MEMOIRS

OF THE

American Museum of Natural History.

VOLUME IX, PART III.

III.—Studies on the Arthrodira.

BY LOUIS HUSSAKOF.

May, 1906.

The Knickerbocker Press, New York

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PART III.—STUDIES ON THE ARTHRODIRA.

By Louis Hussakof.

Plates XII and XIII.

CONTENTS.

I.—INTRODUCTION.

After nearly a century of study, the structure and relationship of the Arthrodira are but imperfectly understood. They have been regarded as allied to the Ostracophores (McCoy, '48, Pander, '57, Huxley, '61, Traquair, '88, Jaekel, '02); Teleostomes (Huxley, '61, Regan, '04); Dipnoans (Woodward, '91, Dean, '95, Eastman, '06); and Chimæroids (Jaekel, '02). In 1899 Professor Bashford Dean advanced the view that they are not in fact fishes (*sensu stricto*), since their gnathal apparatus is not homologizable with the vertebrate jaw, constituted of a modified mandibular arch. He maintained that the Arthrodira, with their allies the Anarthrodira, constitute a major division of the vertebrates which he termed Arthrognathi.

In the present research my aim was primarily to reëxamine the question of the relationship of the Arthrodira; and since the views bearing on this subject have been so largely based upon the mouth parts, or "jaws," in these forms, I directed my attention, as a matter of especial importance, to elucidating the structure and mode of action of these elements.

A study of the jaws and of their manner of attachment led next to a detailed investigation of the structure and interrelationship of all the known Arthrodires. And in tracing the various forms through successive geological horizons, certain evolutionary stages became apparent, so that an attempt was made provisionally to outline the evolution of the group, particularly in its North American forms.

Some of the arthrodiran material is very fragmentary; in fact, several genera (*e.g.*, *Diplognathus*, *Glyptaspis*, and others) are known only from a few isolated plates. Such material is discussed with extreme caution and as far as possible the drawing of inferences from it is avoided, except in the case of elements, whose status is well known in kindred species or genera, *e.g.*, the lower jaws of *Diplognathus*, the upper fang of *Dinichthys lincolni*, etc. And throughout the present research I have endeavored, as far as practicable, to keep distinct, the facts and the theoretical conclusions deduced from them.

This investigation was carried on in the Zoölogical Laboratories of Columbia University and at the American Museum of Natural History. In the latter institution, as Assistant to Professor Bashford Dean, Honorary Curator of Fishes, I have enjoyed the privilege of studying the remarkable Newberry collection of American arthrodiran material, now deposited by Columbia University in the American Museum. I feel deeply grateful to Professor Dean for the innumerable kindnesses he has shown me during the progress of my studies, and for his constant helpful suggestions and criticisms. My thanks are also due to the other officers of the Department of Zoölogy at Columbia for the uniform courtesy shown me during my period of residence, as well as

for a grant from the Dyckman Fund, which they voted me, enabling me to study the marine fauna at the Bermuda Biological Station during the summer of 1903. I am under obligations, also, to Dr. Chas. R. Eastman of the Cambridge Museum of Comparative Zoölogy, with whom a number of my views were discussed, for some valuable suggestions and for the loan of specimens; to Dr. A. Smith Woodward for several important observations on specimens in the British Museum and for a set of casts of a unique *Dinichthys* dentition; to Dr. Lynds Jones of Oberlin College for the loan of a small but valuable collection of dinichthyid plates; and to Professor John M. Clarke Geologist of the State of New York, for permission to reproduce an unpublished figure. I desire also to express my thanks to the Rev. Dr. William Kepler and to Dr. William Clark, the veteran Ohio collectors, for the many kindnesses shown me in the summer of 1905 while exploring the classical dinichthyid localities in Ohio.

II.—THE NOMENCLATURE OF THE ARTHRODIRAN JAW.

Palæontologists are familiar with the number and type of elements composing the arthrodiran jaw. This section, therefore, will be restricted to a discussion of the nomenclature, and to the notice of some details hitherto either unobserved or insufficiently emphasized.

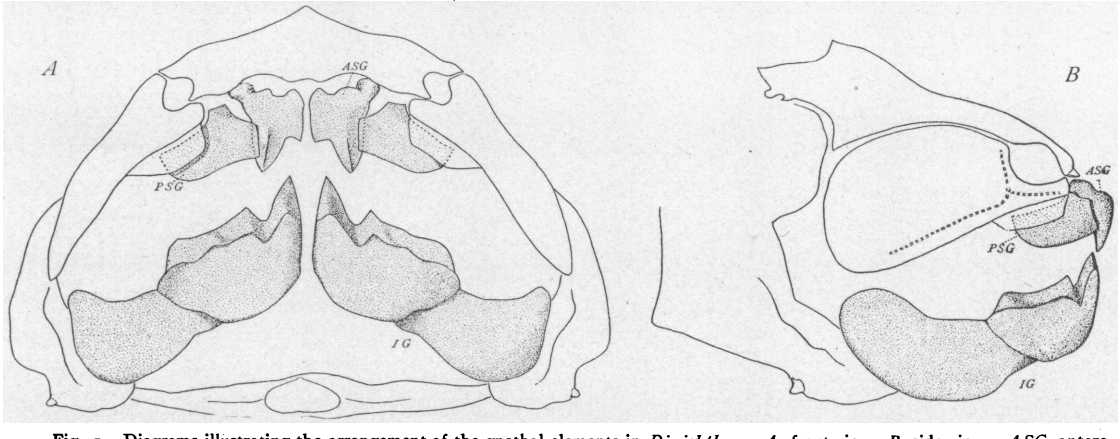

Fig. 1. Diagrams illustrating the arrangement of the gnathal elements in *Dinichthys*. *A*, front view; *B*, side view. *ASG*, antero-supero-gnathal; *IG*, infero-gnathal; *PSG*, postero-supero-gnathal.

Fig. 1, A and B represents diagrammatically the conception of the arrangement of the elements which has been worked out in the course of this research; the evidence for it will be presented in some detail in Section III.

The flattened blades (*IG*) constituting the lower jaw are generally known in the literature as "mandibles," from their *function* which is similar to that of the true mandibles in other vertebrates. In the upper jaw, the anterior pair of elements (*ASG*) are the "premaxillaries"; the posterior pair (*PSG*), the "maxillaries." These terms were introduced by Newberry in 1875, who writes concerning them: "The dentition of the upper jaw consists of what I have called,

for convenience in my description, premaxillaries and maxillaries, without, however, intending to commit myself fully to this view of their homologies" (1875, p. 5). And he adds in a foot-note: "In describing these bones I have called them premaxillaries, because they hold the positions and perform the functions of those organs in other fishes." This view of the non-homology of these elements with mandibles, premaxillaries, and maxillaries proper, is widely recognized. In this paper, therefore, it was deemed advisable to discard these terms and to propose new ones constructed on the same principle as the ones now in general use for other arthrodiran plates. The word *gnathal* which has been proposed by Professor Dean (1901) will be used to designate any one of the jaw elements, and Latin derivatives will be prefixed to designate the relative position of the particular element under consideration. Thus, *antero-supero-gnathal* for "premaxillary"; *postero-supero-gnathal* for "maxillary"; and *infero-gnathal* for "mandible." This terminology has the advantage of clearness and, moreover, suggests no false homologies.[1]

Infero-gnathal.—The form of this element is clearly shown on Plate XII, Figs. 3, 4. Comparative measurements of several of these elements have never been brought together and for that reason the measurements of three specimens of this bone preserved in the American Museum are here given.[2]

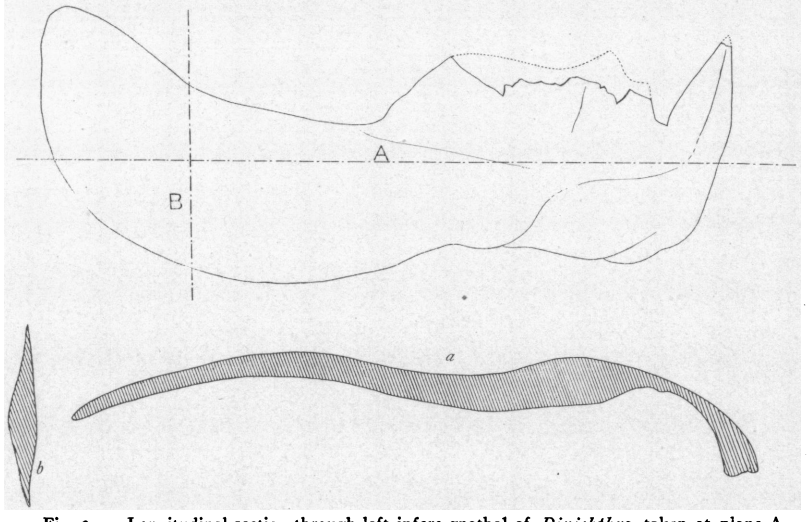

Fig. 2. *a.* Longitudinal section through left infero-gnathal of *Dinichthys*, taken at plane A. *b.* Cross-section of same taken at plane B. The outer surface of the blade is to the left in this figure.

It must be mentioned that the portion of this element termed "tooth," is simply the upturned cusp-shaped end of the plate. Teeth proper do not occur in the Arthrodira.

[1] The term "gnathal" proposed by Professor Dean is by far the most available word. "Dental" though a less clumsy term is too suggestive of "dentary," *e.g.*, in the Teleostomi.

[2] MEASUREMENTS OF THE INFERO-GNATHAL IN *D. terrelli.*

Length	Height at Tooth	Height at Posterior End	Remarks
No. 1 493 mm.	136 mm.	227 mm.	Right inf. gn.
" 2 488 "	149 "	200 "	Left " "
" 3 468 "	142 "	208 " (a little restored)	Left " "

Mode of measurement the same as that proposed by the writer in a previous paper (1905 *a*, p. 29).

A cross-section taken through the posterior half of the blade is shown in Fig. 2 *b*. It is noticed that the external surface is convex from above downward. The internal surface, on the other hand, is frequently concave. Fig. 2 *a* presents a longitudinal section taken in a horizontal plane through approximately the middle of the blade. A striking fact not hitherto observed is that this section is somewhat sigmoidal, antero-posteriorly. This character was noted in three other well-preserved elements belonging to different species. Its significance will be discussed later (p. 115).

Antero-supero-gnathal.—One of these elements is figured in internal aspect on Plate XII. The only point that need be referred to in connection with it is the prominent lateral cusp; this feature has hitherto been insufficiently emphasized.

Postero-supero-gnathal.—One of these elements is figured on Plate XII in internal aspect. In external view it has been well figured by Newberry (1875, 1889) in several different species.[1]

III.—THE MECHANISM OF THE ARTHRODIRAN JAW.

A. In Dinichthys.

1. Orientation of the Jaw Elements.

There are three specimens extant which exhibit the jaw elements in natural association. These must be carefully reviewed before attempting to deduce the mode of jaw movement. Fig. 3 represents the original specimen upon which the genus *Dinichthys* was founded (Newberry, 1873). This is a large portion of the cranium of *D. herzeri* exhibiting the upper and lower dental plates only slightly disturbed from their natural positions. The specimen is not well preserved but shows clearly the two heavy antero-supero-gnathals situated below the anterior edge of the roof of the cranium, with their sharp points apposed to the upturned fangs of the infero-gnathals. The postero-

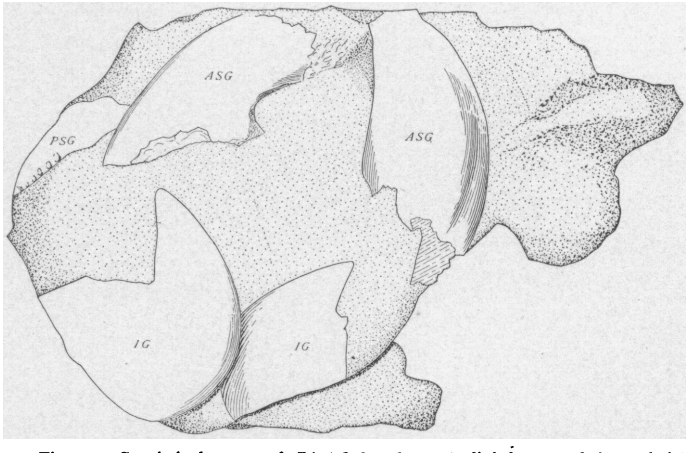

Fig. 3. Gnathal elements of *Dinichthys herzeri* slightly moved from their natural positions. Type specimen × about ½. Huron shale, Ohio. *ASG*, antero-supero-gnathal; *IG*, infero-gnathal; *PSG*, postero-supero-gnathal. Cat. No. 81.

[1] MEASUREMENTS OF THE POSTERO-SUPERO-GNATHAL IN *D. terrelli.*

No.	Length	Width (back of process)	Remarks
53	173 mm.	94 mm.	Left
3559	170 "	75 "	"
26	172 "	85 "	"

supero-gnathals preserved *in situ* indicate that the denticled edges were apposed to the toothed portions of the infero-gnathal blades.

A second specimen, exhibiting the gnathals of one side associated together, is preserved in the British Museum. A drawing (Fig. 4) and casts of this were kindly supplied by Dr. A. Smith Woodward. The specimen is that of *Dinichthys curtus* (?) and confirms the conclusions deduced from the specimen illustrated above.

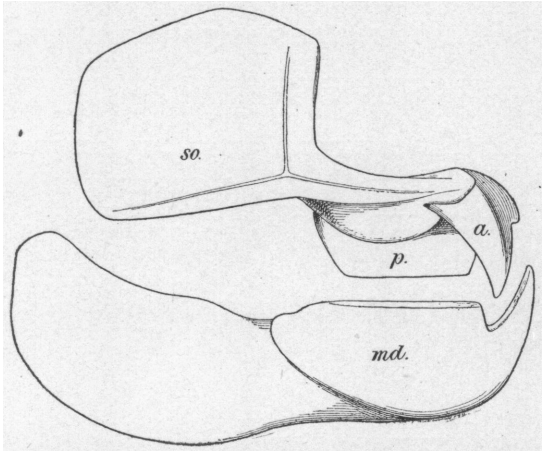

Fig. 4. Specimen of *Dinichthys intermedius* Newb., showing the suborbital and the gnathal elements of the right side in natural association. *a*, antero-supero-gnathal; *md.*, infero-gnathal; *p*, postero-supero-gnathal; *so.*, suborbital. After A. Smith Woodward. Original in British Museum.

The third specimen retaining associated gnathals is one of *D. curtus*. This will be dealt with at some length in Subdivision *3* of this section.

The foregoing evidence demonstrates:

A. That the jaw elements were arranged in pairs (*cf.* Newberry and others), two being above and one below. The upper anterior pair (the antero-supero-gnathals) stood vertically and apposed the upturned "teeth" of the infero-gnathals. The postero-supero-gnathals apposed the cutting portions of the infero-gnathals.

B. That the antero-supero-gnathals closed *over* the outside of the upturned "teeth" of the infero-gnathals. This was clearly recognized by Newberry (1875, p. 5 *et passim*). Thus he writes: The premaxillaries "interlock with and shut over the projecting points of the turned up mandibles, which are received into their concavities" (1875, p. 5).

The correctness of this view is to be deduced from an examination of either the upper or the lower elements alone. An examination shows that:—

1. The antero-supero-gnathals exhibit no trace of wear on their external surfaces.

2. The infero-gnathals, on the other hand, show undoubted wear on their external surfaces.

C. That the antero-supero-gnathals were so oriented that the heavy processes were turned outward (laterally) while the small cusp of either element was situated mesially (Newberry).

This arrangement is noted in the British Museum specimen (Fig. 4). It is shown also in specimen No. 249 in the Newberry collection; and can be inferred from the impressions made in the matrix by the gnathal elements in an available specimen of *Dinichthys curtus* which clearly indicate how the elements must have stood relatively to each other in life so as to have fallen out of their places and become buried in the positions in which they were found.

D. That the postero-supero-gnathal was placed on the inner (visceral)

side of the suborbital flange. *Cf.* the British Museum specimen (Fig. 4). It is also shown, though not so conclusively, in a specimen belonging to Oberlin College.

2. *Distribution of the Lines of Wear.*

A knowledge of the mode of action of the jaws in a fossil can be deduced from three sources:

1. From the shape of the several elements and their manner of insertion considered as a system of interacting levers.

2. From the remains of contemporaries bearing wounds inflicted by the teeth or other jaw structures of the form considered.

3. From the scourings and other wear produced by the working of the upper jaw elements over the lower in biting or tearing, during the life of the individual.

The first line of evidence in the case of the Arthrodira is very unsatisfactory. The remains are seldom found in natural association so that the position of several important skeletal elements is still in doubt. This line of argument moreover would at best be inconclusive, for in a type with no living relatives, the shape and size of the muscular motors are not known, and therefore we can only conjecture as to the movement of any part.

As to the second line of evidence, a dorso-median plate was described by Newberry, (1899, p. 154) which bears tooth marks probably inflicted by a contemporary dinichthyid. To this I will return later.

The third line of evidence is the most fruitful one. Lines of wear are demonstrable in most gnathal elements, clearly indicating the direction of the superimposed plates while in action. The lines of wear on the gnathals must therefore be carefully studied.

