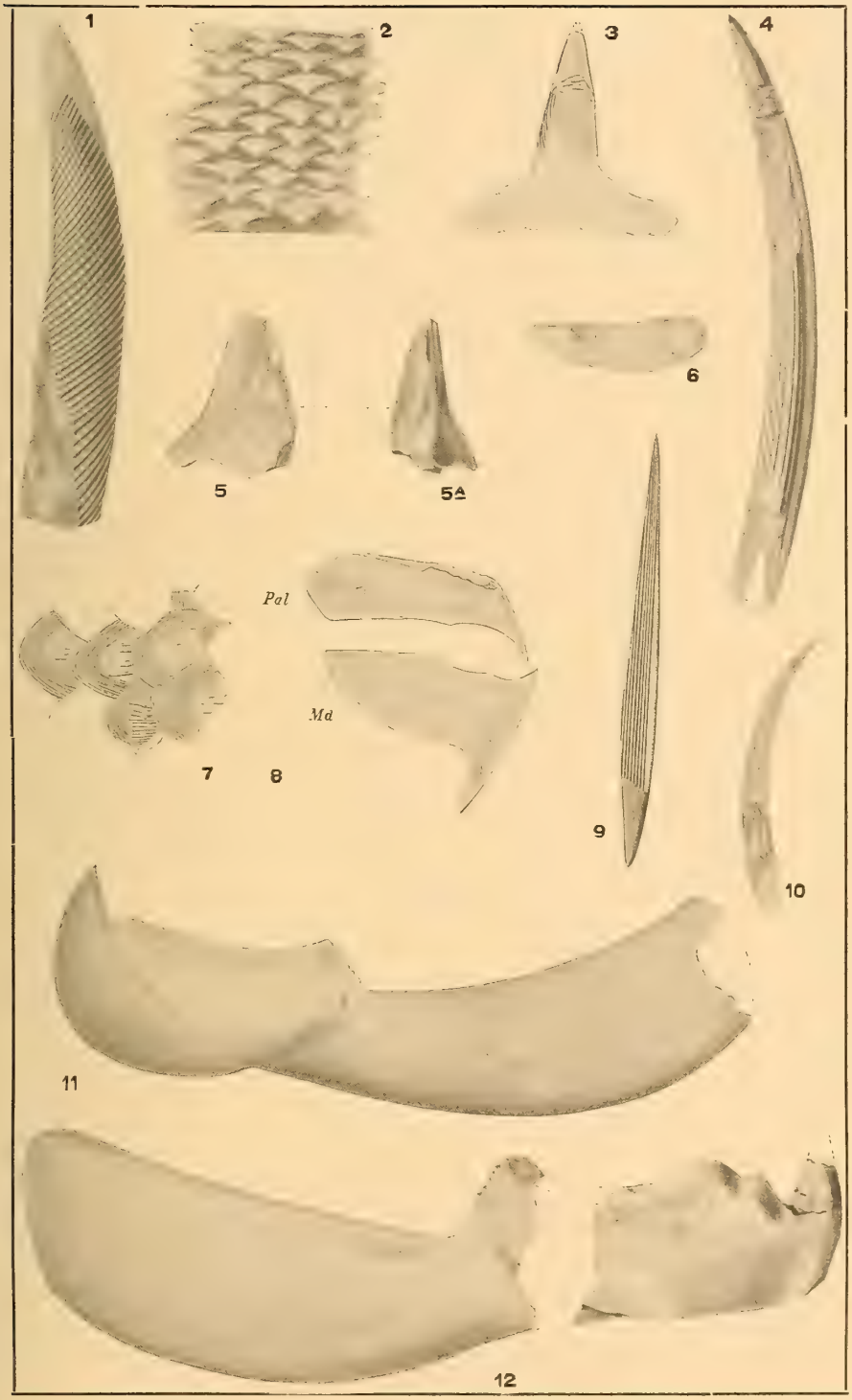

1
2
3
4
5
5A
6
Pal
Md
7
8
9
10
11
12

Plate IV.

Dinichthys pustulosus Eastm. Lower part of the Cedar Valley limestone (Middle Devonian); near Rock Island, Illinois. Dorsal aspect of moderate-sized headshield, showing cranial sutures, sensory canals and other features very distinctly. The median occipital plate is removable, showing conformation of the visceral surface, and median depression for the attachment of muscles, etc. Original collected by Mr. A. S. Tiffany, of Davenport, and now preserved in the Museum of Comparative Zoology, Cambridge. x 1-2. Page.....194

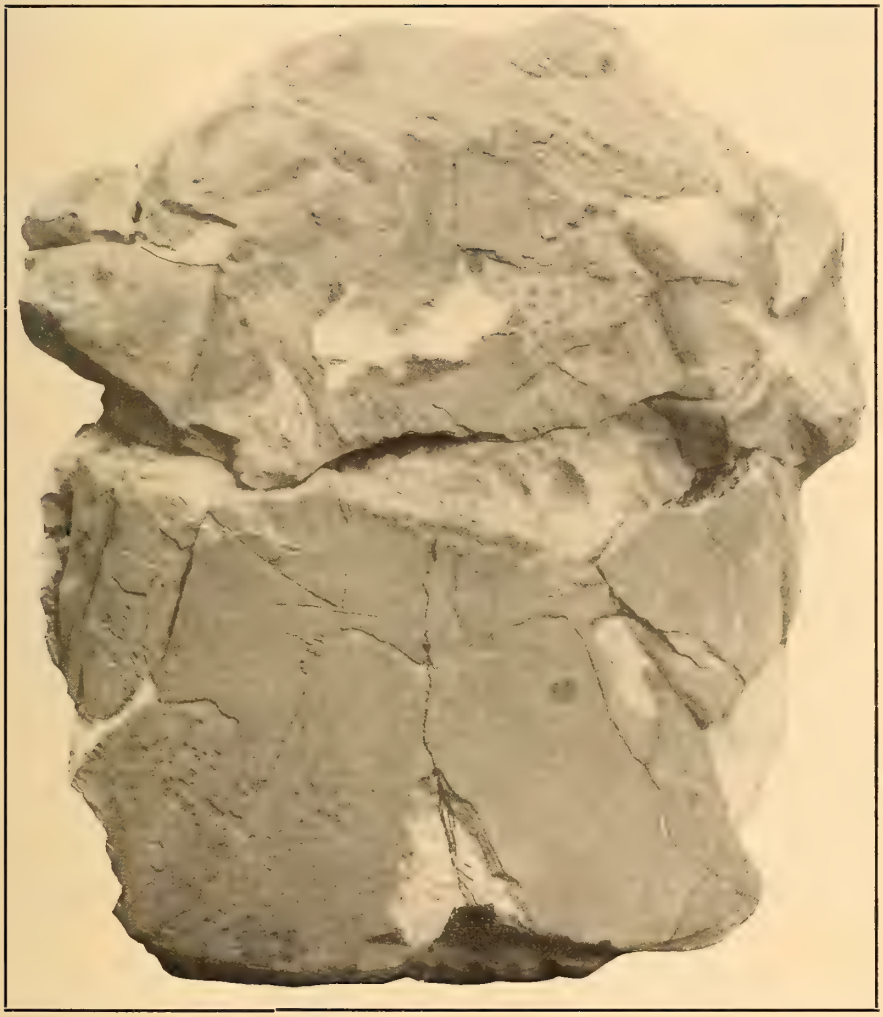


Plate V.

EXAMPLES OF PTYCTODONT DENTITION FROM VARIOUS DEVONIAN LOCALITIES.