Plate XII, Figs. 3 and 4, exhibit the lines of wear and their distribution on the cutting edge of the infero-gnathal. They will be seen to run parallel to the axis of the upturned "tooth." The depression following the "tooth" also bears scourings on its sides which have the same general direction.

Pl. XII, Fig. 1, is from a photograph of the antero-supero-gnathal. Lines of wear are noted on the "tooth" and in the concavity between it and the lateral cusp. They extend vertically upward.

Pl. XII, Fig. 2, exhibits the grooves on the cutting edge of the postero-supero-gnathal. They occur along the entire beveled edge, running vertically downward.

These series of grooves are constant characters and may be demonstrated satisfactorily in any well-preserved gnathal element. It will be granted therefore, I believe, that they indicate the lines of wear. If the elements be apposed along these lines they will occupy the positions they held in life.

3. *The Jaw Mechanism as Illustrated by D. curtus.*

Fortunately a series of dental plates is available which enables me to test the conclusion just reached in a most satisfactory manner. In the Kepler collection at the American Museum there are preserved most of the remains of a single individual of *D. curtus* (Hussakof, 1905 *b*). With these are associated almost the complete dentition, *viz.*, both infero-gnathals, both antero-supero-gnathals, and one of the postero-supero-gnathals. By carefully modeling the wanting element, the right postero-supero-gnathal, the entire dentition is available. The mode of arrangement and the manner of movement of these elements thus become a concrete problem which can be settled by experiment. A series of casts was prepared from these gnathals and with them various experiments in the mode of jaw action were performed. The results were checked by the use of the originals.

Fig. 5, *A* and *B*, exhibits the natural arrangement of these elements of one

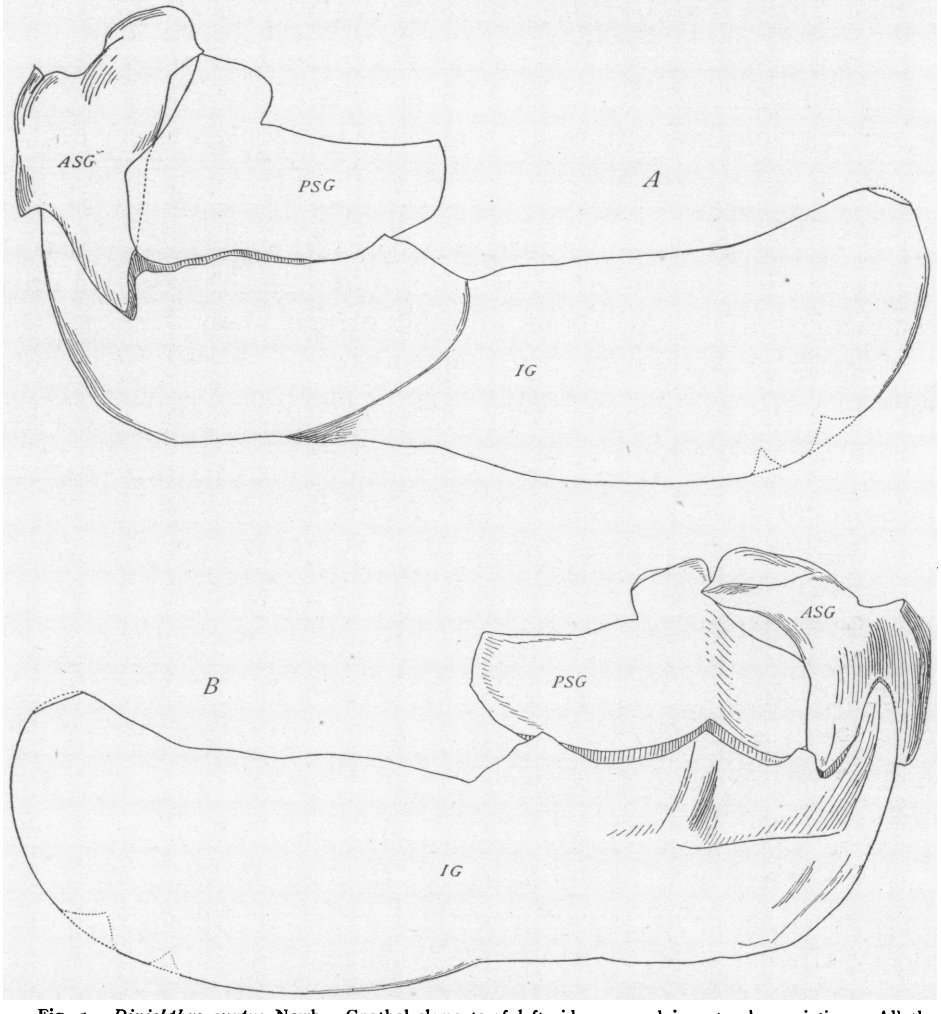

Fig. 5. *Dinichthys curtus* Newb. Gnathal elements of left side arranged in natural association. All the elements excepting *PSG* belong to the same individual. × ⅛. Cleveland shale, Ohio. *A*, external view; *B*, internal view; *ASG*, antero-supero-gnathal; *IG*, infero-gnathal; *PSG*; postero-supero-gnathal.

side, in external and internal views. To determine their mode of motion in life, the beveled edges of the infero-gnathals, and in a second set of the supero-gnathals were coated with a paste of sand and plaster of Paris. This when dry gave a rough, hardened area which readily scoured the uncoated beveled edge of the apposing jaw. By experimenting it was seen that only in one manner can the upper elements move over the lower so as to imitate the actual lines of wear—by a vertical or chopping motion. The suggestion has been made that a certain degree of rotation about a horizontal axis may have occurred in the gnathals. But by making the elements move in such a manner the resulting grooves are different from those actually found to exist.

1. The beveled edge of the infero-gnathal becomes convex instead of plane or slightly concave.

2. The second infero-gnathal cusp digs a deep excavation in the cutting edge of the postero-supero-gnathal not found in the original.

3. The limiting line of the beveled area of the infero-gnathal is worn away merging the beveling into the outer surface of the blade.

4. The upturned "tooth" of the infero-gnathal loses its acuteness, being ground down.

The view has also been advanced that there was some degree of intermovement among the upper gnathal elements else, it was declared, it is hard to see the need for their peculiar processes. This question was carefully examined. On this view the upper gnathals did not hold their relative positions fixed during the down-stroke, but underwent some deviation in their respective directions. But a study of the individual lines of wear, where observation is favorable, shows each line to be continuous in a single direction. Moreover the lines made by the antero-supero-gnathal run quite in the same direction as those made by the postero-supero-gnathal. It is proper to conclude, therefore, that there was no appreciable intermovement between the upper plates while in action. This conclusion is entirely borne out by experiments performed with the plaster casts. The upper plates of one side were firmly imbedded in a plaster setting in their proper relative positions, and the cutting edges thus held fixed

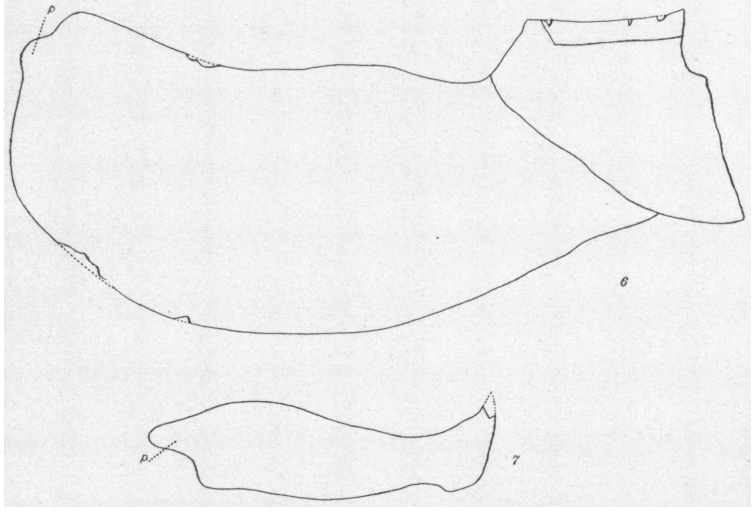

Fig. 6. Posterior portion of the infero-gnathal of *Dinichthys intermedius*, to illustrate the posterior process (*p*). × ½.

Fig. 7. Dental plate of *Rhynchodus pertenuis* Eastm. *p*, process. × ½. After Eastman.

relatively to each other were worked over the cutting edge of the infero-gnathal. The lines of wear thus produced are like those found on the actual specimens.

A matter of great importance is the mode of suspension of the lower jaw. Fig. 6 illustrates the posterior spatular end of an infero-gnathal of a related species—*Dinichthys intermedius*. As is well known the blade is laterally compressed. No articular facet has ever been found among the specimens hitherto brought to light and it may be concluded that none existed. Other evidence strengthens this conclusion. At the posterior end of the blade in well-preserved specimens, there is noted a small semicircular, laterally compressed process, drawn out in the plane of the blade (Fig. 6, *p*). This parallels the condition occasionally found in chimæroid dental plates and is a specialization for firmly lodging the blade in its setting of muscle or cartilage (Fig. 7).

The posterior portion of the infero-gnathal is externally demarcated from the anterior, exposed portion. (See Plate XII, Figs. 3, 4). It does not appear to the eye as dense as the latter. Several infero-gnathals which have been broken across in different regions of the proximal and distal portions show the tubulated spongy structure to extend throughout the entire length of the blade, wanting only in the densest portions, the cutting edge and the "tooth." In the region of demarcation between the anterior and the posterior portions the anastomosing tubules rise obliquely upward towards the "tooth" and cutting edge. I have convinced myself that there is no interruption between the spongy tubulated structure of the exposed and the inserted portions of the gnathal. The relation which exists between the two parts is not that existing between a jaw element and its attached dental plate. Both are intimately connected in their microscopic structure (Fig. 8). Moreover, from experience with these elements I have found that it is almost impossible to cause an infero-gnathal to break along this line of demarcation for even a part of its extent. Among a score of lower jaw elements that I have seen there is none broken clean at this point. The importance of this fact is that it clearly demonstrates that the infero-gnathal is a unit, one portion of which is adapted to insertion in muscle or cartilage, and another to functioning as an exposed cutting blade.

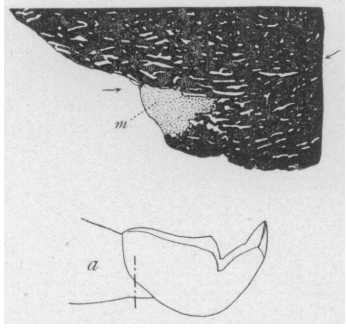

Fig. 8. Cross-section through region of union of the exposed and inserted portions of the infero-gnathal of *Dinichthys*. The arrows indicate the direction in the original of the line of demarcation. *a*, to illustrate the plane of section; *m*, matrix. Enlarged about 6 diameters. Camera.

The superior gnathals from this standpoint present even more interesting conditions. A specimen of the antero-supero-gnathal which had been broken into several pieces shows clearly that the spongy tubulated structure continues uninterruptedly throughout the entire basal process and into the fang; in the latter, however, the tubules becoming fewer in number and more crowded together. As would be expected, the process is the more vascular of the two portions, to allow for the ramification of vessels and nerves.

The postero-supero-gnathal presents a similar condition. As far as one can judge, the articular process differs structurally from the cutting portion only in its lesser density.

Hence the three types of gnathal elements in *Dinichthys* offer a remarkable correspondence in plan of structure. Each is differentiated into a distal, exposed, functioning portion, and a proximal, deeper-lying, inserted portion. That the cutting region of the blade was exposed, or at most covered only by epidermis, is to be inferred from the frequent occurrence of ornamental denticles on these parts (*Dinichthys lincolni*, *D. herzeri*, an infero-gnathal of *D. intermedius*, etc.). The proximal portions, being inserted in muscle, or perhaps in cartilage, are more tubulated. It does not seem proper to differentiate any one of these gnathals into jaw element and dental plate, as can be done, for instance, in the Dipnoans. Microscopic sections show that the non-cutting portions of the gnathals are histologically indistinguishable from the armor plates, *e.g.*, the clavicular or the dorso-median. Hence these gnathals must be regarded as exoskeletal plates which in the region of the mouth have come to be used as jaws. There is no evidence that they were connected with either chondrocranial structures, or with an osseous suspensorium.

Dr. A. Smith Woodward writes: "There is no trace of a hyomandibular bone in the most exquisitely preserved specimens" (1898, p. 64). The infero-gnathal differs profoundly, in regard to suspension, from the true vertebrate mandible, which is so articulated proximally by a pivotal joint as to be capable of motion in only a single plane. There are no facts against the view that the dinichthyid infero-gnathal was capable of moving in at least two planes: 1, a vertical plane, and 2, to and away from the median axis. Indeed, there is evidence for believing that such was the case. Several excellently preserved infero-gnathals of various species of *Dinichthys*, which had not been too much flattened out in fossilization, present a somewhat sigmoid sagittal section (Fig. 2*a*). The gnathal is thus a lever, the muscular force applied at the posterior end causing the anterior portion, while retaining its vertical position, to swing readily to or from the median line.

In this connection the double beak of the lower jaws becomes of great significance. Each upturned "tooth" is complete in itself and shows no evidence of having been united along its inner side to its fellow. It is only at the base of the "tooth," and where this blends with the body of the blade, that there are rugosities for the attachment of the ligaments or membranes which bridged the space between the infero-gnathals while separated. Moreover the presence of symphyseal denticles in allied forms, *e.g.*, *D. herzeri*, *Coccosteus*, *Diplognathus* (Fig. 25, p. 149), goes to strengthen the view that the halves of the lower jaw were not stationary with respect to each other, but were capable of separating at their anterior ends to enlarge the gape of the mouth. The specimen bearing scars inflicted by a dinichthyid, presently to be discussed, lends additional support to this view.

The probable mode of action of the jaws is illustrated in the accompanying diagrams. Fig. 9*A* shows the jaws at rest, Fig. 9*C* illustrates approximately their maximum distension. In closing the jaws, the infero-gnathals approach each other mesially at the same time closing upward.

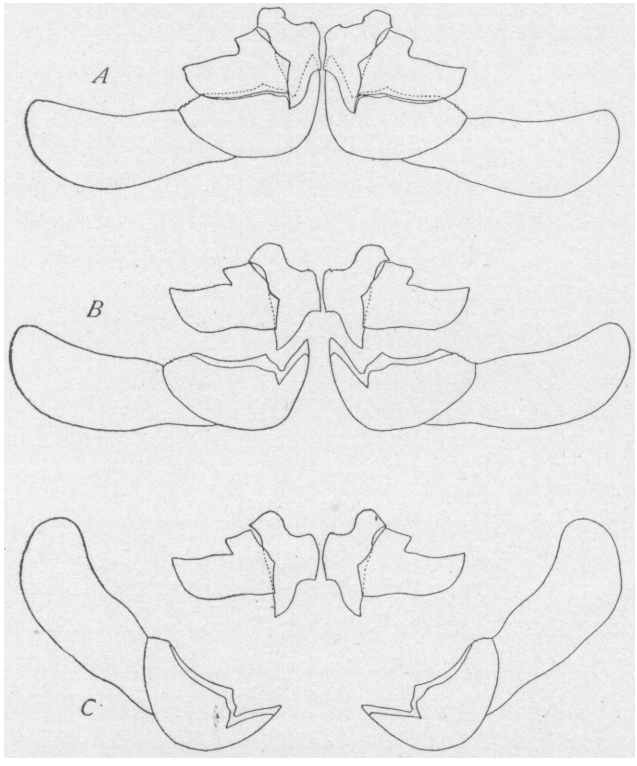

Fig. 9. Diagrams illustrating the mode of action of the jaws in *Dinichthys*. *A*, at rest; *B*, partly distended; *C*, almost completely distended.

This view of the mode of action of the jaws is substantiated in a remarkable way by the dorso-median plate referred to on page 111 which bears wounds inflicted by a contemporary dinichthyid.