All figures reduced a trifle less than natural size.
Originals preserved in the Museum of Comparative Zoology.

Figs. 1-17. *Ptyctodus calceolus* Newb. and Worthen. State Quarry beds (Upper Devonian); Johnson county, Iowa. The distinction between upper and lower dental plates is apparent from the configuration of the symphysial portion, a prominent beak and obtuse descending process being developed in the lower, and the corresponding region of the superior being gently rounded. The lower beaks are preserved in the originals of Figs. 1, 5-9, 16, the last being a nearly complete specimen. Page 133

Figs. 18-27. *Ptyctodus compressus* Eastman. State Quarry beds (Upper Devonian); Johnson county, Iowa. Symphysial beaks of the lower dentition well shown in Figs. 23-27. Page.135

Figs 28-30. *Ptyctodus molaris* Eastman. Middle Devonian; Eifel District, Rhenish Prussia. The holotype, shown in Fig. 28, is a nearly perfect example of the lower dental plate, and shows traces of sutural attachment with its fellow of the opposite side.

Figs. 31-34. *Ptyctodus panderi* Eastman. Middle Devonian; Eifel District, Rhenish Prussia. Figs. 31, 32 show collectively the greater portion of the Rhynchodus-like inferior dental plate, the oral surface of which, however, displays punctate tritoral areas. Detached examples of the tritors are shown in Figs. 33, 34.

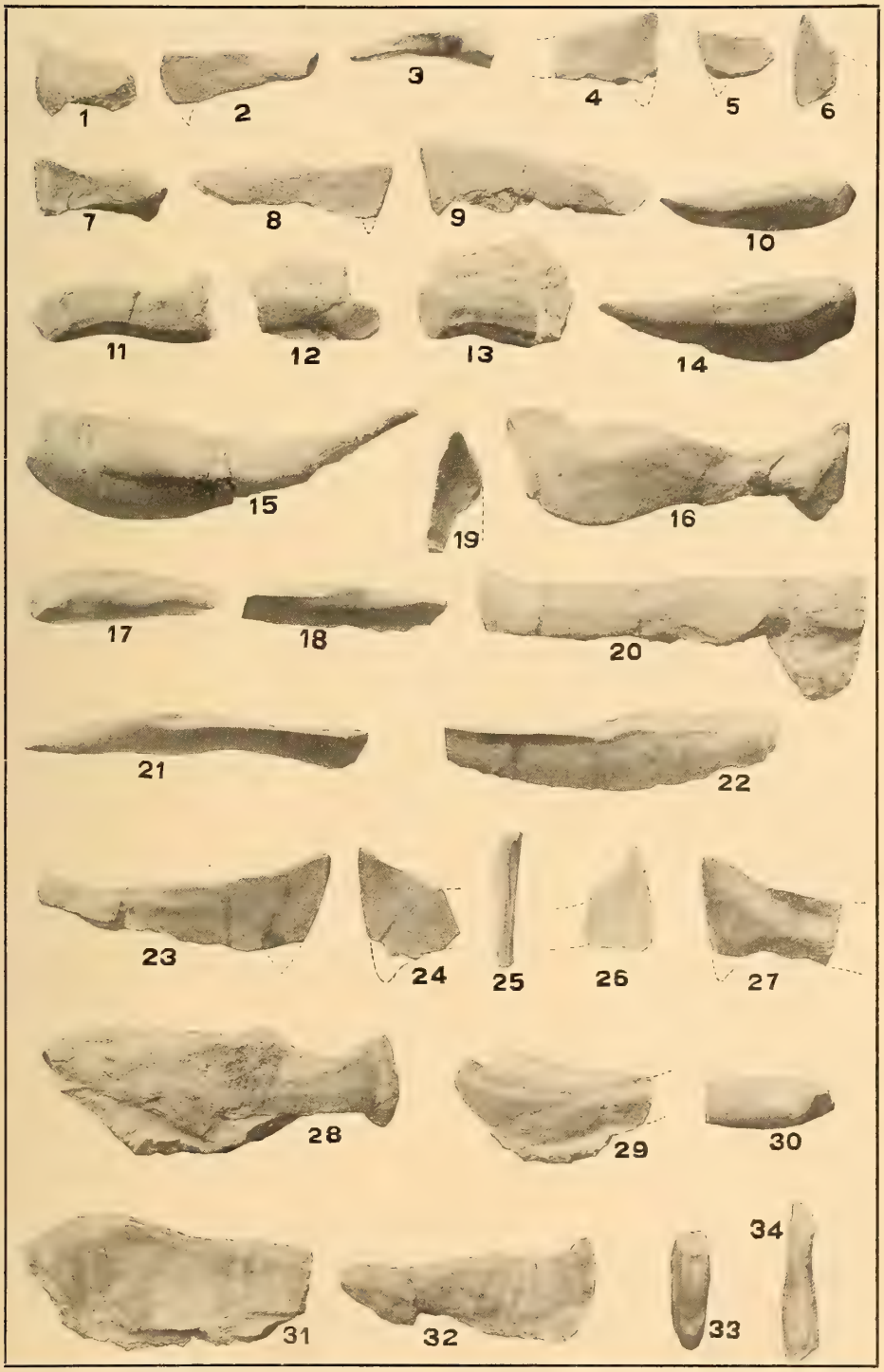

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
19
16
17
18
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34

Plate VI.

EXAMPLES OF PTYCTODONT DENTITION FROM THE IOWA UPPER DEVONIAN.

All figures are of the natural size.

A miscellaneous assortment of detached tritors, all more or less worn by use, and otherwise rolled and abraded, this being the usual condition in which remains of this sort are found in the Old State Quarry beds near North Liberty, in Johnson county, Iowa. The greater number of these tritors belong to *Ptyctodus calceolus* Newb. and Worthen, and are shown of the natural size. Originals in the Museum of Iowa State University. Page 133