Fig. 10 is from a photograph of this specimen. It will be seen to bear two long scars and below them two deep dents. This group of markings will be admitted, I believe, to have been caused by a contemporary dinichthyid. For from our knowledge of the fauna of the Cleveland shale we are led to conclude that an Arthrodire, probably *Dinichthys*, was the only contemporary that could have produced them. Sharks were abundant but they had cladodont teeth; and even assuming that these teeth could pierce the armor of *Dinichthys*, we should expect a long series of marks and not the peculiar group here presented. But if we picture a dinichthyid as causing the scars then they can readily be explained. On such a view the long scars may be regarded as due to the points of the antero-supero-gnathals. These points projected for a short distance below the cutting edge of the postero-supero-gnathals. Hence they would strike sooner than the supero-gnathals, but the resistance of the bone would prevent them from sinking so deep as to allow

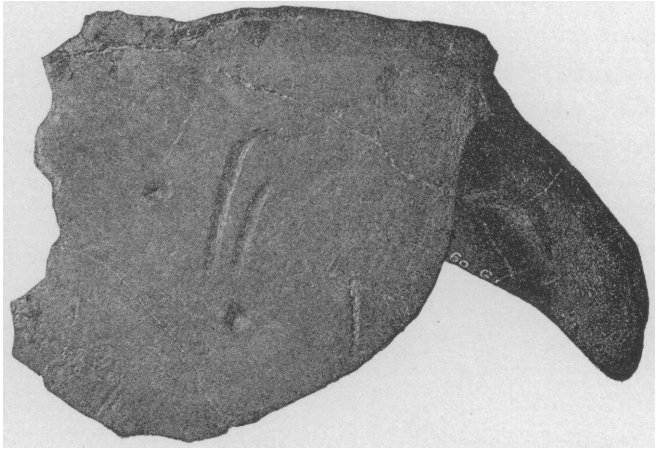

Fig. 10. Dorso-median plate of *Dinichthys intermedius* showing scars inflicted by a contemporary dinichthyid. × ⅓. Cleveland shale, Ohio. The pair of long scars were produced by the antero-supero-gnathals; the circular marks, by the points of the infero-gnathals.

the postero-supero-gnathals to scar. The two circular marks, probably, were made by the infero-gnathal "teeth" which were thrust deep into the bone. They are farther apart from each other than the long scars, because the infero-gnathals, as was explained above, open up laterally as well as vertically. This specimen therefore appears to the writer to bear out the interpretation of the mode of jaw action deduced from a study of the lines of wear.

Incidentally we may note that this specimen affords an interesting commentary on the ferociousness of the dinichthyids, for so deep a set of scars could be produced in the thick shoulder armor only by a sudden and terrific onslaught.

4. *The Jaws in Other Species.*

Dinichthys lincolni *Claypole.*

An antero-supero-gnathal is the only portion of this species known. It is of small size and has a heavy basal process. The external surface of this "tooth" is ornamented by several vertical rows of pointed denticles which are directed somewhat downward. The largest denticles are nearest the tip of the "tooth" becoming in each row gradually smaller upward; also the denticles become smaller the farther they are laterally from the central row. This "tooth" undoubtedly functioned in a manner similar to those in *D. curtus*. The rows of denticles on the external surface with their downwardly directed points, therefore, interfered with its action, since they would check its downward thrust. They are to be interpreted as modified ornamental tubercles; in fact all stages can be traced among them from true "teeth" to mere small flattened tubercles. This antero-supero-gnathal, therefore, taken in conjunction with the facts discussed at page 115, as well as those presently to be mentioned, lends support to the view that *the gnathal elements are merely modified dermal or exoskeletal plates, which are not homologous with the true jaw parts of fishes (sensu stricto)*.

There are other instances among the Arthrodira of gnathal elements ornamented with tubercles. The antero-supero-gnathal of *D. herzeri* (Plate XIII, Fig. 2), bears a single row of seven denticles comparable to the central row in *D. lincolni*. They, also, point downward, and the lowermost ones are the largest. *D. herzeri* (Huron shale) occurs in a somewhat higher geological horizon than *D. lincolni* (Marcellus shale), and hence may be regarded as a more advanced evolutionary stage, being farther away from the primitive type with ornamented gnathals.

The infero-gnathal also occasionally bears traces of a tubercular ornament. Plate XIII, Fig. 5 represents such a gnathal. It is a specimen of an old individual of *D. intermedius* (?) and shows scattered over its surface large, rounded, flattened-down tubercles. This specimen is perhaps a reversionary type.

Facts of this character, it appears to the writer, point to *the origin of the gnathal elements from plates primitively ornamented and homologous to the rest of*

the body plates of the individual. This point was strongly emphasized by Professor Dean (1901), who was the first to call attention to it.

Dinichthys herzeri *Newberry.*

The complete dentition of this form is known. The infero-gnathal has a row of powerful "teeth" (Plate XIII., Fig. 1). In the region of the symphysis there is a row of small denticles (Fig. 11). In comparison with the large size of the element, they are seen to be too delicate to have functioned. They represent the same row which will be described under *Coccosteus* and *Diplognathus*, and which in the latter, were undoubtedly functional. The presence of these denticles is evidence that the two halves of the lower jaw were more or less separable from each other at the symphysis so as to permit of the enlargement of the mouth opening.

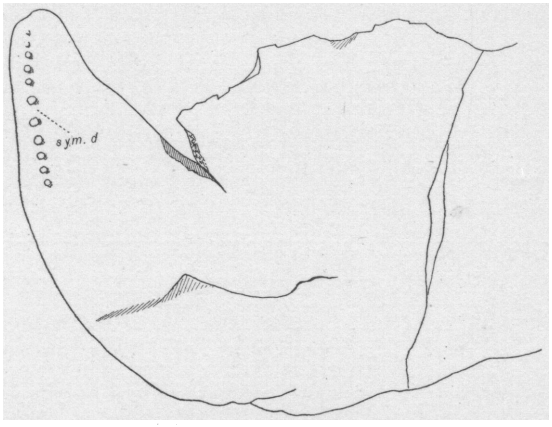

Fig. 11. Anterior portion of infero-gnathal of *Dinichthys herzeri*, inner view, showing the symphyseal denticles (*sym. d.*) Somewhat less than ½ natural size.

The antero-supero-gnathal is figured on Plate XIII, Fig. 2, from which its general character will be seen. The presence of ornamental denticles on its external surface has already been referred to.

The postero-supero-gnathal exhibits a double row of "teeth" along the cutting edge. The only known example of this plate (Plate XIII, Fig. 3) is unfortunately broken and cannot be considered in detail in relation to the other jaw elements. The general mode of action of the jaws was probably similar to that in *D. curtus*, the knife-life edges, however, being replaced by rows of powerful conical serrations about a centimeter in height (Plate XIII, Fig. 4).

Dinichthys intermedius and D. terrelli *Newb.*

These species are entirely similar in plan of jaw structure to *D. curtus* and may be considered together. In both species, vestigial denticles occur along the posterior portion of the cutting blade, both in the postero-supero- and in the infero-gnathal. These have been recorded by several investigators in *D. curtus* and *D. intermedius;* I have recently found them in two infero-gnathals and in two postero-supero-gnathals of *D. terrelli.* They are to be interpreted as an inheritance from an earlier evolutionary stage in which they were functional. They are reduced in size and not composed of the dense bone of which the functional portion of the blades is made. They are, moreover, situated on curved surfaces

which, as can be definitely shown in the associated gnathals of *D. curtus* (Fig. 5, page 112), were not in contact.

In addition to the species of *Dinichthys* discussed, other dinichthyids are known more or less completely but their jaw structures fall under one or another of the above types and so need not be reviewed in detail.

B. The Jaws in Other Genera.

1. **Mylostoma** *Newberry.*

This genus is remarkable among Arthrodira for the possession of crushing instead of cutting-and-piercing jaws. Judging by analogy with *Dinichthys* to which *Mylostoma* is closely related, three, and only three, pairs of gnathals should be referred to the jaw mechanism. The almost complete body-armor described by Professor Dean (1901) had that number associated with it.[1]

Professor Newberry (1889) made the first suggestion as to the orientation of the six jaw elements. He properly referred the "mandibles" to the lower jaw and the other elements to an upper crushing pavement. Professor Dean, (1901), put forward a definite theory of their mode of action. It was argued that since the upper two elements are situated close together in the specimen then described, they must be in their natural association. Hence if one of the infero-gnathals be fitted with its crushing surface against them, the mode of action of the jaws could be inferred. A tubercle on a superior gnathal seemed to fit into an oval depression in the infero-gnathal. It thus appeared that for the tubercle to produce the oval-shaped depression, the gnathals must have had a somewhat rotary movement upon each other.

This view has recently been criticised by Dr. Eastman (1906, p. 136), who can find no evidence whatever for the theory of jaw-rotation. His argument is based on the associating of dental plates of *Mylostoma* which have been found isolated, and upon a unique form *Dinomylostoma*. Concerning the latter, it appears to the writer, who, thanks to the kindness of Dr. Eastman, has had the opportunity of studying the originals, that it has not been demonstrated that the gnathals which were found in the same concretion really belong to one individual, for the two upper elements of one side cannot be arranged so as to completely cover the oral face of the lower one, leaving more than a third of it uncovered. As to associating isolated gnathal elements, Professor Dean urges the objections that we are not sure that, 1, these elements belong to one species, and, 2, that they belong to individuals of the same size. Professor Dean further maintains

[1] The evidence recently brought forward by Dr. Eastman (1906, p. 138; also Fig. 1.) for the presence of an additional pair of upper elements seems to the writer insufficient to establish that point. The additional pair ("vomerine teeth") figured, are sufficiently suggestive in form of the succeeding two types of dental plates to leave open the probability that they represent one of those pairs belonging either to a juvenile individual or to a new species. Moreover, introducing this additional pair of elements would give us a total of four pairs instead of the three occurring in the most closely related forms, *Dinichthys* and *Coccosteus*.

that a proper solution of this problem is to be sought in a series of dental elements which unquestionably belong to a single individual.

As to the remains described by Professor Dean (1901), which beyond question represent a single individual, I am not prepared to say that these put the problem beyond all doubt. That the jaws should rotate during their downstroke would be a phenomenon so anomalous among vertebrates that the evidence for it must be of a most cogent character before such a view is accepted. It seems best to defer a final solution of the problem of jaw action in *Mylostoma* until additional material representing entire sets of dental plates shall be found.

Summary.—The dentition of *Mylostoma* was of a crushing type. The upper elements were evidently imbedded in cartilage. The infero-gnathals were probably somewhat separable at the symphysis. This fact is inferred from the extent to which the grinding surface extends downward in the symphyseal region, which for some distance is smooth, with no roughness for the attachment of ligaments.

2. **Titanichthys** *Newberry.*

Some species of this genus attained huge size as is evidenced by a cranium of *T. clarkii* in the American Museum which measures 56 inches in width. The infero-gnathals are the only portions of the jaw thus far discovered. In the absence of all knowledge of the upper elements, no theory can be brought forward as to the mode of action of the jaws. Both Newberry and Claypole have indicated the presence of large blades of bone, or "teeth," in the gnathal groove. But the so-called "tooth" figured by Newberry (1889, Pl. XLIII, Fig. 4), is really one of the pair of triangular plates belonging on either side of the pineal on the under side of the cranium. These have a characteristic striation which makes their determination quite certain. Claypole's figures of the "teeth" are not convincing, and since no one else has recorded them, their existence must still remain questionable.

3. **Coccosteus** *Agassiz.*

It has sometimes been supposed that the postero-supero-gnathal element was wanting in *Coccosteus*, the genus differing in that respect from *Dinichthys*.[1] Nevertheless the presence of such an element has been inferred by different investigators from an examination of the denticled edge of the infero-gnathal, which obviously could not appose the suborbital since the latter bears no denticles.

Dr. Traquair in describing a very favorably preserved specimen writes: "No teeth are, as usual, seen on the maxillæ [=suborbitals of American

[1] See the restorations of Dr. Traquair and Dr. Smith Woodward.

writers], but internal to them and between them and the contiguous mandibular ramus is seen a row of conical teeth evidently placed on the edge of a palatal or palato-pterygoid bone, which I have not yet seen in its entirety" (1890, *b*). This "palatal" or "palato-pterygoid" the writer believes to be the postero-supero-gnathal.

Fig. 12 represents a portion of a specimen of *C. decipiens* in the American Museum (No. 7104), recently secured by Professor Dean in Europe. The elements figured are those in the matrix to the left of the cranium. *PSG* is the postero-supero-gnathal. It is a small, somewhat elliptical element, 15 mm. long and 4 mm. wide. On the lower edge it retains two denticles and several others have probably been weathered away. Reasons for regarding it as the postero-supero-gnathal:

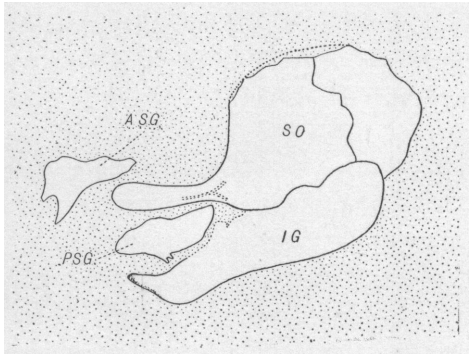

Fig. 12. *Coccosteus decipiens*. Gnathal elements and suborbital, natural size. *ASG*, antero-supero-gnathal; *IG*, infero-gnathal; *PSG*, postero-supero-gnathal; *SO*, suborbital. (No. 7104.)

1. General resemblance in shape to that element in *Dinichthys* (*cf.* Pl. XII, Fig. 2.)

2. The size and shape of its lower toothed edge are such as to exactly fit the denticled portion of the infero-gnathal.

3. Its association in the matrix with the jaw elements suggestive of belonging with them.

Pander (1857) figured such an element (Pl. I, Figs. 6*a*, 6*b*), but at that time, *Dinichthys* not having been discovered, it was impossible to place it.

The specimen of *Coccosteus* here described also throws light on the character of the antero-supero-gnathal in this genus. Because of its small size and delicate structure this element is usually fragmentary or quite weathered away, and so has never been adequately described. In the present specimen (Fig. 12, *ASG*) it is seen to possess both a "fang," a smaller cusp, and a drawn-out basal process, like its homologue in *Dinichthys* (*cf.* Pl. XII, Fig. 1). It is the element from the left-hand side of the animal with its outer (anterior) face toward the observer.

Dimensions:

Height at main cusp, 10 mm.
Width across both cusps, 5 mm.
Width at process, 11 mm.

These facts establish for the first time, the entire similarity between *Coccosteus* and *Dinichthys* in the *number* and *kind* of elements composing the jaw.

Hugh Miller was the first to call attention to the presence of symphyseal denticles in the infero-gnathal, and in a cast of his type specimen kindly secured for me by Professor Dean[1] the writer was able to study these structures. The

[1] From the original in the Edinburgh Museum, by courtesy of Dr. R. H. Traquair.

anterior end of the gnathal is bent inward, making an obtuse angle with the rest of the blade, and the edge where the symphysis should be is occupied by a row of six denticles standing out horizontally one above the other, with their points on a slightly higher level than their bases. They are pointed and comparable in size to the denticles along the upper cutting edge. What could have been the function of such denticles? From a close study of their appearance in the cast, and from analogy with *Diplognathus*, it appears that they were functional. They cannot be regarded as of use in interlocking the two halves of the lower jaw, because for such a purpose they should be truncated at the tips, and not pointed. Furthermore it is inconceivable that such structures could interlock the gnathals since they do not stand out horizontally but point slightly upward. Their presence and character go to strengthen the view already deduced in the case of *D. curtus* (page 115), that the arthrodiran infero-gnathals were separable at the symphysis to allow of widening the gape. This capability existed in addition to that of opening the mouth vertically (*cf.* also p. 140.)

What the exact function of the symphyseal denticles was cannot be definitely ascertained, especially in view of the extreme rareness of well-preserved gnathals showing these denticles. They probably served in the prehension of food, as suggested by Newberry. In later forms they are gradually reduced (*D. herzeri*) and finally disappear (*D. terrelli*, etc.).

4. **Diplognathus** *Newberry.*

The infero-gnathals described by Newberry are preserved in his collection at the American Museum. Along the upper edge there are in different specimens from fifteen to seventeen strong "teeth"; in the symphysis, four. A close study of the latter in the specimens thus far known would seem to indicate that they probably were functional. They consist of the same dense bone of which the "teeth" along the cutting edge are composed, and in at least one favorably preserved specimen, they show wear. Unfortunately no other structures belonging to this genus are known, so that here, as in *Coccosteus*, no clue to their exact mode of action is available. Professor Newberry suggested (1889, p. 159) that they served in seizing slippery kinds of prey, such as worms or eel-shaped organisms.

The theoretical importance of this type of gnathal is obvious: the evidence it offers taken together with that afforded by other forms would indicate that in at least certain genera of Arthrodira, there was the capability of separating the halves of the lower jaw at the symphysis.

5. **Selenosteus** *Dean.*

This is another genus which possessed symphyseal denticles, as described and figured by Professor Dean (1901, Plate VI, Fig. 37).

C. General Conclusions.

The most important conclusions arrived at in the preceding section may here be briefly summarized.

1. The recurrence of functional symphyseal "teeth" in three genera (*Coccosteus*, *Diplognathus*, *Selenosteus*); the presence of vestigial symphyseal denticles in *Dinichthys herzeri*, and the evidence mentioned in the case of other species of *Dinichthys*, and in *Mylostoma*, indicate that *the halves of the lower jaw in the Arthrodira were separable from each other at the symphysis.* In this regard the Arthrodira differ from all true fishes.

2. The wide occurrence of ornamental denticles on the gnathals demonstrates the dermal origin of the latter, *i.e.*, from plates which in the mouth region gradually lost their original form and ornamentation and assumed the function of jaws.

3. Teeth in the strict vertebrate sense are unknown. The "teeth" which may be present on the margins of dental plates are in reality the tuberculate surface ornaments of dermal elements. They are composed of osseus tissue which is more compact than, but not different from, that in the rest of the dermal element. *No dentine is present.* This is especially significant in a comparison with the dental plates of Dipnoans.

4. The infero-gnathals were not pivoted posteriorly so as to be restricted to moving in a single plane. They were set in muscle, or perhaps cartilage, in a manner analogous to the dental plates of the Chimæroids.

5. There is no trace of a Meckelian cartilage.[1]

These points indicate that the dental mechanism of the Arthrodira is not homologous with the jaws of other Vertebrates.

IV.—THE RELATIONSHIP OF THE ARTHRODIRA.

It is not the purpose of this section to review the earlier theories regarding the Arthrodira, for their interest is mainly an historical one. Moreover an admirable discussion of them is to be found in Pander's 'Ueber die Placodermen des Devonischen Systems.' This section accordingly will be restricted to matters which are to-day under discussion.

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[1] The best case in favor of the presence of this cartilage has been made out, recently (1906), by Dr. Eastman. It appears, however, that the infero-gnathals of the new form *Dinomylostoma* (which, thanks to the kindness of Dr. Eastman I have had the opportunity of studying) do not establish this point conclusively. The elements which are described as the Meckelian cartilages occur obscurely; there is clearly a fragment of a cartilage-like tissue near the posterior end of the blade of one of the infero-gnathals and there may have been a similar fragment on the other blade. Dr. Eastman's paper ('Structure and Relations of *Mylostoma*,' Bull. Mus. Comp. Zoöl., 1906, pp, 2—29) treating of this subject *in extenso*, has been received only after the proof of the present paper had been corrected. Its discussion, therefore, must be reserved.

1. *The Supposed Relationship to the Teleostomi.*

Huxley was the first to institute a comparison between *Coccosteus* and the Teleosts; he recognized in the coccosteids, the Palæozoic forerunners of the Teleostei (1861). Subsequent discoveries have greatly extended our knowledge of the Arthrodira, and have led to the abandonment of this view. At the time Huxley wrote (1861), the evolutionary idea had not been applied in detail to the study of fishes, and the succession of forms and the gradual rise of the Teleostei had not been induced. But it is indeed surprising to find a somewhat similar view advocated recently. In 1904 Mr. C. Tate Regan announced that in his opinion the Arthrodira, and with them the Ostracophori, must be regarded as specialized descendants of Crossopterygians.

Very little evidence was advanced in support of this view:

1. The head shield of *Coccosteus* is compared with the cranium of *Rhizodopsis* and the former is declared, on the evidence of a similar arrangement of the elements, to be an "almost typical Crossopterygian."

2. A resemblance in the dorsal fin-supports; these being in each case arranged in two regular series.

3. "The structure of the ventral fin,—which appears to be essentially similar to that of *Polypterus*."

The first of these arguments was promptly challenged by Dr. Eastman,[1] and need not occupy us here except to point out that a far stronger case had been made out by Huxley in favor of the supposed homology with the Siluroids.

As to the other two statements, were even both of them positively demonstrable, it would still be doubtful whether their weight would be adequate to lead to the affiliation of the Arthrodira with Crossopterygians. But as the case stands, the third item enumerated is not only undemonstrable, but the gravest doubts must even be entertained as to whether paired fins existed in the Arthrodira at all.

Nothing is said by Regan of the presence in Arthrodira and the absence in Crossopterygii, of the dorsal and ventral plate systems; and these are features so characteristic of the arthrodiran plan of structure that any view professing to deal with the affinities of the Arthrodira must take them into consideration.

On the whole a far stronger array of facts will have to be presented to lead to the acceptance of so radical a conception of the Arthrodira; and until such facts are forthcoming the theory of their Crossopterygian ancestry may be dismissed.

2. *The Supposed Relationship to the Chimæroids.*

In an interesting paper entitled 'Ueber Coccosteus und die Beurtheilung der Placodermen' (1902), Professor Otto Jaekel advanced the view that the Arthrodira are related to the Chimæroids. Points of similarity are enumerated between the Arthrodira and (1) Ganoids, (2) Chimæroids, and (3) Tetrapoda

[1] Amer. Journ. Sci., XVIII, 1904, pp. 141–144.

and the discussion is summarized in following wise: "Nach alledem scheinen mir die Placodermen echte Fische zu sein und unter ihnen die Coccosteiden eine ancestrale Stellung gegenüber den Ganoiden und namentlich den Chimæriden einzunehmen" (p. 115).

Professor Jaekel enumerates the following characters which he regards as possessed in common by Chimæroids and Arthrodires.

1. Shape of cranium.
2. Structure of the nasal region.
3. Course of the canals.
4. Presence, position, and support (*Befestigung*) of the dorsal spine.
5. Dorsal fin beneath the same.
6. Type of dentition of the lower jaw.
7. Beginning of the formation of a pelvic arch.
8. Supposed large size of the pectoral fins.

Some of these characters can be rejected as hardly of any value for purposes of morphologic comparison. It is doubtful, for instance, whether the mere "Form des Schädels" is in this connection of significance, for the cartilaginous cranium of a Chimæroid is certainly not homologizable with the dermal bones constituting the head shield of an Arthrodire.

As to the assumed similarity between the Chimæroids and Arthrodira in the "presence, position and support of the dorsal spine," I believe it will not be generally admitted that a chimæroid-like spine exists in the Arthrodira. Professor Jaekel evidently regards as such a spine in *Coccosteus*, the sharp, pointed prolongation of the dorso-median.

Again, the observation that the dorsal fin is situated *beneath* this spine probably rests upon a specimen in which the fin had been shifted from its original position. "In a very good specimen in the British Museum," Dr. Traquair finds the dorsal fin "a little beyond the apex of the plate just mentioned [dorso-median]" (1890*b*, p. 131).

The sixth point, *viz.*, that there is a resemblance between the Chimæroids and *Coccosteus* in the "type of dentition of the lower jaw" is the strongest point in the argument. There is indeed a resemblance between the dental elements in shape and manner of insertion, especially in the case of the dinichthyids. This similarity extends in some cases to the presence of a similar posterior process for securely lodging the blade in its setting (see Figs. 6, 7, p. 113). But this resemblance cannot be regarded as other than a parallelism, both types of lower jaw being similarly adapted to their supports.

As to the supposed pelvic arch, *e.g.*, in *Coccosteus*, I think it is doubtful whether the small *ossified* elements sometimes regarded as a pelvic girdle can properly be interpreted as such. Dr. Eastman has already pointed out that the identification by Professor Jaekel of the "ileum" is probably erroneous.[1]

[1] Amer. Jour. Sci., XVIII, 1904, p. 144.

The point concerning the large pectoral fins assumed to have existed in *Coccosteus* seems to the writer unsubstantiated by evidence. In fact Professor Jaekel's reason for believing that pectorals existed at all is not convincing: "Der tiefe Ausschnitt, der sich am Hinterrand des Halsskeletes genau an der Stelle zeigt, wo eine Pectoralis zu erwarten wäre, und die seitliche Auschbuchtung des Hinterrandes der Cleithra kann über die Lage und Stellung der Brustflossen keinem Zweifel Raum geben" (1902, p. 111). Nevertheless, no trace of pectorals has been found, even in specimens which have retained well-preserved dorsal and caudal fins.

It thus appears that Professor Jaekel's view of the relationship of the Arthrodira to the Chimæroids is based mainly upon characters which are not conceded to be of value in demonstrating homology, or upon such interpretations of structural features as are not generally recognized. The single resemblance as regards the form of the lower jaw, therefore, is best explained as a parallelism.

3. *The Supposed Relationship to the Dipnoans.*

The view that the Arthrodira are Dipnoans was first advanced by Newberry (1875), who based it more especially upon certain resemblances in the mandibles of *Dinichthys* and *Protopterus*. Since then other anatomical features have been brought into this comparison, with the result that, in one form or another, this view is held at present by some of the leaders in palæichthyology.

The number of structural features that have been introduced into the discussion of this subject are so many that for the sake of convenience, it will be advisable to summarize in parallel columns the arguments for and against the Dipnoan theory of the Arthrodira.

Evidence for Affiliating the Arthrodira with the Dipnoans.	*Evidence against.*
PAIRED FINS.	
A pair of elongate triangular elements in the abdominal region have been regarded as constituting a pelvic girdle ("Ileum," Jaekel) and hence pelvic fins are inferred to have existed.	These elements are present but they have not been demonstrated to be pelvic elements. They are ossified. The view that they constitute a pelvis is only conjectural. No satisfactory evidence for the presence of paired fins has yet been found in any of the hundreds of specimens of *Coccosteus* that have been obtained. Pectoral fins are generally admitted to be absent.[1]
CRANIUM.	
The presence in some Dipnoans (*e.g.*, *Ceratodus*) of a series of unpaired median elements suggests the condition in the Arthrodira.	This is only a superficial resemblance seen chiefly in *Ceratodus*. It is not so apparent in the other living Dipnoans and is not demon-

[1] "Of the pectoral pair (of fins) no trace whatever has been preserved, nor do we even know that a girdle was present" (Eastman, 1906, p. 142).

strable in the earliest fossil Dipnoans. Several important Dipnoan cranial elements are not found in the Arthrodira; *e.g.*, *parasphenoid*, *pterygoids*, *vomer*, rod-like *occipital rib*. The preorbital element not ossified in the Dipnoans; great fenestration of the cranial roof in *Lepidosiren* and *Protopterus*, never found in the Arthrodira. Articulatory condyles in posterior lateral region of cranium, absent in Dipnoans.

DORSAL AND VENTRAL ARMOR.

The complicated dorsal and ventral plate systems present in all known Arthrodires, absent in all Dipnoans.

There is some resemblance in form, but homology, by relating the elements to the cranium and dorsal armor, cannot be demonstrated.

Operculum (dipnoan) = "clavicle" (arthrodiran).
Interoperculum = lateral appendage.

MECKELIAN CARTILAGE.

No positive evidence for its presence. The Dipnoan (*e.g.*, *Ceratodus*) splenial is deeply concave on the outer surface for lodging this cartilage; in the arthrodiran " mandible" the outer surface is always convex along its entire depth (see Fig. 2*b*, page 108), with no groove. The furrow near the inner anterior end may as well be regarded as functioning in lodging the ligaments, etc., which united the halves of the jaw.

JAWS.

The Arthrodire "mandible" is homologous with the Dipnoan splenial. In *Mylostoma* there is a crushing pavement comparable to that of the Dipnoi.

Probably a mere parallelism just as the arthrodiran "mandible" parallels that of some early Chimæroids (p. 125). The other Dipnoan jaw elements (*e.g.*, dentary, angular, articular) not accounted for.

Mylostoma is a late specialized form clearly traceable back to a coccostean ancestry. Hence its dentition is secondary.

The frequency of rows of surface denticles, all gradations of which can be traced up to small ornamental tubercles, proves the jaw elements of the Arthrodira to be modified armor plates (see p. 117).

The presence of large symphyseal "teeth" in three genera, and their presence in a vestigial condition in another, proves that the lower jaws in the Arthrodira were in many forms (if not universally), capable of separat-

	ing from each other and were not interlocked at the symphysis. This condition is unknown among the true fishes.

VERTEBRAL SPINES.

Neural and hæmal spines each ossified about a cartilaginous core.	

TAIL.

Tail in *Coccosteus* probably diphycercal as in *Ceratodus*.	Imperfect knowledge as to the caudal of *Coccosteus*. Has not been established what the shape of tail was.

From this list of *pros* and *cons* for the Dipnoan relationship of the Arthrodira, it will be noted that while there are some characters which favor such a view, yet there are many others, and to the writer's mind a preponderating number, against it. That there are at least *some* unanswered criticisms against this supposed relationship, no one, I believe, will deny. For instance, the presence in the Dipnoan cranium and jaws of some eight elements which have not been shown to be present in any Arthrodire. Or again, as was pointed out by Kemna (1904), upholders of the Dipnoan theory cannot well argue that the pectoral fins have entirely disappeared while the pelvics have degenerated, for this is opposed to the course of fin evolution in all other fishes: the pelvics always degenerating and disappearing before the pectorals.

Moreover the staunchest upholders of the Dipnoan theory do not maintain that the degree of relationship is a close one; the Arthrodira are not regarded as standing in the same relationship to the Dipnoans as, for instance, *Ceratodus* does to *Protopterus*. On the contrary, the relationship is regarded as phylogenetically very distant, the branches of the supposed pro-Dipnoan-Arthrodire stem having already undergone long divergent specialization at the earliest period at which they are known.[1]

For these considerations, and because of the evidence advanced in the preceding pages, it appears to the writer preferable to separate the Arthrodira from the Dipnoi. Moreover their strong resemblances in many important structures to the Antiarcha, lead one to separate them from the fishes (*sensu stricto*) and to group them as a separate subdivision having no other features in common with the fishes except that, like them, they are descended from the common pro-vertebrate stock.

4. *The Degree of Relationship to the Ostracophori.*

There has been much difference of opinion concerning the relationship of the Arthrodira to the Ostracophori. McCoy in 1848 united them with several genera of the latter into a single family, the Placodermata.[2] This view was

[1] See especially Eastman, 1906. [2] Originally *Placodermi*.

adopted by Pander (1857), Huxley (1861),[1] Traquair (1888).[2] More recently a similar view has been maintained by Jaekel (1902) and by Regan (1904). The opposite opinion, *i.e.*, that the Ostracophori and the Arthrodira are widely distinct, has been urged by Cope, Woodward, and others, and is held at present by a majority of investigators.

The term Placoderm has of late come to be used in a rather broad sense, as referring indiscriminately to all primitive armored vertebrates, *e.g.*, Ostracophores and Arthrodires: this usage is a perversion of the sense of the original definition and I would therefore call attention to the history of the term in order to bring out its proper meaning.

As defined by McCoy [3] the Placodermata were constituted a family of Ganoids to include Agassiz's group Cephalaspidæ (=*Pterichthys*, *Coccosteus*, *Chelyophorus*, etc.), with the exception of the genus *Cephalaspis* Ag., plus three genera included by Agassiz in his *Cœlacanthi*, *viz.*, *Bothriolepis*, *Asterolepis*, *Psammosteus*. A decade later the researches of Kner and Huxley led to the breaking up of the genus *Cephalaspis* Ag., into *Pteraspis* and *Cephalaspis*, the types respectively of our orders Heterostraci and Aspidocephala. These orders therefore are clearly not included in the original significance of Placodermata.

Pander [4] employed the term in this restricted sense. He defines it as a family, "die sich durch ihre knöchernen, fest an- und aufeinander gewachsenen Kopf- und Körper Schilder von allen übrigen unterscheidet." He restricts it to five genera: *Asterolepis*, *Coccosteus*, *Homosteus*, *Heterosteus*, and *Chelyophorus*.

Hence it is evident that the earlier use of the term limited it to our present groups Antiarcha and Arthrognathi as far as at that time known. Its very *raison d'être*, as Egerton [5] clearly recognized, was to draw a trenchant distinction between forms having the head only encased in armor (Heterostraci and Aspidocephali), and those having both head and trunk so encased (Placodermata). The use of the term *Placodermata* ought therefore to be restricted exclusively to the Antiarcha and Arthrognathi. Those feeling the need of a more comprehensive term to include all the primitive armored vertebrates have therefore to coin one.

A number of similarities between some of the Ostracophores, especially the Antiarcha and the Arthrodira, have again and again been pointed out. I need only cite such familiar examples as:

1. The hard bony casing of the anterior portion, and the unarmored condition of the posterior portion of the body.
2. The correspondence in number and arrangement of the ventral plates.
3. The articulation of the dorsal armor to the cranium by a pair of ginglymoid joints.

That there is a close resemblance between the two groups in these regards, no one, I believe, will deny. What then is its significance? There seem to be two possible interpretations:

1. Either these similarities are merely analogies, *i.e.*, a series of parallelisms in phylogenetically unrelated forms, or—

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[1] Huxley's view is tersely stated as follows: "No one doubts that wherever *Coccosteus* goes, *Pterichthys* must follow." (1861, p. 37).

[2] Dr. Traquair, however, later referred them to the Teleostomi.

[3] Ann. and Mag. Nat. Hist. [2], II, 1848.

[4] Ueber die Placodermen des Devonischen Systems, 1857 p. 43.

[5] Palichthyologic Notes, No. 12, Q. J. Geol. Soc., XVI, 1860.