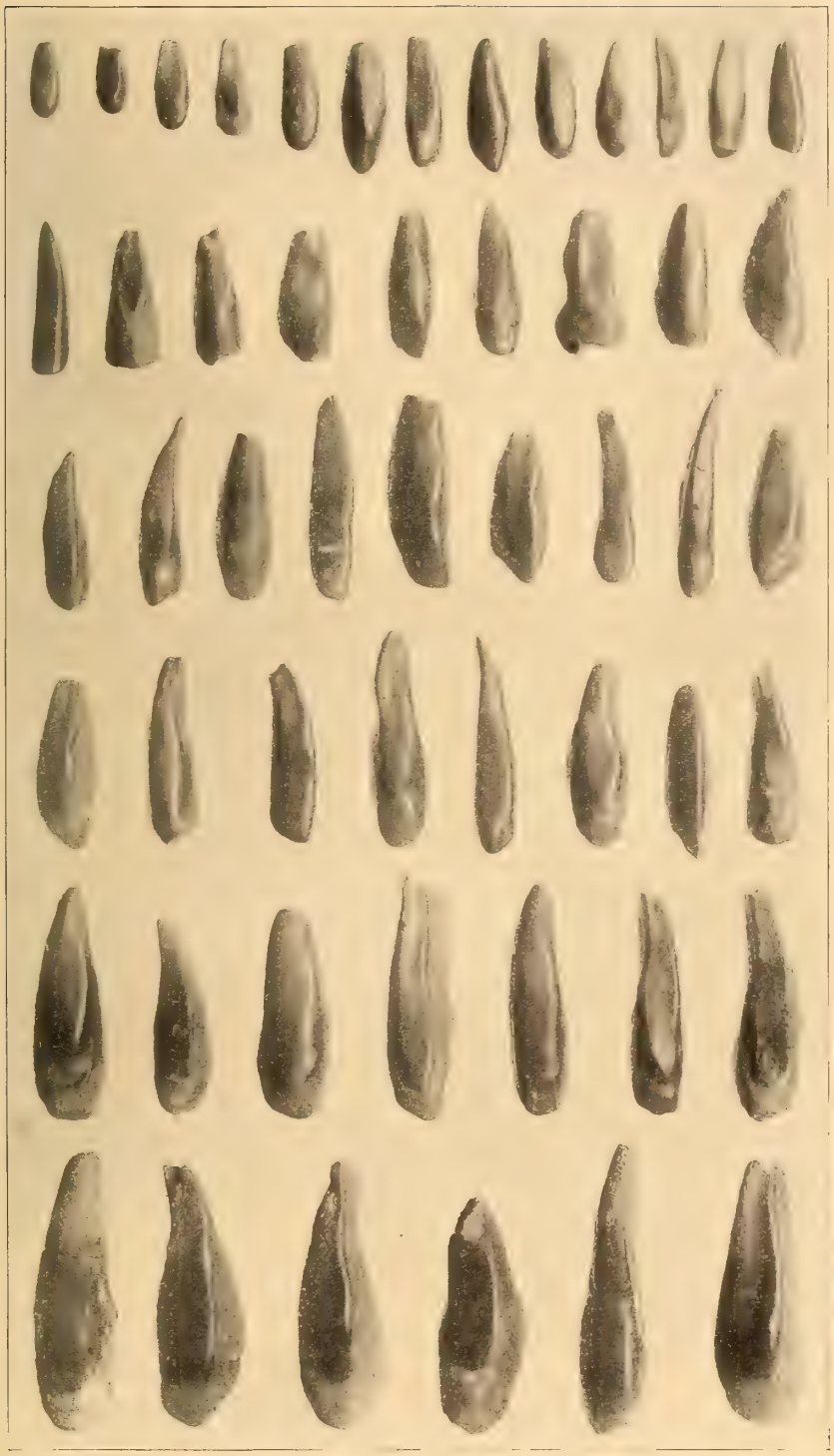


Plate VII.

EXAMPLES OF CTENODIPTERINE DENTITION, MOSTLY FROM THE IOWA UPPER DEVONIAN.

All figures are of the natural size.

Figs. 1-4. *Dipterus nelsoni* Newberry. Chemung; Warren. Pennsylvania. In Fig. 1 is shown a right upper dental plate of the so-called "*D. flabelliformis*" type, and in Figs. 2-4 the corresponding mandibular dental plates of both sides of the mouth. The original of Fig. 2 is one of Newberry's cotypes of this species, and is now preserved in the Peabody Museum at Yale University. The others are the property of the Museum of Comparative Zoology at Cambridge. The original of Fig. 3 is also shown in Plate II, Fig. 11, 11*a*. Page.....223

Figs. 5-9. *Dipterus mordax* Eastman. State Quarry beds (Upper Devonian); Johnson county, Iowa. Small sized examples of the inferior dental plates, to be compared with those shown in Plate II, Figs. 4, 5. Page.....220

Figs. 10-15. *Dipterus pectinatus,* sp. nov. State Quarry beds (Upper Devonian); Johnson county, Iowa. Lower dental plates represented in Figs. 10, 13, 14; upper in Figs. 11, 12, 15. The original of Fig. 13 is also shown in Plate II, Fig. 2. Page..222

Figs. 16-25. *Dipterus digitatus,* sp. nov. State Quarry beds (Upper Devonian); Johnson county, Iowa. Lower dental plates represented in Figs. 16-19, 25; upper in Figs. 20-24. The original of Fig. 20 is also shown in Plate II, Fig. 6. Page.....221

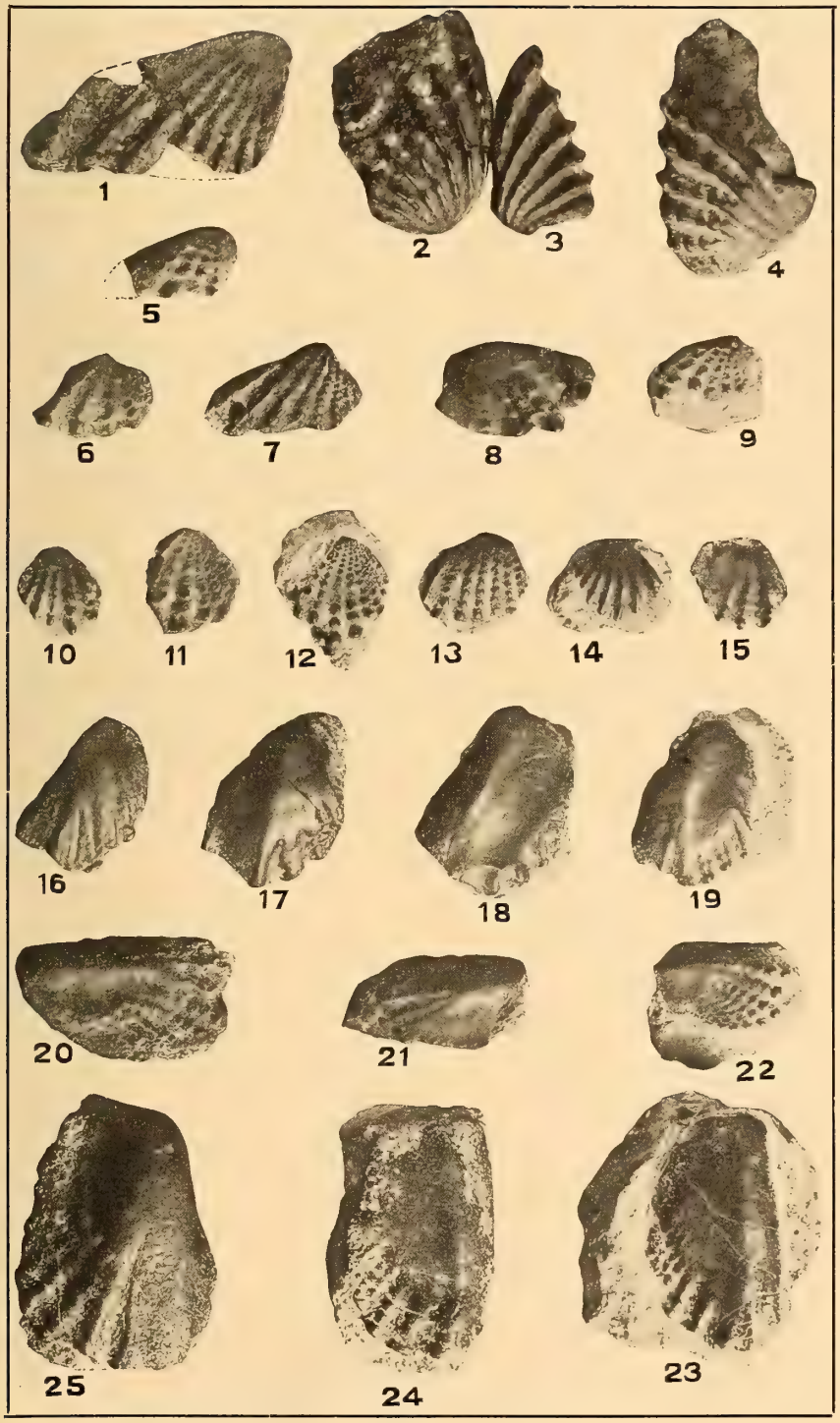

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
25
24
23

Plate VIII.

EXAMPLES OF STATE QUARRY CTENODIPTERINE DENTAL PLATES.

All figures very nearly of the natural size.

The greater number of specimens selected for illustration in this Plate (all except Figs. 16, 20, 29, 34) are determined as belonging to *Conchodus variabilis,* sp. nov., and form a representative series, showing the wide range of variation exhibited by the detached dental structures, and with evanescent traces of coronal plications (seen especially at the bottom of Figs. 13, 15, 28, 33, etc.). The four exceptional figures are probably worn or otherwise imperfect specimens of *Synthetodus calvini,* all from the State Quarry beds near North Liberty in Johnson county, Iowa.

Originals preserved in the Museum of Iowa State University.

Pages.....230 and 233

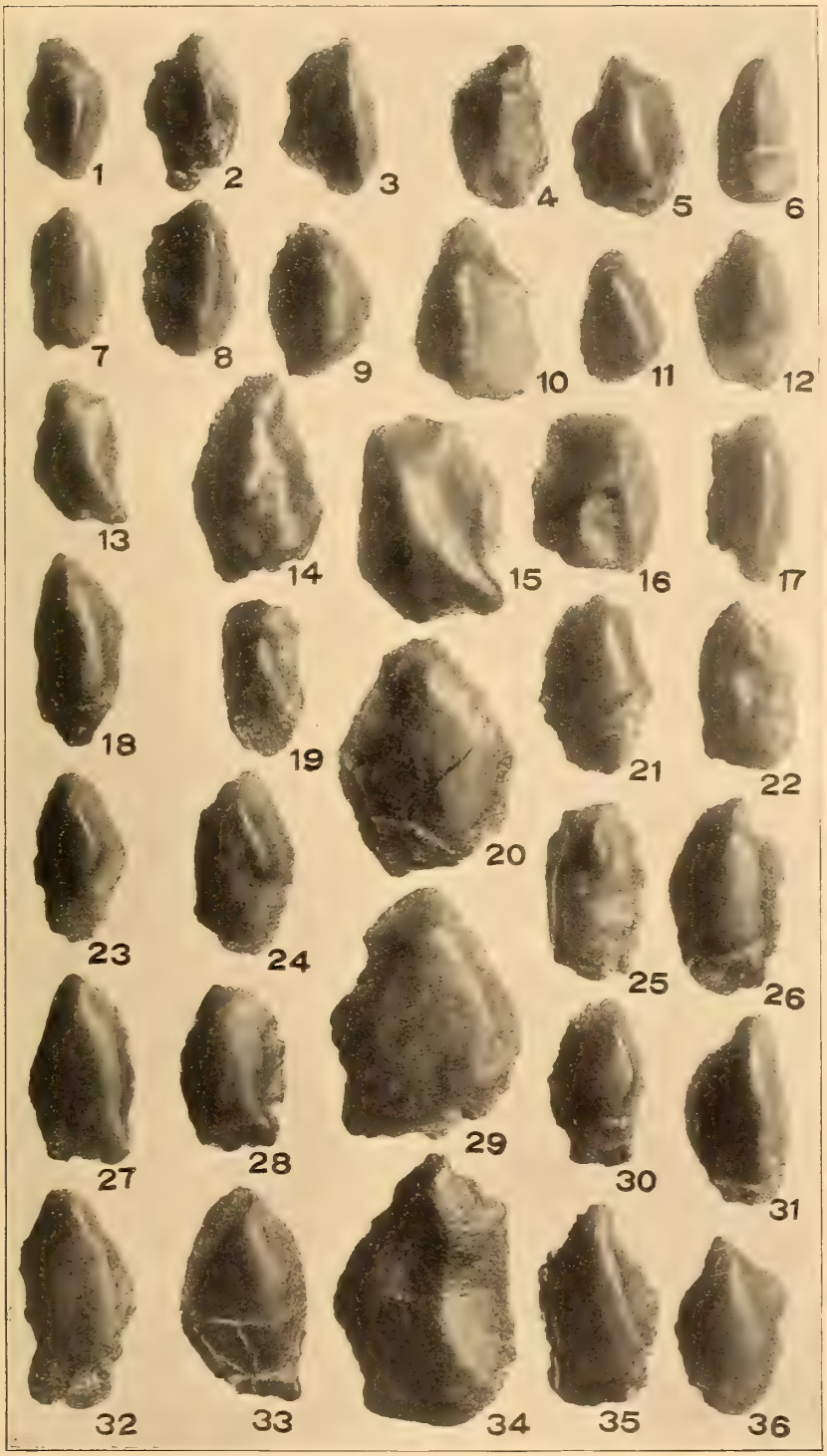

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

Plate IX.

EXAMPLES OF STATE QUARRY SYNTHETODONT DENTAL PLATES.

All figures reduced slightly less than the natural size.

In this plate is shown a representative assortment of the compound dental plates of *Synthetodus trisulcatus,* with perhaps one or two mutilated examples (Figs. 19, 32) of *S. calvini,* all from the State Quarry beds near North Liberty, in Johnson county, Iowa. The two upper rows represent the normal expression for the type species.

Originals preserved in the Museum of Iowa State University. Pages.....231 and 233