2. They are homologies, *i.e.*, characters indicative of phylogenetic relationship.

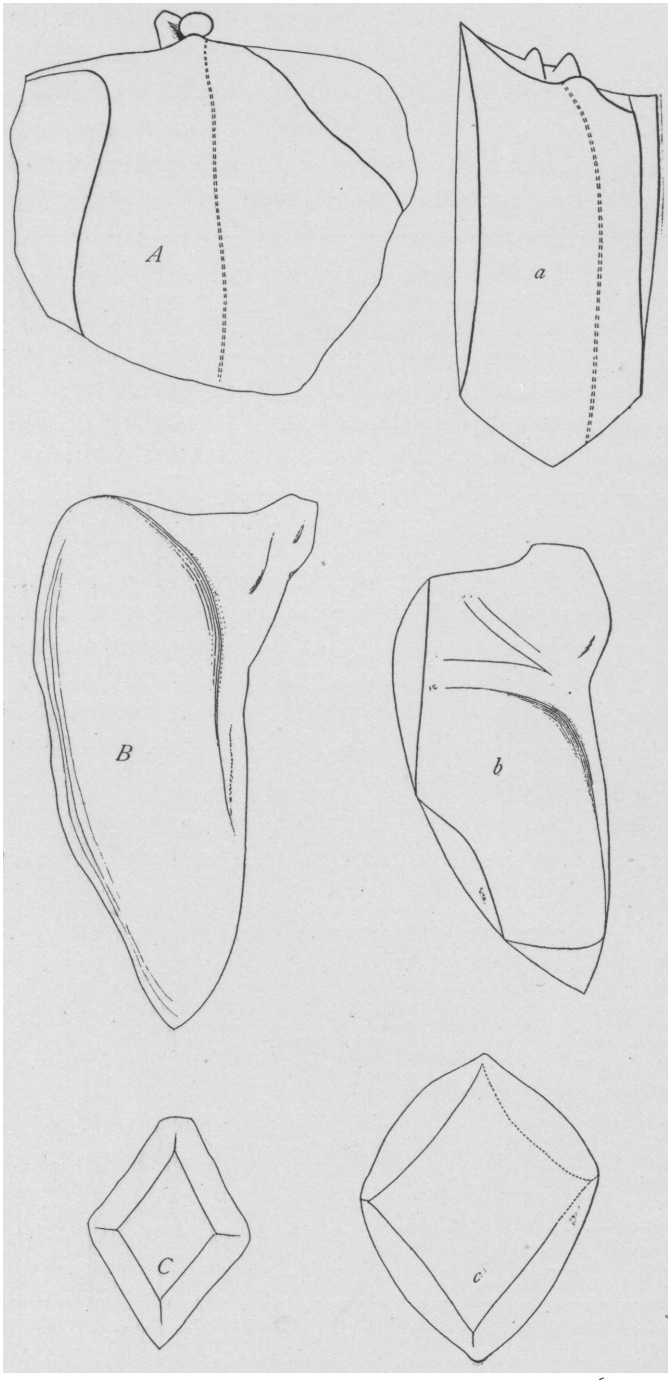


Fig. 13. Body plates of Arthrodires (*A*, *B*, *C*) and Ostracophores (*a*, *b*, *c*) compared. *A*, right antero-dorso-lateral of *Dinichthys minor* Newb. × $\frac{2}{3}$. (Cat. No. 69). *a*, antero-dorso-lateral of *Asterolepis*. After Traquair. *B*, right antero-ventro-lateral of *D. intermedius* Newb., inner view. × $\frac{1}{4}$. *b*, the same element in *Asterolepis*. After Traquair. *C*, postero-ventro-median of *Coccosteus*. After Pander. *c*, the same in *Asterolepis*. After Eastman.

I will endeavor to show which of these views is the more probable one, but before doing so I will briefly refer to a few points, in the following order: (1) ventral armor, (2) dorsal armor, (3) cranial shield, and (4) lateral appendages.

Ventral Armor.—In regard to this, I would point out that there is not only a similarity in plan of structure, but that some of the individual plates closely resemble corresponding elements in the Arthrognathi. (Fig. 13, *B*, *C*).

Dorsal Armor.—In both groups this is built on the same plan; but in the Antiarcha there is one plate more than in the Arthrodira—the posterior median-dorsal. In other regards the resemblance extends quite closely. Both anterior and posterior dorso-laterals are traversed by lateral lines, which have the same direction in the two groups. Some of the anti-archan plates might well be compared in detail with corresponding elements in the Arthrodira, *e.g.*, the antero-dorsol-laterals. (Figs. 13, *A*, *a*).

Cranial Shield.—It is not my intention to maintain that there is an exact correspondence, element for element, between the cranial shields of Antiarcha and Arthrodira. But I desire to point out that in some regards, at least, there

is a remarkable degree of similarity; what its significance is will presently be seen.

The two types of crania on a first glance are so different that their underlying similarity in plan has been generally overlooked.[1] One difficulty has been that the asterolepid cranium, as usually represented, has associated with it the suborbitals ("extra-laterals" Traquair, "operculars" Pander), whereas the arthrodiran cranium is usually figured without them. Concerning these extra-laterals, I fully concur in the opinion of Professor Jaekel, that they are homologues of the arthrodiran suborbitals. They hold the same position as in the latter forms, *i.e.*, external and anterior to, the marginal plates of the head, and are but loosely articulated with the other cranial elements. Writing of one of these plates, Dr. Traquair says: "Forming the lateral margin of the buckler external to the lateral plate on each side, this element attains large size in *Pterichthys*, and seems to have been only loosely articulated to the side of the head, as it so frequently occurs dislocated and removed from its position, while the other cranial plates will cohere together."[2]

Fig. 14, *A*,*B*, presents for comparison the cranial shields of *Bothriolepis* and of

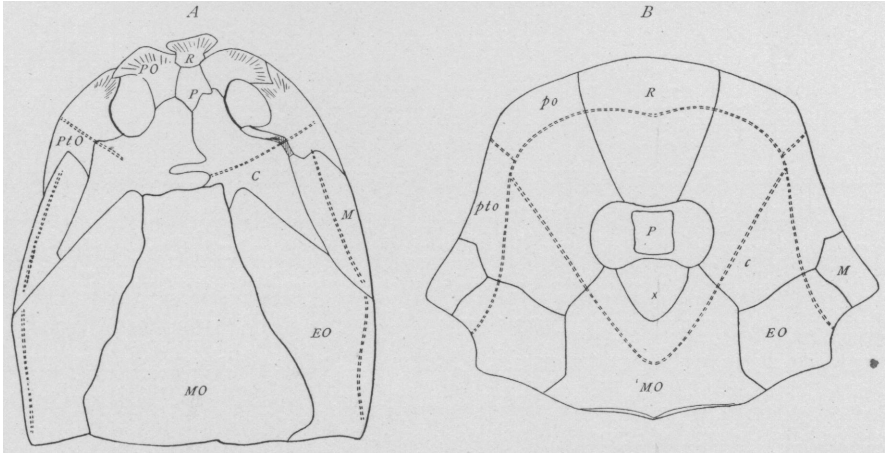


Fig. 14. Cranial shields of *Homosteus* and *Bothriolepis* compared. *A*. *Homosteus milleri* Trq. After Traquair. *C*, central; *EO*, external occipital; *M*, marginal; *MO*, median occipital; *P*, pineal; *PO*, preorbital; *Pt O*, postorbital; *R*, rostral. *B*. *Bothriolepis canadensis* Whit. (Homologies of elements lettered in small type doubtful.) *c*, central; *EO*, external occipital; *M*, marginal; *MO*, median occipital; *P*, pineal; po, preorbital; *pto*, postorbital; *R*, rostral; *x*, element of uncertain homology.

Homosteus. My interpretation of the homologies of the elements agrees largely, but not entirely, with that of Professor Jaekel.[3] It will be noted that the main difference between the two types of crania is in the region of plates, which in the Arthrodira are very variable and sometimes fused. The posterior region

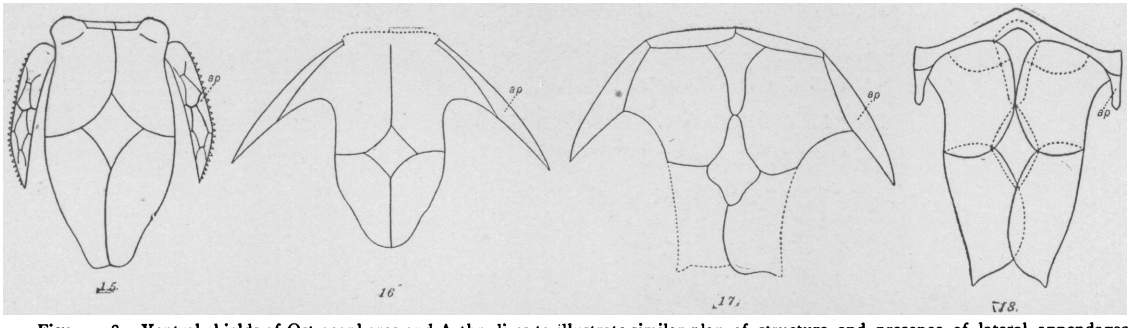
[1] Jaekel, however, has recently instituted a careful comparison between the arthrodiran and the asterolepid crania (Ueber die Organization u. syst. Stellung der Asterolepiden. Zeitsch. der Deut. Geol. Gesell., Bd. 55, 1903, pp. 41–60).

[2] A Monograph of the Fishes of the Old Red Sandstone of Britain. Part II, No. 1. The *Asterolepidæ*. Palæont. Soc., XLVIII, 1894, pp. 63–90.

[3] *Ibid.*

of the cranial shield (median occipital, external occipital, marginal) is identical in all genera of Arthrodira and Antiarcha. In the present instance, moreover, the comparison is fortified by the evidence afforded by the sensory canals traversing the plates. These, in the main, have a similar distribution on the head and shoulder armor.

The orbits in the Antiarcha are approximated, and dorsal in position, while those in the Arthrodira are usually lateral. But the position of these organs is no index of homology since we know from other groups (*e.g.*, Elasmobranchs) that their position may shift in adaptation to a special environment. The approximation and dorsal position of the orbits in the Antiarcha have been regarded by various writers as a specialization for bottom living.



Figs. 15-18.—Ventral shields of Ostracophores and Arthrodires to illustrate similar plan of structure and presence of lateral appendages (*ap*). Fig 15. *Pterichthys*. After Traquair. Fig. 16. *Acanthaspis*. After A. S. Woodward. (Regarded by some as an Ostracophore and by others as an Arthrodire.) Fig. 17. *Phlyctænaspis*. After Traquair. Fig. 18. *Coccosteus*. Modified from Traquair.

Lateral Appendages.—These are present in the Antiarcha and in all of the Arthrodira which have been completely studied. The complicated mode of articulation to the ventral plates is absent in the Arthrodira. But, it is highly significant that in the Arthrodira spines do occur, and that they appear especially well marked in the more primitive forms (Figs. 15–18, 19).

To sum up: in addition to marked similarity in time-relations and distribution the Arthrodira resemble the Antiarcha in:

1. Plan of dorsal armor.
2. Plan of ventral armor.
3. Unarmored condition of the caudal half of body.
4. General similarity in lateral line systems.
5. An underlying similarity in cranial structure.
6. Union of cranium and dorsal armor by a pair of complicated ginglymoid joints.
7. A similar tendency to develop lateral spines.
8. To these points may be added the existence of connecting or intermediate forms, *e.g.*, *Acanthaspis*.
9. A similar "potential of evolution," shown in the progressive antero-posterior shortening of the armor.

How shall these similarities be regarded, as homologies or as analogies? It seems to me that the former is the view more in accord with the facts; for it

is inconceivable that conditions of life, however similar, should so profoundly affect the structure of two wholly unrelated groups as to build them on parallel plans, and constrain them to pass through similar phases of evolution. It appears to the writer that the Arthrognathi and the Antiarcha are related,

Fig. 19. Right "clavicular" of *Dinichthys intermedius* Newb. to show the presence of a vestigial lateral appendage (*ap*). × about ¼. (Cat. No. 5.)

although at the earliest period at which they are known, they had already long diverged, each of the branches having followed out a different evolution, though still retaining evidence of a common origin. It is further evident that the

amount of divergence between the two is best expressed by such a division as an order or a subclass.

It must be stated that in this affiliation of the Antiarcha with the Arthrognathi, the other Ostracophori are not included. It seems to the writer that the long-accepted view that the Ostracophori form a natural group is without sufficient evidence, and that therefore the Antiarcha should be separated from the lower forms with which they are usually classed, in a manner similar to that proposed by McCoy (1848). The group *Ostracophori* as at present understood, embraces two or more divisions which are united more upon negative evidence, *i.e.*, because they have no similarities with any of the other divisions of the Vertebrata, rather than for the possession of a series of common characters. What community of structure is there between *Pteraspis* and *Asterolepis?* What evidence is there for homologizing the single ventral shield of the former with the five or six plates of the latter; and how, too, can we account for the absence of the lateral spines in *Pteraspis?*[1] No one, I believe, can deny that there is a closer similarity in structure between *Asterolepis* and *Coccosteus* than between the former and, say, *Cyathaspis.*

There are a few objections which will readily occur to any one, against systematically relating the Antiarcha to the Arthrognathi. These objections must be briefly noticed.

1. The presence in the Arthrodira and the absence in the Antiarcha of neural and hæmal arches. Against this objection it may be stated that the Antiarcha are not here regarded as on the same level of evolution as the Arthrodira; they retain many primitive characters and among these a notochord which has not yet developed ossified neural or hæmal arches.[2] The presence of a notochord is of course quite generally conceded by the very fact that these forms are classed as vertebrates.

2. The absence of internal fin-supports. Primitive internal fin-supports would be rather delicate and unossified, and hence would not be favorable to preservation. Moreover, in some instances where the animal had been preserved more or less intact, the internal elements are concealed by the external covering.[3]

3. Mouth parts. It is now recognized that the pair of "mentals" in the Antiarcha are jaw elements (for a good figure see Patten, in Biol. Bull., VII, 1904, p. 117, fig. 3). And Professor Patten has recently found an additional

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[1] Professor Patten's conjecture that the "lateral eye openings" may turn out to be notches for the attachment of appendages (Amer. Naturalist, XXXVII, 1903, pp. 827–865), still lacks confirmation.

[2] "One may infer from the outline of the trunk that a notochord was present. It was probably surrounded by a membranous sheath of no more consistency, if as much, than that in *Amphioxus.*" (Patten, *l. c.*, p. 114.)

[3] Fossilized cartilaginous structures are extremely rare even among the Arthrognaths. There is only a single specimen of *Dinichthys* known, which shows the notochord, and even this is defined by the position of the arches rather than by the substance of the cord (Dean, 1896 *a*).

pair of elements in the jaw region of *Bothriolepis*.[1] The antiarchan jaw, however, is much inferior in development to that of the Arthrodira.

It has thus far been shown, I believe, that the Arthrodira and the Antiarcha, though divergently specialized, retain a sufficient number of characters in common to indicate a relationship.[2] This relationship is perhaps as remote as that existing between the present-day Elasmobranchs and Teleosts; it is closer, in fact, than that between the Elasmobranchs and the more aberrant Teleosts.

Hence, it appears to the writer that there are good grounds for accepting the view which has been maintained by McCoy, Pander, and others, *viz.*, that the Antiarcha and the Arthrognathi are allied forms. And it seems best to retain for these forms McCoy's term *Placodermata*, though in a slightly wider sense so as to include the more recently discovered allied genera. The group *Placodermata* as here defined is to be regarded as a division of the Vertebrata coördinate with fishes (proper), or *Cyclostomi*.

The *Placodermata* thus comprise two divisions:

1. Antiarcha (Cope), as generally defined.
2. Arthrognathi (Dean), including:

a. Anarthrodira (Dean) representing forms like *Macropetalichthys*, which in some characters seem transitional between the Antiarcha and the Arthrodira.

b. Arthrodira (Smith Woodward).

For the group including the Ostracophori as commonly understood, minus the Antiarcha, it seems advisable to introduce a new term, and **Euostracophori** is here proposed.

Classification of the Primitive Vertebrates.

1. Euostracophori.[3]
2. Placodermate.

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[1] Biological Bulletin, VII, 1904, pp. 113–124.

[2] A similar view, though based upon evidence of a different kind has recently been urged by Kemna (1904). "Ce qui nous semble bien établie, ce sont les rapports d'étroite parenté entre Astérolépidés et Arthrodiriens, mais dans le sens d'une commune origine, et non dans la descendance d'un groupe de l'autre. Les différences sont des modifications divergentes d'un type commun, qui a pu ê tre quelque chose comme *Acanthaspis*, ballotté entre les deux groupes, Astérolépidé pour Smith Woodward, énergiquement réclamé comme Coccostéidé par Traquair" (Kemna, 1904, p. 78).

[3] It is rather doubtful whether Traquair's order Anaspida belongs here, or whether it should be raised in rank as a separate subdivision. From Dr. Traquair's careful description it would appear that these forms do not possess a large number of characters in common with the Euostracophori; perhaps only three:

1. Presence of dermal tubercles,
2. Dorsal fin,
3. Absence of paired fins.

On the other hand they differ from them in the following characters:

1. Compressed fish-shaped body,
2. Presence of a series of shark-like gill (?) openings,
3. Flanks armored with parallel series of plates.

Further research may perhaps demonstrate their affinity with the primitive Elasmobranchs.

3. Cycliæ.
4. Cyclostomi. 5. Pisces.[1]

V.—GENERAL CONCLUSION: THE POSITION OF THE ARTHROGNATHI.

In conclusion I desire to bring together the various strands of the argument which has been made and to indicate the view regarding the position of the Arthrognathi to which it has led.

In Section III evidence was brought forward for the conclusion that the Arthrodira are unique among vertebrates:

1. In having the power to separate the halves of the lower jaw in the symphyseal region (pp. 115, 118, 123).

2. In the absence of the Meckelian cartilage (pp. 123, 127).

3. In having jaw elements derived from ornamented armor plates.

4. In Section IV it was shown that it is doubtful whether paired fins at all existed in the Arthrodira. Pectoral fins are generally conceded to be absent (p. 126). And there is no conclusive proof of the presence of pelvic fins. It is equally questionable whether the so-called pelvis in *Coccosteus* is really such, since it is ossified (p. 126).