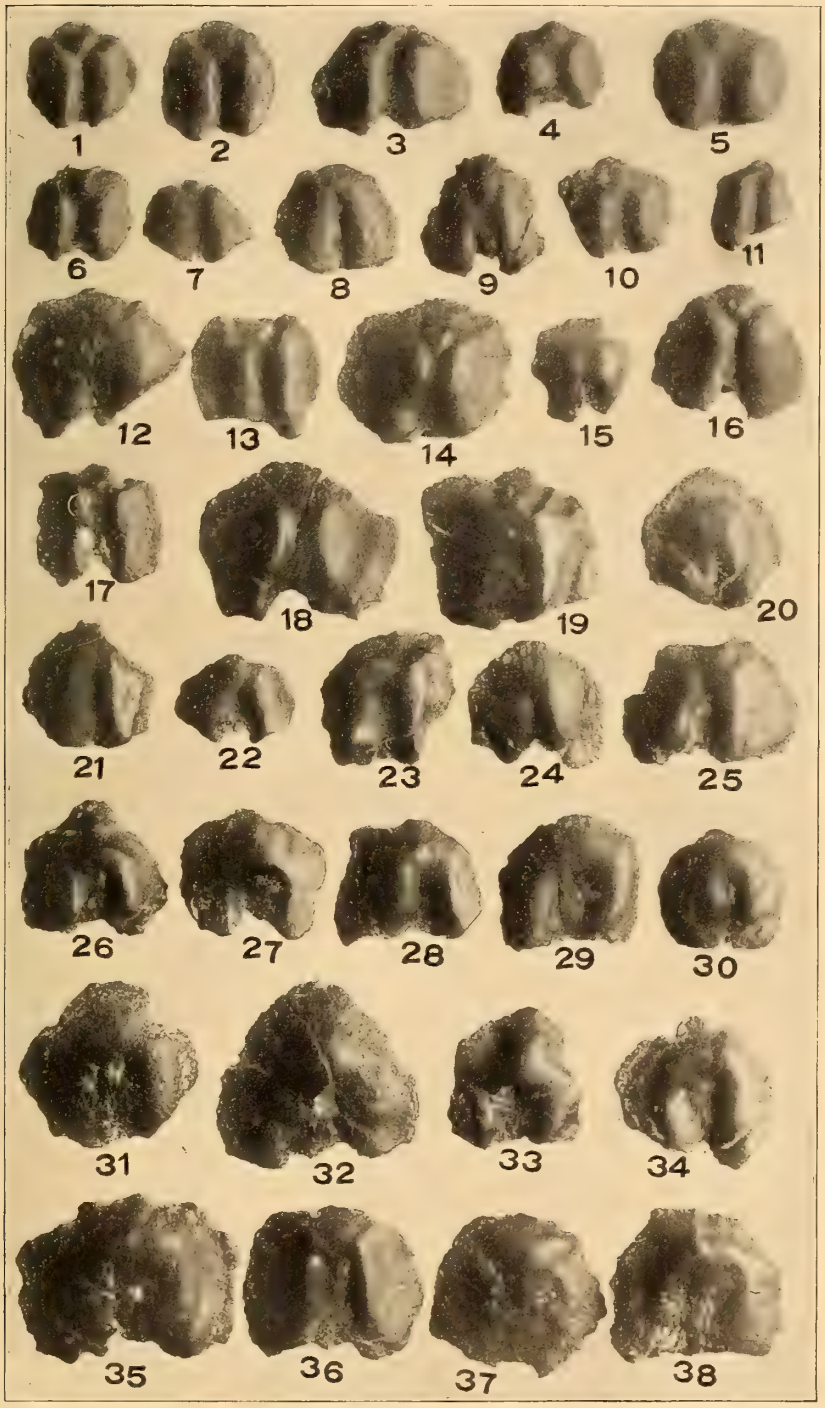

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38

Plate X.

EXAMPLES OF STATE QUARRY SYNTHETODONT DENTAL PLATES.

All figures reduced slightly less than natural size.

The larger specimens in the middle row and at the bottom of the Plate are determinable as belonging to *Synthetodus calvini,* the remainder as imperfect examples of *S. trisulcatus;* all from the State Quarry beds near North Liberty, in Johnson county, Iowa.

Originals preserved in the Museum of Iowa State University.

Pages .....231 and 233

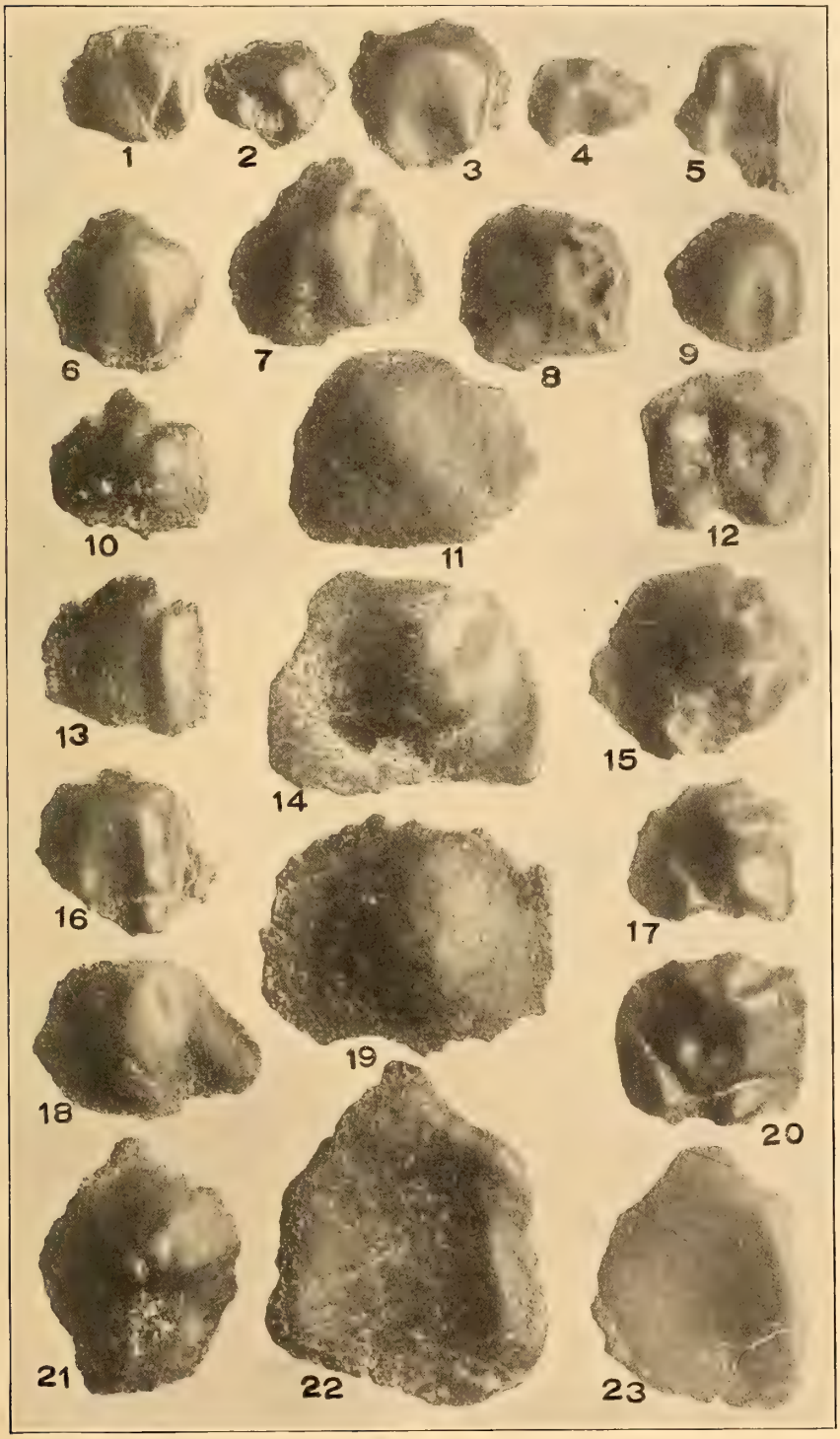

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Plate XI.

EXAMPLES OF STATE QUARRY SYNTHETODONT DENTAL PLATES.

All figures reduced slightly less than the natural size.

The smaller plates with more or less distinct sulci, such as the originals of Figs. 6, 8, 10, 15, 22, 23, 25, etc., are determinable as belonging to *Synthetodus trisulcatus,* the larger ones, which are apparently simple, as somewhat imperfect examples of *S. calvini;* all from the State Quarry beds near North Liberty, in Johnson county, Iowa.

Originals preserved in the Museum of Iowa State University.