5. In the different subdivisions of Section IV, also, it was shown that the Arthrognathi cannot be regarded as even distantly related to, (1) Teleostomes; (2) Chimæroids; (3) Dipnoans.

6. Evidence was advanced for regarding them as related, though remotely, to the Antiarcha; together with which they constitute the group *Placodermata*.

7. The *Placodermata* are one of the major subdivisions of the Vertebrata, coördinate in rank with such divisions as *Pisces* or *Cyclostomi*.

VI.—THE EVOLUTION OF THE ARTHRODIRA IN NORTH AMERICA.[2]

In this section an attempt is made to outline the evolution of the Arthrodira in North America. The conclusions set forth should be accepted as provisional only, for the material studied has been partly fragmentary, so that the results attained may at any time be upset by new discoveries.

1. *The Origin of the Arthrodira in North America.*[3]

The first problem that arises concerns the place of origin of the Arthrodira. Did the American forms originate independently of any other stock, or did they

[1] The character of the two forms described by Dr. Traquair under the generic names of *Gemündina* and *Hunsrückia* is highly problematical and for the present they must be retained as *Insertæ sedis*.

[2] I am under obligations to Prof. A. W. Grabau of Columbia for a number of suggestions in connection with the geological data discussed in this section.

[3] A paper read before the American Society of Vertebrate Palæontologists, New York meeting, Dec. 27, 1905.

find their way into the American seas from some other center, in the course of their adaptive radiation? The evidence at hand, it appears to the writer, points conclusively to the latter alternative.

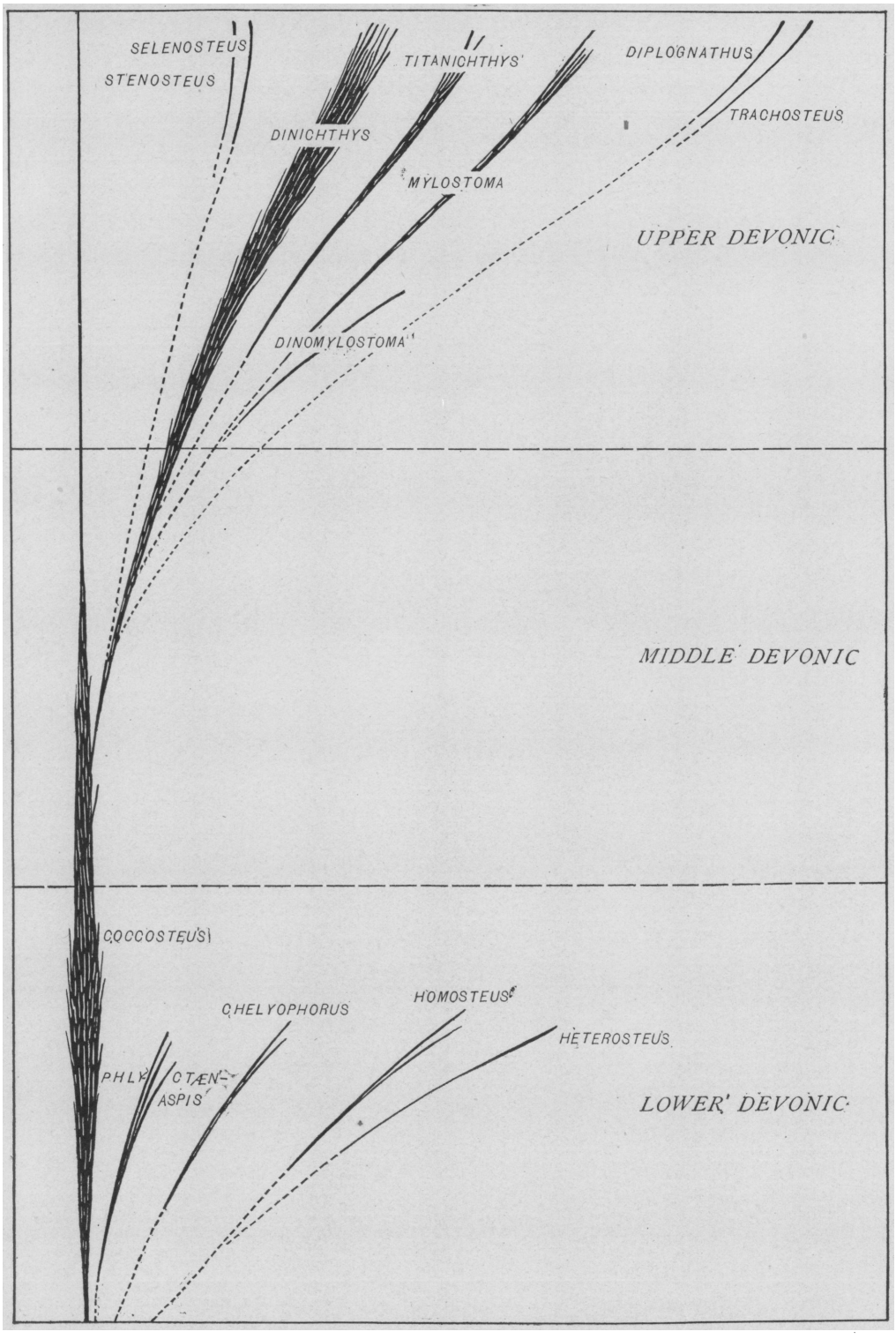
GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE EARLIER ARTHRODIRA.

	WESTERN EUROPE.	NORTH AMERICA.
MIDDLE DEVONIC	Dinichthys eifeliensis *Kays.* " pelmensis *Eastm.* " bohemicus *Barr.* " trautscholdi *Eastm.*	Dinichthys canadensis *Woodw.* " pustulosus *Eastm.* " lincolni *Clayp.* " halmodeus *Clarke.* " precursor *Newb.* Coccosteus occidentalis *Newb.*
LOWER DEVONIC	Dinichthys livonicus *Eastm.* Coccosteus decipiens *Ag.* " minor *Miller.* " hercynius *von Meyer.* " angustus *Trq.* Phlyctænaspis anglica *Trq.* " germanica *Trq.* Heterosteus asmussi *Ag.* Homosteus milleri *Trq.* " formosissimus *Trq.* Chelyophorus primigenius *von Eichw.* " verneuili *Ag.* Coccosteus ? agassizi *Barr.* " ? primus *Barr.*	Phlyctænaspis acadica *Whit.*

Arthrodira occur in the Devonic of both Europe and North America. The above table gives for comparison the geological distribution of the earlier forms in the two regions. It is noted, 1, that arthrodira appear much earlier in Europe than in North America; 2, that the variety of arthrodiran forms in Europe in these horizons is greater; 3, that no genera appear in America that are not first found in Europe, the difference in common forms being only specific. These facts indicate apparently that a wave of migration took place from the European to the American sea. This view is strongly supported by geological evidence. It is generally recognized that toward the close of the Siluric and perhaps even into the Devonic (Onondaga limestone), a channel extended across the Atlantic region between Europe and North America. This afforded the opportunity for an arthrodiran migration westward. The variety of forms and the relative abundance of individuals found in the lower Old Red Sandstone of Scotland indicate that the coccosteids were in a period of "evolutionary prosperity" and hence would certainly radiate in search of a new environment.[1]

[1] The Ostracophores probably found their way to North America in a similar manner. This is shown by the earliest American types (U. Siluric and L. Devonic), being generically identical with European forms: *Palæaspis* Clayp. (=*Holaspis* Lankester), *Cyathaspis*, *Cephalaspis*.

GEOLOGICAL DISTRIBUTION OF THE ARTHRODIRA



At the beginning of the Devonic, the American sea became separated from the European, and during the vast period of time until the seas again merged, as there is reason to believe, toward the close of the Devonic, the Arthrodira in the eastern and western centers followed out their respective evolutions.

The earliest Arthrognaths whose remains have been found in North America are: *Phlyctænaspis acadica* (Lower Devonic, Canada), *Coccosteus* (Middle Devonic, Ohio), and *Macropetalichthys* (Middle Devonic, Ohio).

Of these the first named is a very primitive type—much more so than *Coccosteus;* and the last is avowedly not related to the main arthrodiran stem but is best to be interpreted as a lateral branch.

2. *The Coccosteids.*

The earliest true coccosteid in America was *Coccosteus occidentalis* found in the Delaware limestone of Ohio, described and figured by Professor Newberry (1875). Only two of its plates are known: a dorso-median and a median ventral. But Newberry has clearly shown that these belong to *Coccosteus* and that they differ from their homologues in the typical *C. decipiens* only in unessential details.

The genus *Coccosteus* stands near the bottom of the evolutionary series. All investigators will agree that compared with such forms as *Dinichthys* and *Titanichthys* it is primitive. This is shown in many of its features.

1. The body plates are less specialized: they are simpler in outline, smaller in size, and articulate more frequently by simple overlap rather than by complex peg-and-socket joints.

2. The dorso-median terminates posteriorly in a pointed process and not as in the dinichthyids in a specialized structure. The median carina is not as well developed as in *Dinichthys.*

3. The ventro-laterals are but little removed from a subcircular form.

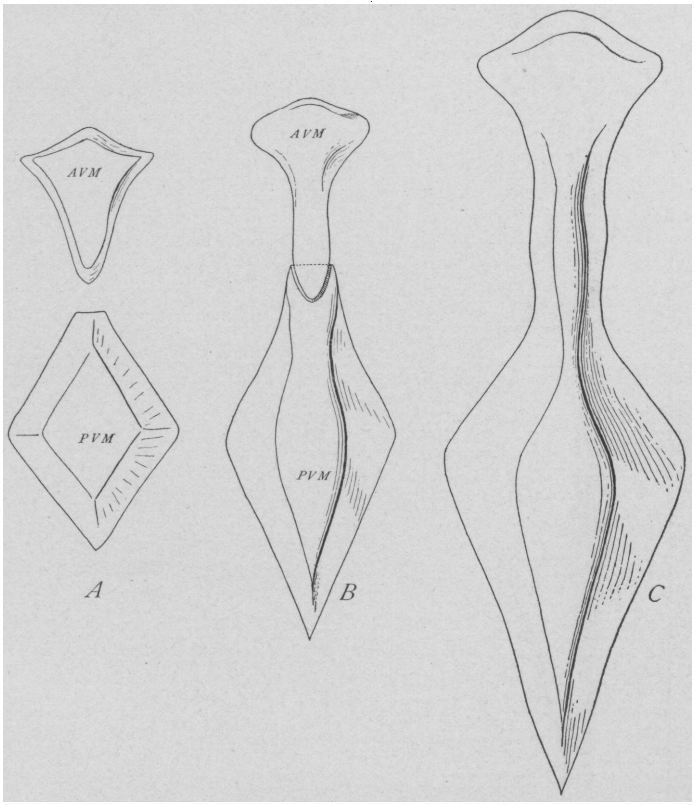


Fig. 20. Types of median ventral elements in the Arthrodira. *A*, *Coccosteus decipiens* Ag.; primitive type of median ventrals. After Pander. *B*, *Dinichthys intermedius* Newb ; more specialized type, the elements interlocking by a socket joint *C*, *Dinichthys terrelli* Newb.; highly specialized type, the elements fused. *AVM.*, antero-ventro-median ; *PVM*, postero-ventro-median.

4. The anterior median-ventral plate neither interlocks nor fuses with the posterior one (Fig. 20).

5. The ornamentation of the body plates consists of simple tubercles not arranged in any pattern.

6. The infero-gnathal possesses a row of symphyseal denticles.

In this connection a few words must be devoted to the small gnathal described by Newberry as *Liognathus spatulatus* (1873), and subsequently identified by himself and others with *Coccosteus*. Newberry's main reason for associating it with *Coccosteus* seems to have been its occurrence in close proximity to the plates of *C. occidentalis*, suggesting a possibility of belonging with them. In the figure a gnathal of *C. decipiens* and that of *spatulatus* are given for comparison (Fig. 21, *A*, *B*). I would call attention to the points of difference between them since these have not been sufficiently emphasized. In *spatulatus* it is noted, (1) that the anterior end rises into a Dinichthys-like "tooth." (2) The denticles are different. The typical *Coccosteus* presents a row of some seven denticles all in the plane of the blade and directed mesially. In *spatulatus* they are not arranged in one plane but are scattered irregularly along the edge. They do not appear to have been so pointed, although in this regard the element of wear should not be left out of consideration. From these facts it is proper to conclude that whether this element falls within the limits of *Coccosteus* or not, it undoubtedly represents a form which in respect to gnathals has advanced beyond the *C. decipiens* stage in the direction of *Dinichthys*.

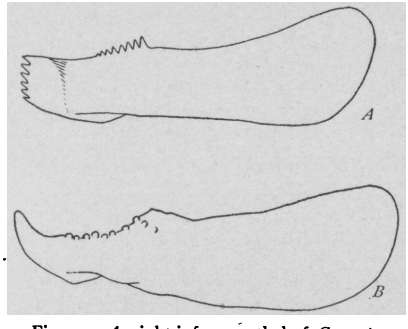


Fig. 21. *A*, right infero-gnathal of *Coccosteus decipiens* Ag., inner view. × 1. *B*, right infero-gnathal of *Coccosteus* (*Liognathus*) *spatulatus* Newb., inner view. × 1. Type specimen. (Cat. No. 325).

No other arthrodiran remains have thus far been found in Ohio proper to enable us to trace the successive stages up to *Dinichthys herzeri* of the Huron shale. In western New York, however, the advancing line is found. The forms from the latter locality are undoubtedly descended from the coccosteid stock which migrated to North America and which gave rise to *Coccosteus occidentalis*.

3. *The Dinichthyids.*

D. halmodeus Clarke.—This is the earliest American form referrable to the genus *Dinichthys*. In many characters it closely resembles *Coccosteus;* and therefore it calls up the question of the distinction between these two genera.

All familiar with the Arthrodira will agree, I believe, that no sharp line can be drawn between *Coccosteus* and *Dinichthys*. A series of transition stages between the two can be arranged for almost every structural character. Dr. Eastman several years ago (1897) indicated one feature which seemed to separate the two genera: the presence in *Dinichthys* and the absence in *Coccosteus* of a

dorso-median process with a spoon-shaped excavation. But this criterion cannot always be applied, for in some of the most primitive dinichthyids (*e.g.*, *D. halmodeus*), the process has not been demonstrated. Another difference formerly believed to exist between the two genera was in the number of jaw elements. This, also, can no longer hold, for as was shown at page 121 there is an

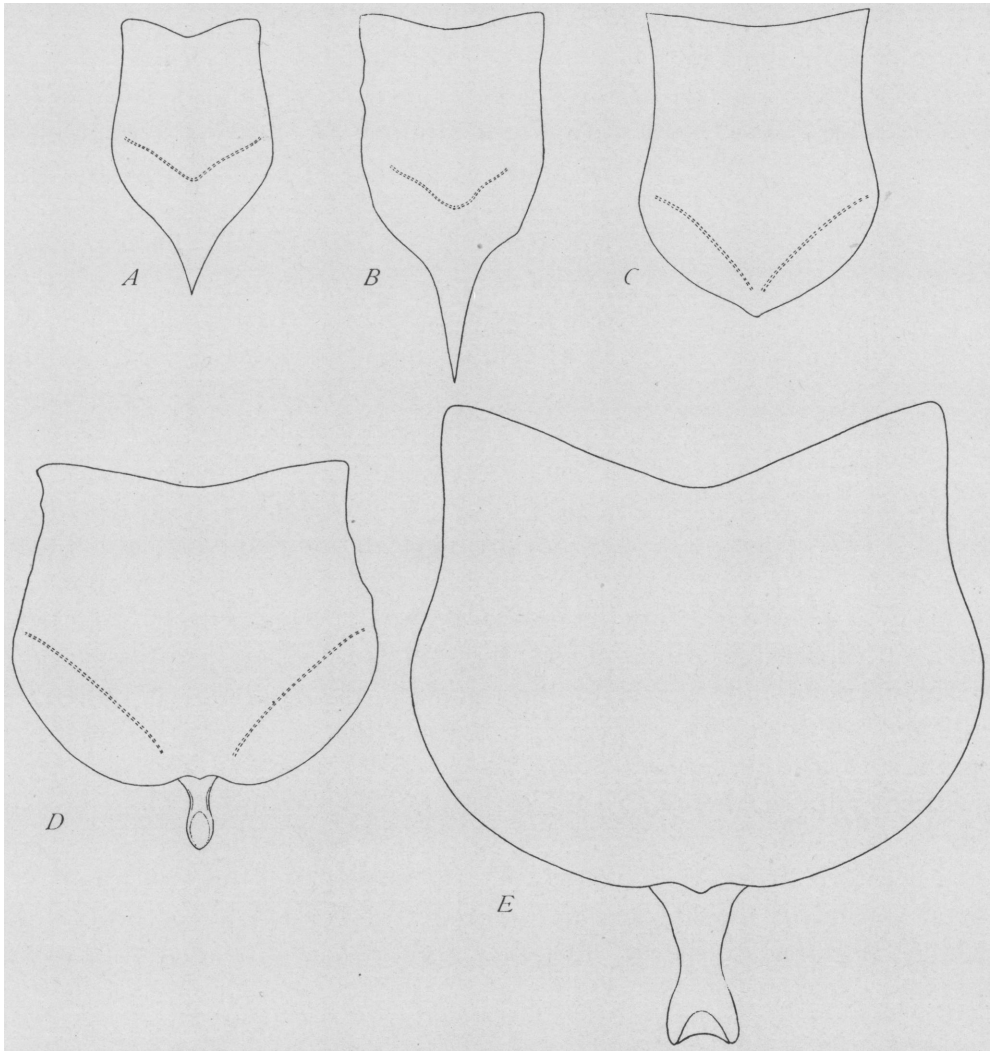


Fig. 22. To illustrate the evolution of the dorso-median plate. Note especially the progressive antero-posterior abbreviation. *A*, *Coccosteus decipiens* Ag. × ½. Lower Devonic. *B*, *Coccosteus occidentalis* Newb. × ½. Middle Devonic. From type specimen. (Cat. No. 313.) *C*, *Dinichthys halmodeus* Clarke. × ¼. Middle Devonic. After Eastman. Original in N. Y. State Mus. *D*, *Dinichthys pustulosus* Eastm. × ¼. Middle Devonic. From specimen in the Cambridge Mus. Compar. Zoöl. (Cat. No. 1389.) *E*, *Dinichthys terrelli* Newb. × ⅛. Upper Devonic.

entire similarity between *Coccosteus* and *Dinichthys* in this regard. In general it may be stated that no line can be drawn between the coccosteids and the most primitive dinichthyids. It is only in the extremely specialized forms that differences are marked. The separation of the lowest dinichthyids from *Coccosteus* should be based upon a consideration of the state of specialization of the animal as a whole.