Pages .....231 and 233

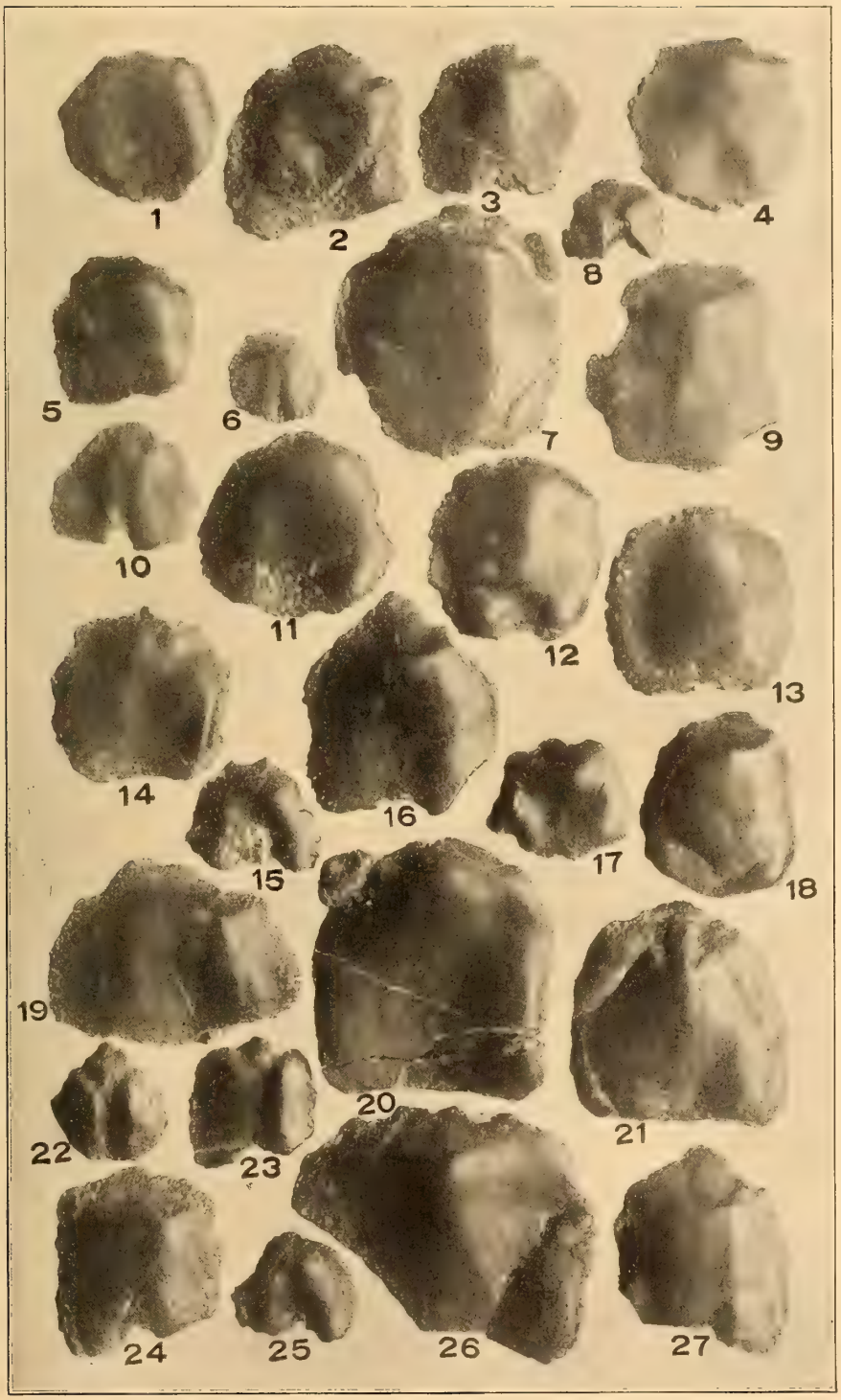

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27

Plate XII.

EXAMPLES OF STATE QUARRY SYNTHETODONT DENTAL PLATES.

All figures reduced slightly less than the natural size.

In this Plate is shown a representative assortment of dental plates belonging to *Synthetodus calvini.* The originals of Figs. 7, 9, 12-15, are interpreted as constituting the lower, and the remainder, with the exception of Fig. 16, as the upper pavement dentition of this species. In Fig. 16 is seen a unique calcified vertebral body, also from the State Quarry "fish-beds," whose relations are considered problematical.

Originals preserved in the Museum of Comparative Zoology at Cambridge, Mass. Pages.....147 and 233

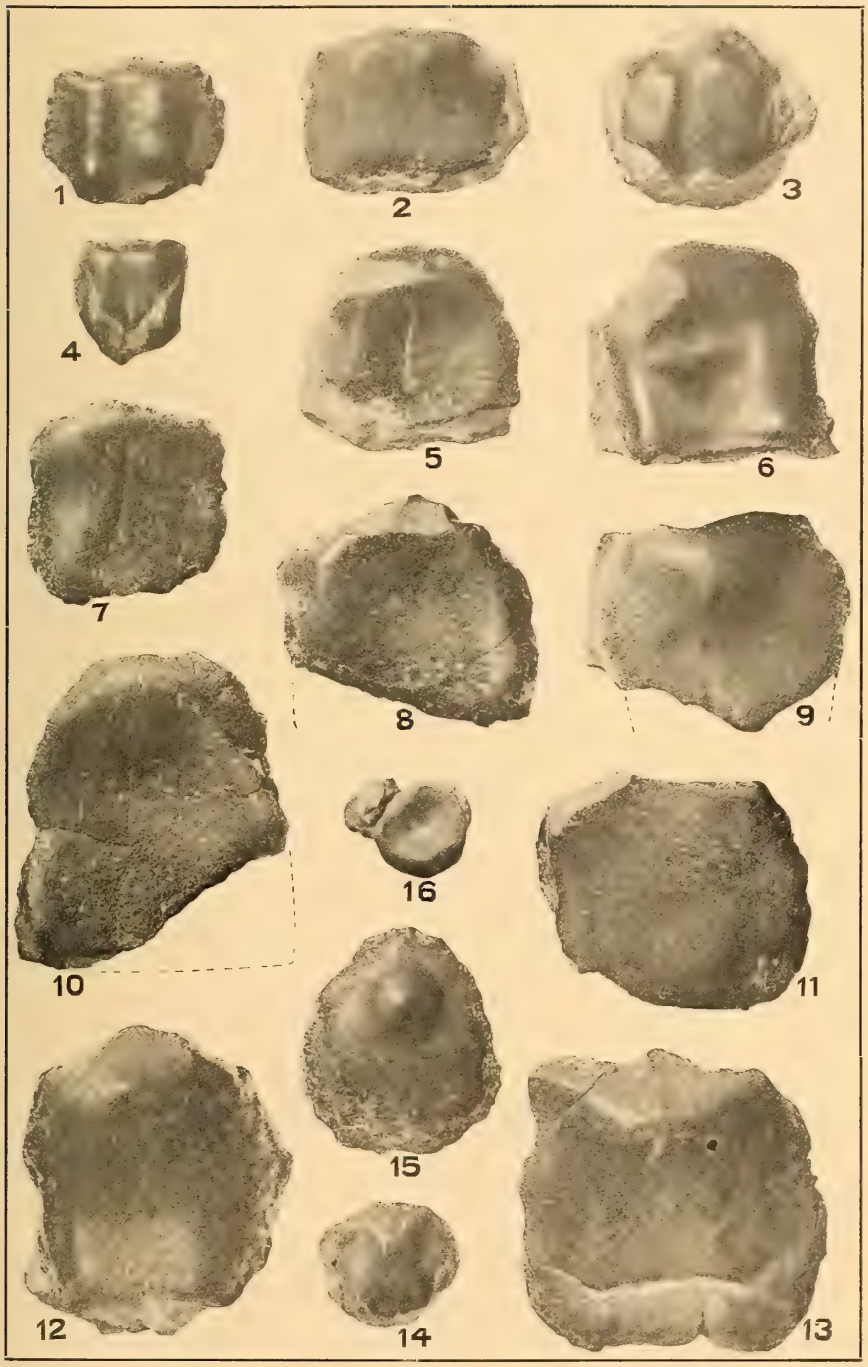

1
2
3
4
5
6
7
8
9
10
16
11
15
12
14
13

Plate XIII.

CRANIA OF *RHADINICHTHYS DEANI*, SP. NOV.

All figures are represented of the natural size.

A series of phosphatic nodules from the base of the Waverly near Junction City, in Boyle county, Kentucky, which have been cleaved in such manner as to display their organic nuclei. In the case of each specimen here illustrated, this consists of the headshield, sometimes with other naturally associated parts of a new species of Rhadinichthys. The cranial roof may be exposed, with or without the superficial ornament, according to the position of the plane of fracture; and in a few fortunate instances, an example of which is furnished by Figs. 8, 9, the cranial roof has been lifted off so as to reveal the structure of the mineralized brain, auditory organs, and arterial blood-vessels. Most of these specimens, like the originals of Figs. 8 and 9, 14 and 15, are preserved in counterpart. The first of these pairs is also shown in text-figure 40, *A-B*.

Originals preserved in the Museum of Comparative Zoology at Cambridge, Mass. Page.....264

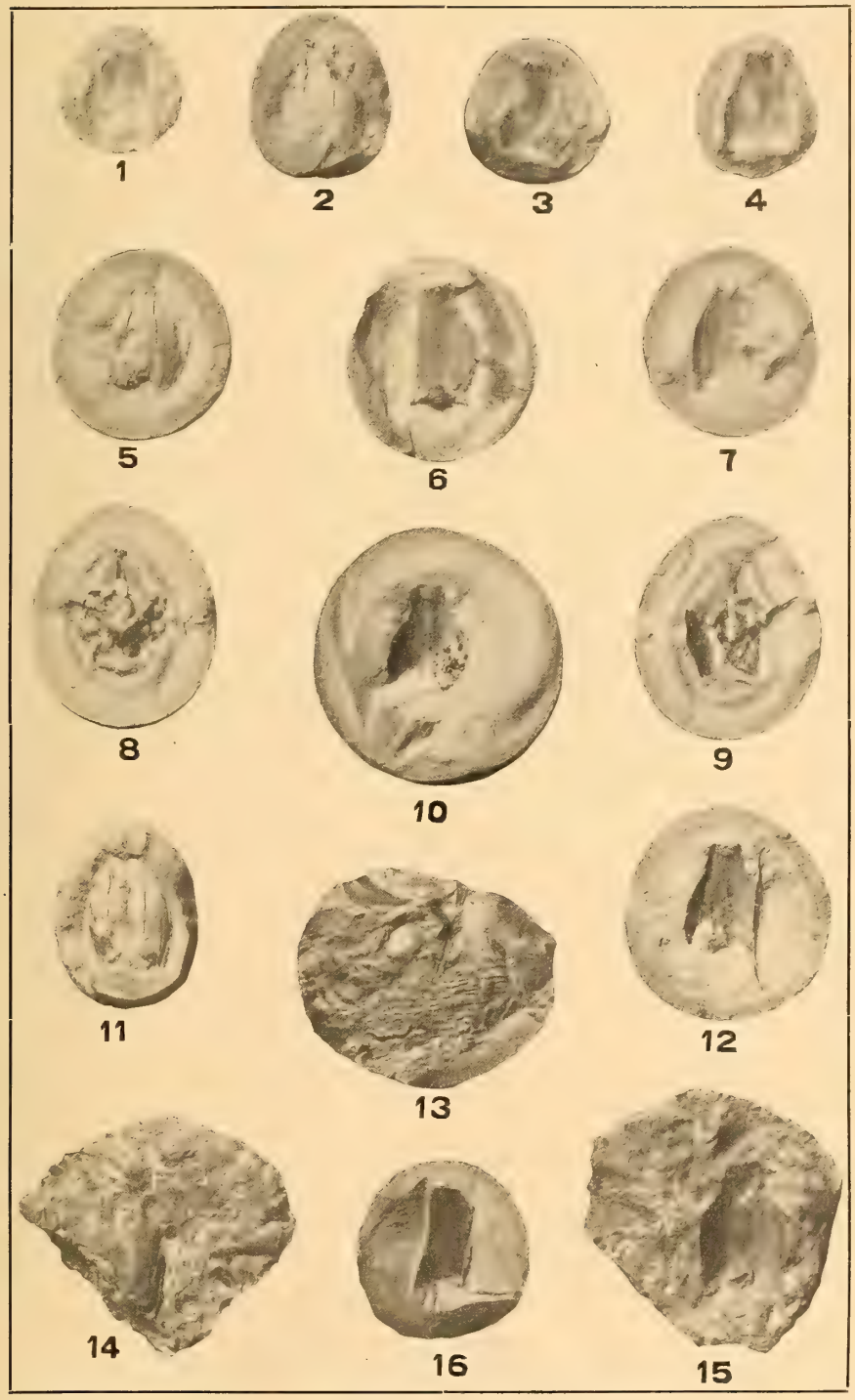

1
2
3
4
5
6
7
8
10
9
11
13
12
14
16
15

Plate XIV.

Areal Map of North American Middle Devonian

Professor Schuchert's reconstruction of Middle Devonian palæogeography at the close of Onondaga time. Noteworthy is the large extent of the interior continental area, the western borders of which are only conjecturally indicated.


ARCTIC OCEAN
DAVIS STRAIT
HUDSON BAY
DOMINION OF CANADA
PACIFIC
HUDSON
GASPE


CORDILLERAN
OHIOAN
MISSISSIPPIAN
APPALACHIA
GULF OF MEXICO
CARIBBEAN SEA
SOUTH AMERICA
ATLANTIC OCEAN
MIDDLE DEVONIC PALEOGEOGRAPHY
CLOSE OF ONONDAGA TIME

MIDDLE DEVONIC PALEOGEOGRAPHY
CLOSE OF ONONDAGA TIME

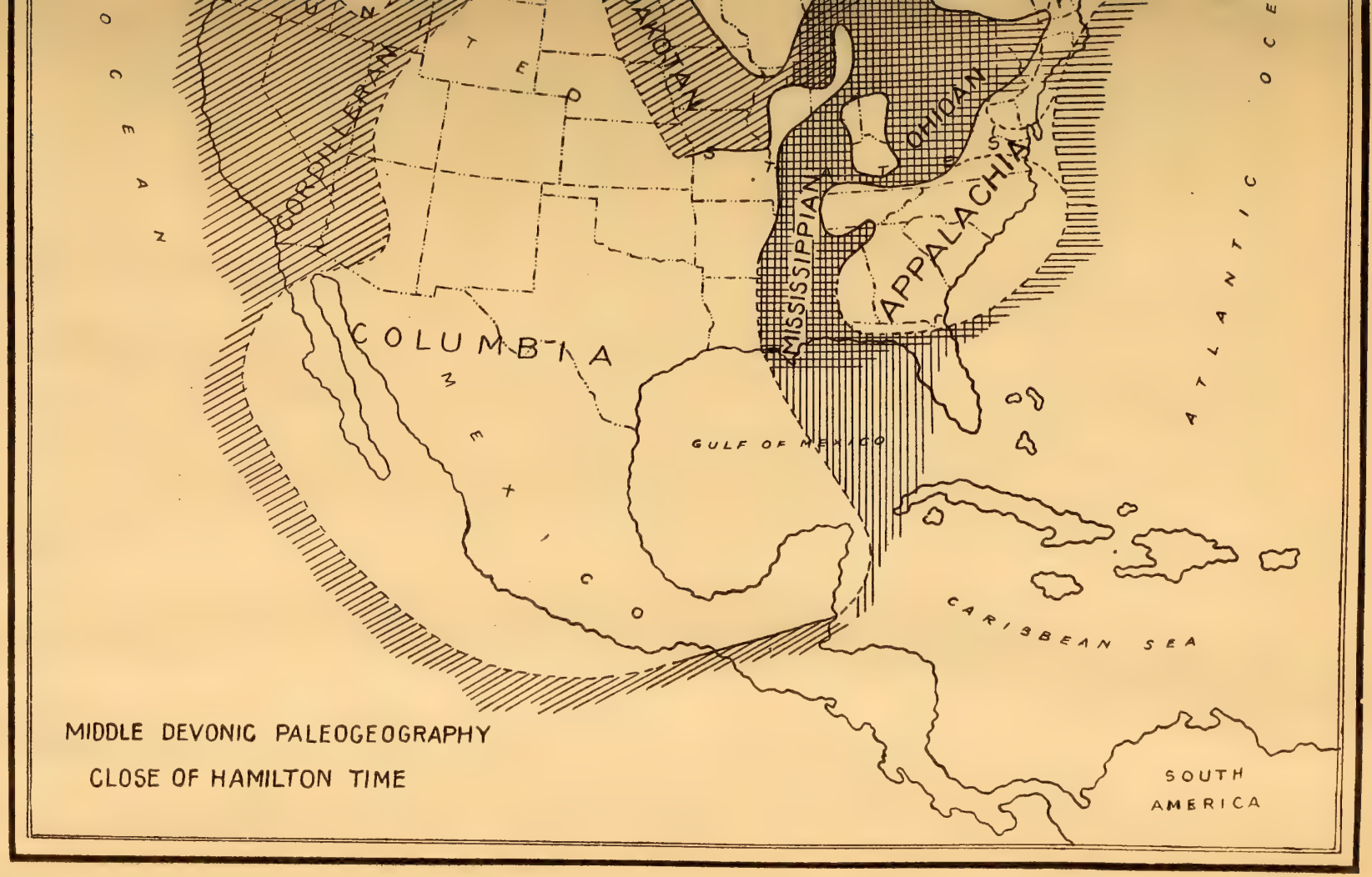
CLOSE OF ONONDAGA TIME
(MODERN TIME)