In most regards *D. halmodeus* is primitive—as primitive as *Coccosteus*. It retains a tubercular ornamentation and exhibits an identical configuration of cranial plates. Nevertheless, it shows certain advances over *Coccosteus*, for instance in the size and relative shortening of the dorso-median (Fig. 22, *C*, p. 141).[1]

Dinichthys lincolni Claypole.—This has already been discussed at page 117, where its bearing on the evolution of the gnathals from denticled armor-plates was considered. This species likewise occurs in the Marcellus shale though some 3–6 feet higher up than the preceding form. Unfortunately, nothing more of it is known than an antero-supero-gnathal. This is interesting because it proves that the Arthrodira were fast evolving in point of size.

Dinichthys pustulosus Eastm.—From the Hamilton of Milwaukee, Wisconsin, Dr. Eastman has described this interesting and in many respects very primitive form (1898). This species has been recorded also from the Hamilton of Kentucky, Iowa, Illinois, and northwestern (?) New York. Recently I have found fragments of apparently the same species in a small collection of fish remains from the Hamilton of Michigan. The head, shoulder armor, and the infero-gnathal were carefully described by Dr. Eastman. These elements prove that with undoubted advances along the dinichthyid line, this species still retained many primitive coccosteid characters. Dr. Eastman enumerates ten such characters:

1. Cranium strongly arched from side to side.
2. Tubercles.
3. Sutures undulatory.
4. A narrow band along the sutures generally striated and destitute of tubercles.
5. Centrals in contact with one another mesially throughout their entire length.
6. Sensory canals, "more curved," especially the preorbital.
7. An occasional antero-dorso-lateral canal terminating blindly.
8. Dorso-median traversed by canals.
9. Union of dorso-lateral plates by simple overlap, not by peg-and-socket joints.
10. Slight anterior emargination of dorso-median.

Hence with undoubted advances in structure this dinichthyid has not yet departed widely from the coccosteid type. Nevertheless, our present knowledge places it undoubtedly in the genus *Dinichthys*.

The most important advance made by *D. pustulosus* is in the line of dentition. It has of course all the gnathal elements of the typical dinichthyid—a fact which is inferred even from the infero-gnathal alone. This element has progressed beyond the primitive type. It is entirely devoid of denticles along the cutting edge but has instead, a sharpened blade like that seen in several of the later

[1] A detailed study of this form has just been prepared for publication by Dr. Eastman, and therefore I have deemed it unnecessary to enter into a lengthy discussion of its structure.

Ohio forms. A few vestigial denticles are retained near the posterior portion of this cutting edge.

What was the relation of this species to the dinichthyids found in higher horizons, particularly in Ohio? Geological considerations indicate that *D. pustulosus* was not in the direct line of the Ohio forms, but that it represented a lateral branch which became extinct. If a line be drawn on a map through the localities at which *D. pustulosus* has been found, it would extend in a curve from Kentucky, through Iowa, around the lakes, through Wisconsin, Michigan, to northwestern (?) New York. Ohio and the States adjoining it on the east are not included. The forms associated with *D. pustulosus* are characteristic chimæroid (Ptyctodont and Rhynchodont) and dipterine teeth, associated with a few Ichthyodorulites. It has been commented on[1] as a striking fact, that these species are characteristic of the Hamilton in the Iowa–Wisconsin region, and that none of them is found in the New York–Pennsylvania region. In fact an entirely different fauna occurs in the Chemung of the eastern States; a fauna characterized by *Holoptychius* and *Bothriolepis*. There seems to have been no mingling of the vertebrates of the Upper Hamilton of the Iowa–Wisconsin region with those of the Chemung of the New York–Pennsylvania region.

What was the barrier which prevented the one fauna from passing over and mingling with the other? It certainly was no uplift between the two regions, for Ohio was probably covered by sea all through the Middle and Upper Devonic. It must be concluded, therefore, that it was the physical character of the Ohio sea which prevented migration. I shall refer presently to the character of the rocks in Ohio as indicating peculiar conditions. It is highly suggestive in this connection, also, that no representatives of the fauna of either the eastern or the western regions are represented in Ohio.

These considerations lead to the conclusion that *D. pustulosus* is not in the line of descent of the highly specialized dinichthyids found in the higher horizons in Ohio. The latter represent a series which is carried much farther along the line of specialization until the time of their extinction at the close of the Devonic. A stage in evolution, in regard to gnathals, comparable to that attained by *D. pustulosus*, is passed through by the Ohio fauna at a much later period (*D. intermedius*, Cleveland shale).

The Upper Devonic of Ohio is composed of the well-known Ohio shale of which three formations are generally recognized:

1. Huron Shale;
2. Erie Shale (Chagrin Formation, *Prosser*);
3. Cleveland Shale.

These massive beds of shale rise in some localities in northern Ohio to a thickness of 2600 feet. Their exact correlation with other Devonic formations is a vexed problem about which a whole literature has sprung up. In the words

[1] Claypole, 1896, p. 355. Also C. R. Eastman: On Upper Devonian Fish Remains from Colorado. Amer. Jour. Sci., XVIII, 1904, pp. 253–260.

of Claypole: "It would suffice to maintain that, as a whole, it [the Ohio shale] is the contemporary of the New York series from the base of the Genesee to the top of the Catskill."[1]

A word must here be said concerning the character of these shales. It has been remarked by several geologists that these Ohio formations are peculiar for their high content of carbonaceous material. Newberry, who studied these shales most carefully, concluded that they must represent a sort of

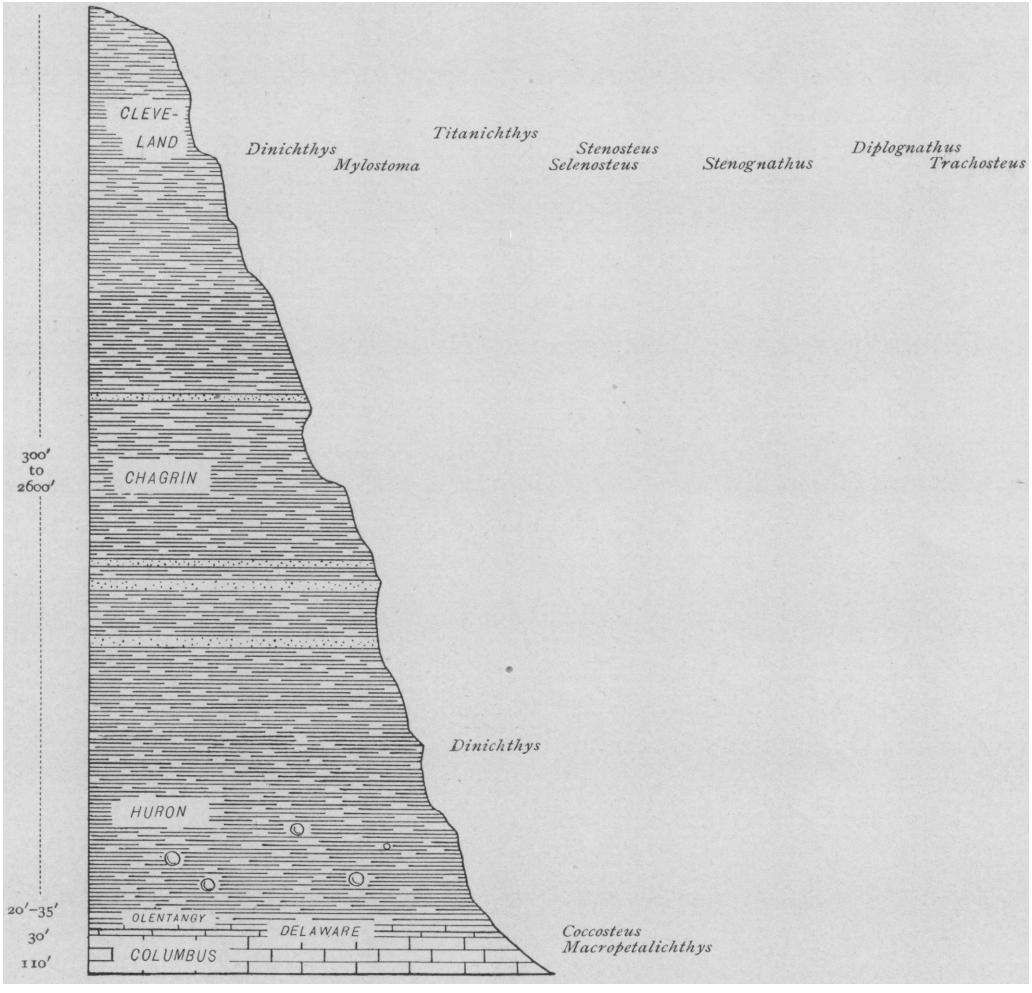


Fig. 23. Devonic formations in Ohio and distribution of the genera of Arthrodires.

Sargasso sea. This view is maintained by several investigators and among them Professor Henry Shaler Williams, who has devoted many years to a minute study of the American Devonic. In a recent work Professor Williams thus speaks of the Ohio shales: "Faunally they are distinguished by a marine fauna containing a few, generally minute, invertebrates, many traces of plants, and often the spore cases of rhizocarps, together with the bones of large fish

[1] Amer. Geologist, XXXII, 1903, p. 98.

distributed irregularly among the sediments. These peculiarities indicate quiet conditions of sedimentation—conditions not enough disturbed by currents or even wave action to affect the smoothness of the sediments on the bottom—and show that the sources of the sediments were at a considerable distance. The indications also point strongly to some kind of Sargasso sea, as suggested by Newberry; and it is possible that this coating of the surface of the sea by a living vegetation may account both for the black character of the sediments and for the absence of any considerable marine population."[1] Several of these conclusions as to the character of this sea are arrived at independently by Professor Dean upon the evidence of the manner of fossilization of the sharks of the Cleveland shale.[2]

In the lowest member of the Ohio shales, the Huron, we come upon the earliest of the great "Placoderms" of Ohio—*D. herzeri* Newb. The cranium and several of the body plates of this species are known, and these for the most part resemble those of later dinichthyids in shape, differing only somewhat in proportions. In the period since the deposition of the Delaware limestone, the Arthrodira in Ohio had rapidly evolved in point of size, for this species is almost as large as any that followed it.

The most remarkable features of *D. herzeri* are the gnathals. These have already been considered (p. 118). The denticles and other unique features of these elements stamp them at once as primitive—far more so, in this respect, than those of *D. pustulosus* of the Hamilton. The nature of the gnathals precludes the idea of the latter species being related to the former.

This type of *Dinichthys* was evidently not successful, for, in higher horizons it is replaced by species characterized more especially by the possession of knife-like, untoothed gnathals. What was the origin of the knife-gnathal types of the Cleveland shale? Are they the direct descendants of the *herzeri* type; or are they the outcome of a distinct stem of Arthrodires, descended, of course, from the primitive American ancestor, but which in an outre-Ohioan region evolved the cutting type of gnathal, then invaded Ohio and replaced the toothed (*herzeri*) type of gnathal? This matter must be carefully examined.

In 1885, Dr. John M. Clarke described an infero-gnathal from the Genesee shales of New York which he termed *D. newberryi*. Associated with it were a postero-supero-gnathal and fragments of the antero-supero-gnathal. An isolated dorso-median has also been referred to this species. The infero-gnathal has no trace of denticles along the upper edge, being entirely sharpened into a cutting blade. Hence, contemporaneous with *D. herzeri* there existed a species of *Dinichthys* with a cutting gnathal and in a region not very remote from that occupied by the former. Two views are therefore possible as to the relationship between these forms:

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[1] The Correlation of Geological Faunas. U. S. Geol. Surv. Bull., No. 210, 1903, p. 110.

[2] The Preservation of Muscle-fibers in Sharks of the Cleveland Shale. Amer. Geologist, XXX, 1902, p. 278.

1. *D. newberryi* is not phylogenetically related to the Cleveland shale fauna.

2. This species entered the Ohio waters, replaced the awkward, toothed type (*D. herzeri*), and gave rise in later horizons to *D. intermedius*, *D. terrelli*, and the other species known from that formation.

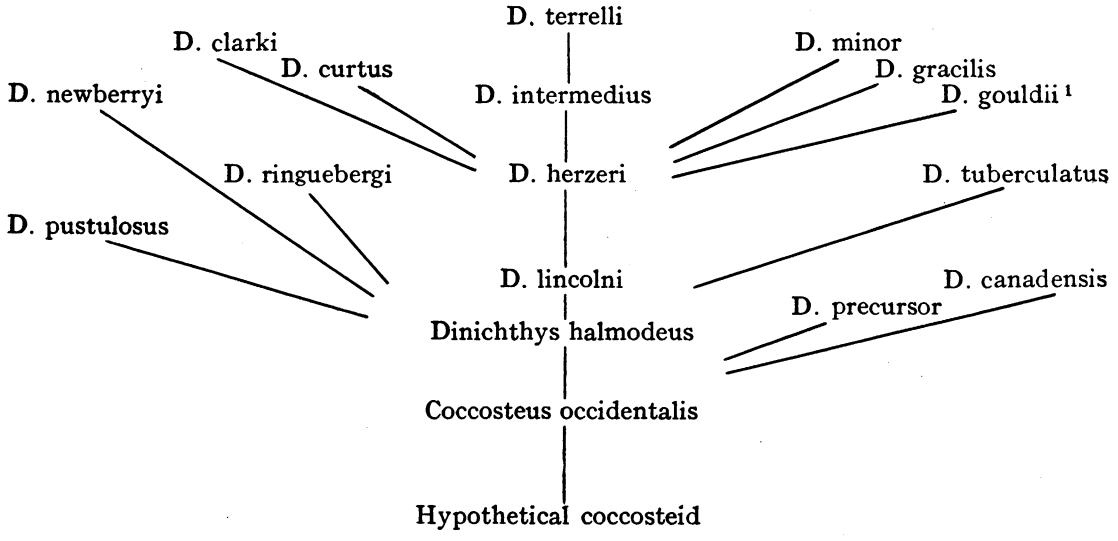
In the present state of our knowledge of this species, with only a single gnathal available for study, it is impossible to conclude whether the first or the second of these views is the correct one. A few considerations, however, lead to the belief that the first is the more probable interpretation.

1. The infero-gnathal is entirely destitute of any trace of vestigial denticles, whereas the Ohio forms of relatively the same size, which upon the hypothesis of lineal relationship would be derived from it, show well-marked vestigial denticles near the posterior portion of the cutting edge (*e.g.*, *D. curtus*, *D. intermedius*). Even *D. terrelli* occasionally shows such denticles (see p. 118).

2. In relative proportions "it agrees quite closely with those of *D. herzeri*, while *D. terrelli*, having a greater width in proportion to its length, has a stouter jaw" (Clarke). This may be interpreted to mean that though an accelerated species as far as the loss of denticles is concerned, it was still on a level with its contemporary *D. herzeri* in regard to proportion.

A final solution of this question, as of so many others in the phylogeny of the Arthrodira, cannot be expected until additional material is obtained.

EVOLUTION OF THE GENUS *Dinichthys* IN NORTH AMERICA.



The first Cleveland shale form that I will consider is *D. intermedius*. This is selected as typical of the Cleveland shale dinichthyids. It was said by

[1] *D. gouldii* Newb. is probably identical with *D. prentis-clarki* Clayp.