Plate XV.

Areal Map of North American Middle Devonian.

Professor Schuchert's reconstruction of Middle Devonian palæogeography at the close of Hamilton time. Partial submergence is indicated for the interior continental area, the two principal land-masses (designated as "Laurentia" and "Columbia") being separated by the encroachment of the "Dakotan sea." The "Ohioan sea" is represented as being in less open communication with oceanic bodies on the east and south than during the period immediately preceding.


ARCTIC OCEAN
DAVIS STRAIT
LAURENTIA
HUDSON BAY
PACIFIC
OF CANADA
HUDSON
ONTARIO


CORDILLERAN
DAKOTAN
MISSISSIPPIAN
OPIDAN
APPALACHIA
COLUMBIA
GULF OF MEXICO
CARIBBEAN SEA
SOUTH AMERICA
ATLANTIC OCEAN
MIDDLE DEVONIC PALEOGEOGRAPHY
CLOSE OF HAMILTON TIME

MIDDLE DEVONIC PALEOGEOGRAPHY
CLOSE OF HAMILTON TIME

FIGURE 3 DEVOND BALLOON HARBOGRAPHY
CHORE OF HAMILTON TIME

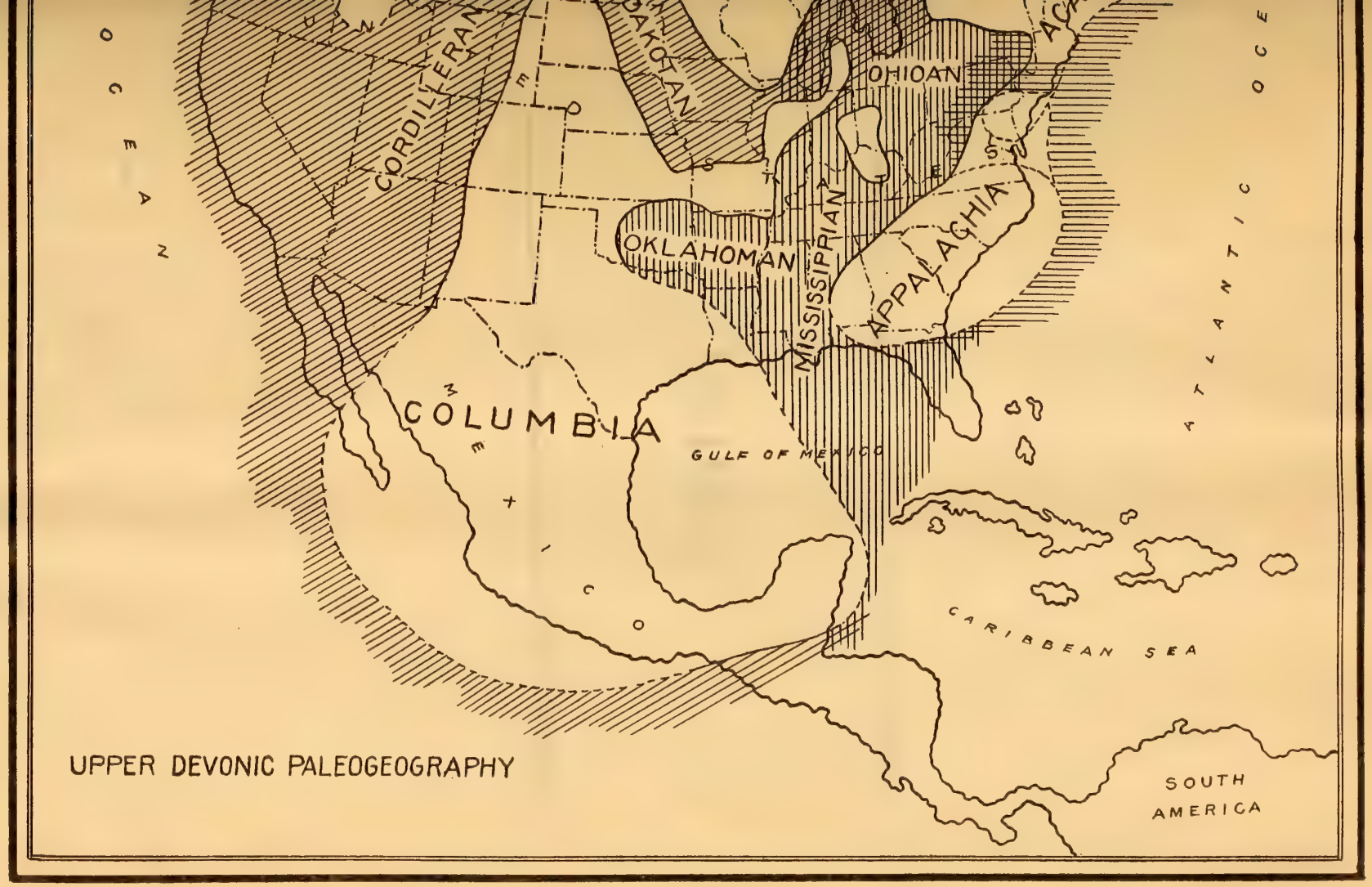
Plate XVI.

Areal Map of North American Upper Devonian.

Professor Schuchert's reconstruction of Upper Devonic palæogeography. The Appalachian and Columbian land-masses are represented as more shrunken in area than during earlier periods of the Devonian, and a westward extension of the Mississippian sea receives the name of Oklahoman. In the Cordilleran region it is probable that a larger land-mass was elevated above sea level than is here conjecturally represented.

MAP OF GERMANY


ARCTIC OCEAN
DAVIS STRAIT
HUDSON BAY
LAURENTIA
PACIFIC
OF CANADA



UPPER DEVONIC PALEOGEOGRAPHY

UPPER DEVONIC PALEOGEOGRAPHY

ÜBER DEN ATLANTIC OCEAN

INDEX

Figures in Italics refer to pages on which descriptions are given.

A

C

M

N

O

Q

R

T