Claypole (1896 *c*) to occur some eighteen feet below the level at which *D. terrelli* is found. But my observations in the field fail to confirm this statement. The vestigial denticles which persist in the gnathals I regard as reminiscent of the condition seen in *D. herzeri*.

From the same geological formation we have the remains of *D. terrelli*. In this form the knife-like jaws are carried to an extreme. But even in this species, a careful study of the available specimens has revealed the occasional presence of vestigial denticles. Two specimens of postero-superognathals and two of infero-gnathals preserved in the Newberry collection exhibit these along the posterior cutting margin.

Contemporaneous with *D. terrelli* there was another large form *D. clarki*. This had a row of powerful functional "teeth" instead of a cutting blade The upturned fang of the infero-gnathal is much larger than that in *D. terrelli*. The body plates, some of which

Explanation of letters same as at p. 131.

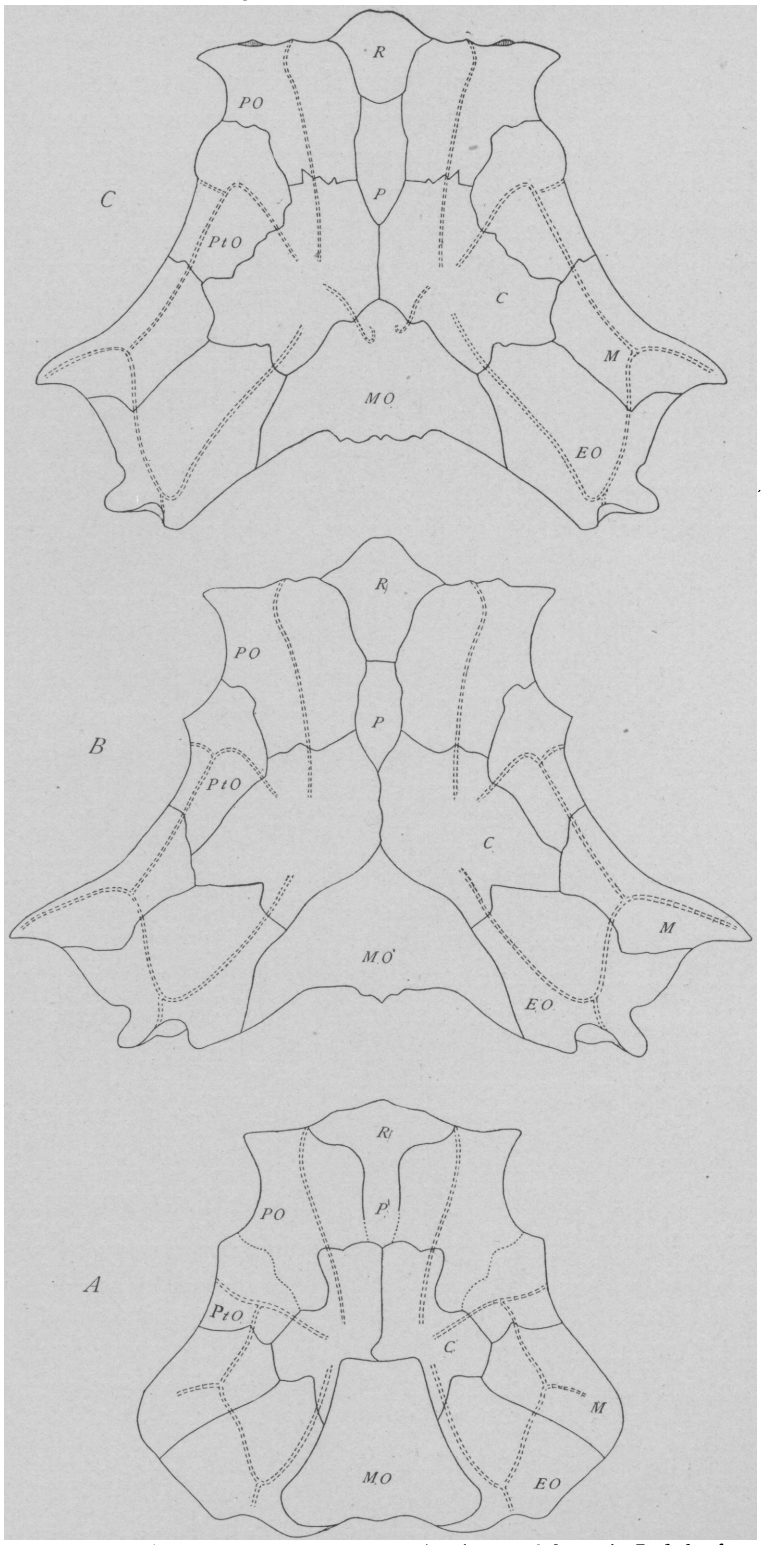


Fig. 24. To illustrate the evolution of the cranium in *Dinichthys*. *A*, *D. halmodeus* Clarke. × ⅛. Marcellus shale. After Eastman. (By permission of Prof. J. M. Clarke.) *B*, *D. intermedius* Newb. × ⅛. Cleveland shale. *C*, *D. terrelli* Newb. × ⅛. Cleveland shale.

the writer has recently described (1905 *b*) are similar in form to those of *D. terrelli* differing only in specific features.

In this discussion of the phylogeny of the Ohio dinichthyids stress has been laid especially upon the gnathals, for two reasons:

1. The gnathals, because of their vital importance to the Arthrodira, are preëminently subject to transformation in response to a changing environment.

2. These elements are better known than any of the other arthrodiran plates. This is mainly because the dense character of their structure was favorable to their preservation.

But other elements when available show progressive specializations. This can be seen, for instance, in a series of dorso-median plates (Fig. 22, *A–E*), or in a comparison of well-preserved crania. Fig. 24, *A*, *B*, *C*, presents the cranial shields of three successive species of *Dinichthys*. The last (*C*) is larger, heavier, and more abbreviated antero-posteriorly—characters in which it has become more specialized than *D. intermedius* or *D. halmodeus*.

4. *Other Genera.*

When we consider that of *Dinichthys* some seven species are known from the Cleveland shale, and that individuals, considering the limited locality, are relatively abundant, we must conclude that competition among them was severe, so that different "expression points" would be seized upon, so to speak, and new forms would appear. The result is that side by side with *Dinichthys* we have a bizarre assemblage of forms, each highly specialized in certain structures. In this class we must include the still imperfectly known genera *Mylostoma*, *Titanichthys*, *Selenosteus*, *Stenosteus*, *Trachosteus*, *Glyptaspis*, and *Diplognathus*. One of these genera is known as yet only by gnathals, *e.g.*, *Diplognathus*, and of the others our knowledge of the dermal plates is far too inadequate to allow of their being brought into a phylogenetic discussion. To each of these genera, therefore, only a few words need be devoted.

Mylostoma and *Titanichthys* are side branches of the dinichthyid stem. The former developed crushing dental plates; but these did not save it from extinction. Of *Titanichthys* some species were probably the hugest of all the Arthrodira. A restoration of the cranium of *T. clarkii* in the American Museum measures 56 inches in width. With an increase in size, however, came a decrease in thickness of armor, in order probably not to cumber the individual with too much weight. Structurally considered, *Titanichthys*, as far as known at present, became more specialized than *Dinichthys*, 1, in cranium, and 2, in gnathals.

1. The cranial shield, though retaining the contour and general structure found in that of *Dinichthys* is, relatively, much more abbreviated antero-posteriorly.

2. The gnathals have developed along a new line (see p. 120). It is at present indeterminable whether the gnathal groove was lined with a hard shell-

like substance, or whether it was set with a few large "teeth." Both hypotheses have been maintained. The view has been advanced that *Titanichthys* was a vegetarian, but the facts as known do not yet allow of final decision. Claypole sums up on this subject as follows: "The suggestion has been made that *Titanichthys* was a vegetarian and used his long jaws and their teeth for collecting sea-weed. Such a mode of life is possible but far from probable. Few fishes, so far as we know, live on sea-weed, and very few large fishes are not carniverous."

The closely related genera *Selenosteus* Dean, and *Stenosteus* Dean, represent another departure from the main dinichthyid stem. These forms were of relatively small size with plates that were thin and delicate. The gnathals were denticled in the symphysis. These forms are at present known only from the two type specimens, and more material is needed for a determination of their exact relationships.

Diplognathus.—All that is known of this genus are the infero-gnathals, and these have been discussed in another section (p. 122). They have departed widely from the Dinichthys-type, and resemble most closely, and probably are related to, *Trachosteus.*

Of great interest are the small jaws described as *Callognathus.* Several species are recorded from the Ohio shales but in the absence of all other structures but infero-gnathals, they cannot be affiliated with any particular division of the Arthrodira.

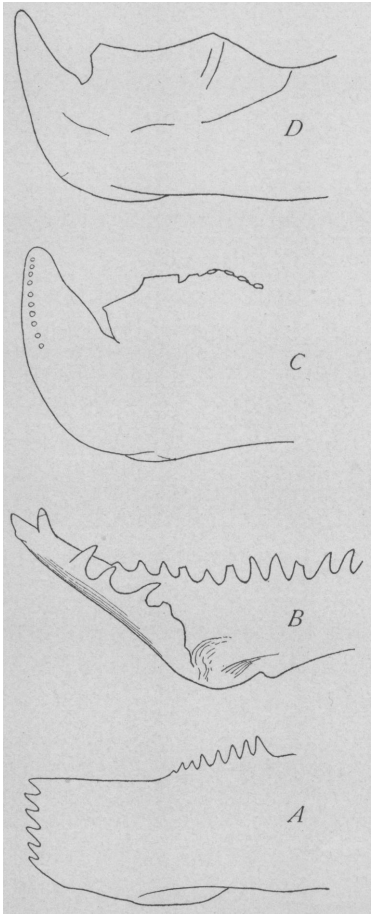


Fig. 25. Anterior portions of four infero-gnathals, inner view, to show the region of the symphysis. In *A*, *B*, and *C* note symphyseal denticles. *A*, *Coccosteus decipiens* Ag. *B*, *Diplognathus mirabilis* Newb. *C*, *Dinichthys herzeri* Newb. *D*, *Dinichthys terrelli* Newb. (No symphyseal denticles.)

This completes our brief survey of the phylogeny of the Upper Devonic Arthrodira of Ohio. While these forms were undergoing changes, other members of this group, in other localities, were also being transformed, *e.g.*, in Europe; but unfortunately too little is known about the forms in the latter region. Moreover, the European forms as now known do not appear ever to have equaled, in size and in diversity of specialization, those in Ohio.

Towards the close of the Devonic, communication seems to have been once more established between the eastern portion of the American sea, *i.e.*, the New York–Pennsylvania region, and the European sea, and hence the fauna of these regions again mingled. The evidence for this mingling of faunas was brought forward first by Max

Lohest (1888). He enumerated the following species as common to eastern North America and to western Europe:

Dipterus flabelliformis. *Holophychius giganteus.*
" *nelsoni.* *Dinichthys tuberculatus.*

And among invertebrates, conspicuously, *Spirifer disjunctus.* Other species have since been added to this list and from localities which perhaps throw light upon the probable extension of this inter-continental sea. Dr. A. Smith Woodward has recorded *Holophychius giganteus* from the Upper Devonic of Spitzbergen and *Holoptychius nobilissimus* from east Greenland.

It must be noted here that while the coccosteid stem was giving rise to the species of *Dinichthys* and their allies, the genus *Coccosteus* still continued throughout the Devonic both in Europe and North America, for several species of *Coccosteus* are recorded from the Middle and Upper Devonic of Europe, and from the Upper Devonic of North America (*C. macromus* Cope, and *C. canadensis* Woodward).

I will conclude this section with some remarks on the probable cause for the total and simultaneous extinction of all the Arthrodira at the close of the Devonic. We can perhaps find a reason for it in the great increase in the number of species and individuals which is evidenced by the relative abundance of remains in such a restricted area as Ohio, and to the increased struggle for food. Added to this we must take into consideration the competition of the sharks which just then were usurping the supremacy of the seas. We notice, too, that among the sharks from this period on, there is a tendency to evolve crushing or grinding, in place of the piercing, teeth which had distinguished them during the Devonic period. This may mean the selection of forms with a crushing type of tooth and may indicate, indirectly, a decrease in the quantity of prey for predaceous forms. The sharks varied abundantly in this direction and soon monopolized the waters. The Arthrodira made several attempts, also, in the same direction, *e.g.*, *Dinomylostoma*, *Mylostoma*, but the arthrodiran plan of structure was apparently most effective in conjunction with predaceous habits and hence became entirely extinct.

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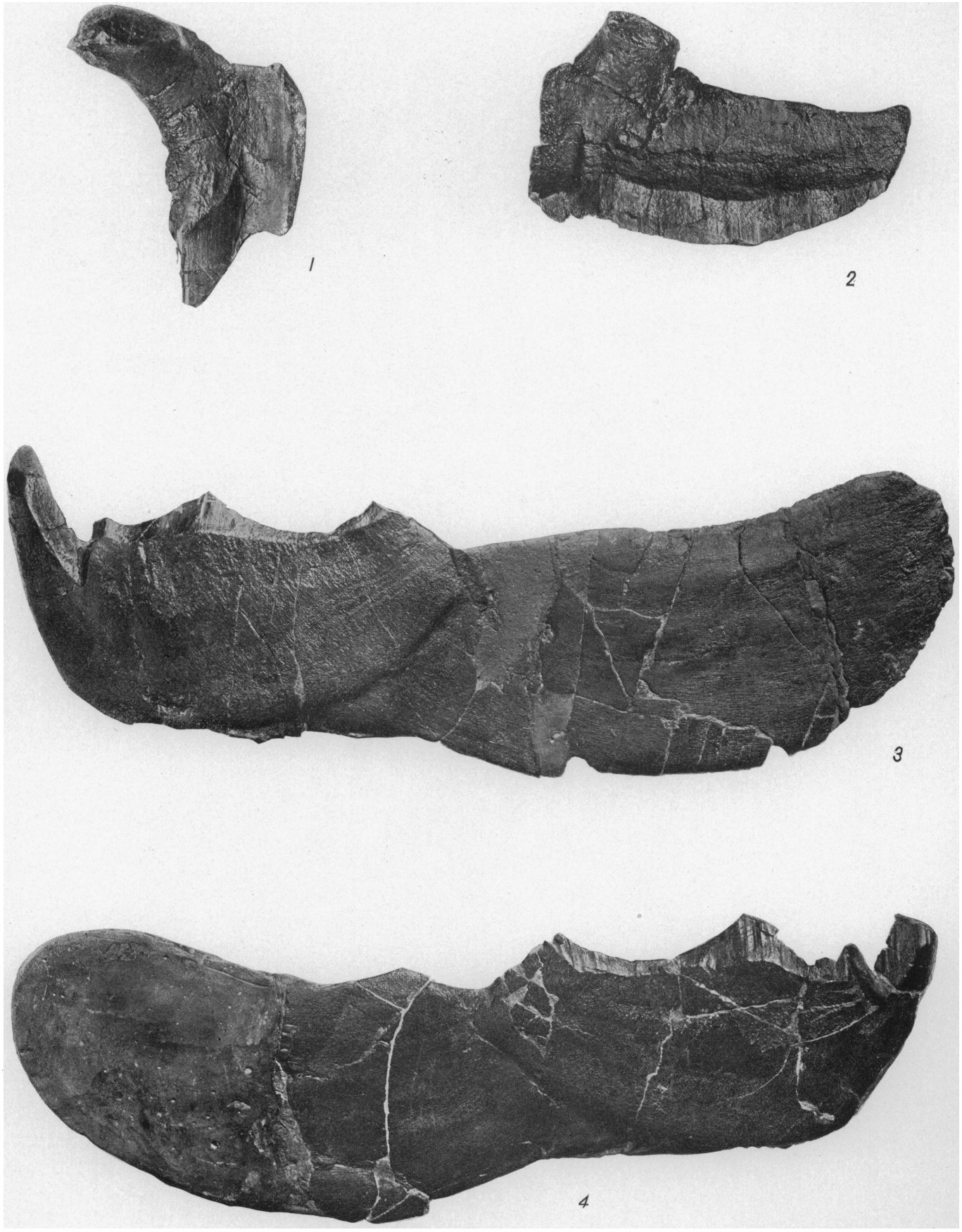
PLATE XII.

EXPLANATION OF PLATE XII.

Gnathal elements of *Dinichthys curtus* Newb. × ¾. Cleveland shale, Ohio. Photographs by Mr. A. E. Anderson.

FIG. 1.—Left antero-supero-gnathal, inner view. Cat. No. 7057.
FIG. 2.—Right postero-supero-gnathal, inner view. Cat. No. 7299.
FIG. 3.—Left infero-gnathal, outer view. Cat. No. 7055.
FIG. 4.—Right infero-gnathal, outer view. Cat. No. 7054.



Dinichthys curtus.

PLATE XIII.

EXPLANATION OF PLATE XIII.

Gnathal elements of *Dinichthys herzeri* Newb. and *D. intermedius* Newb. Photographs by Mr. A. E. Anderson.

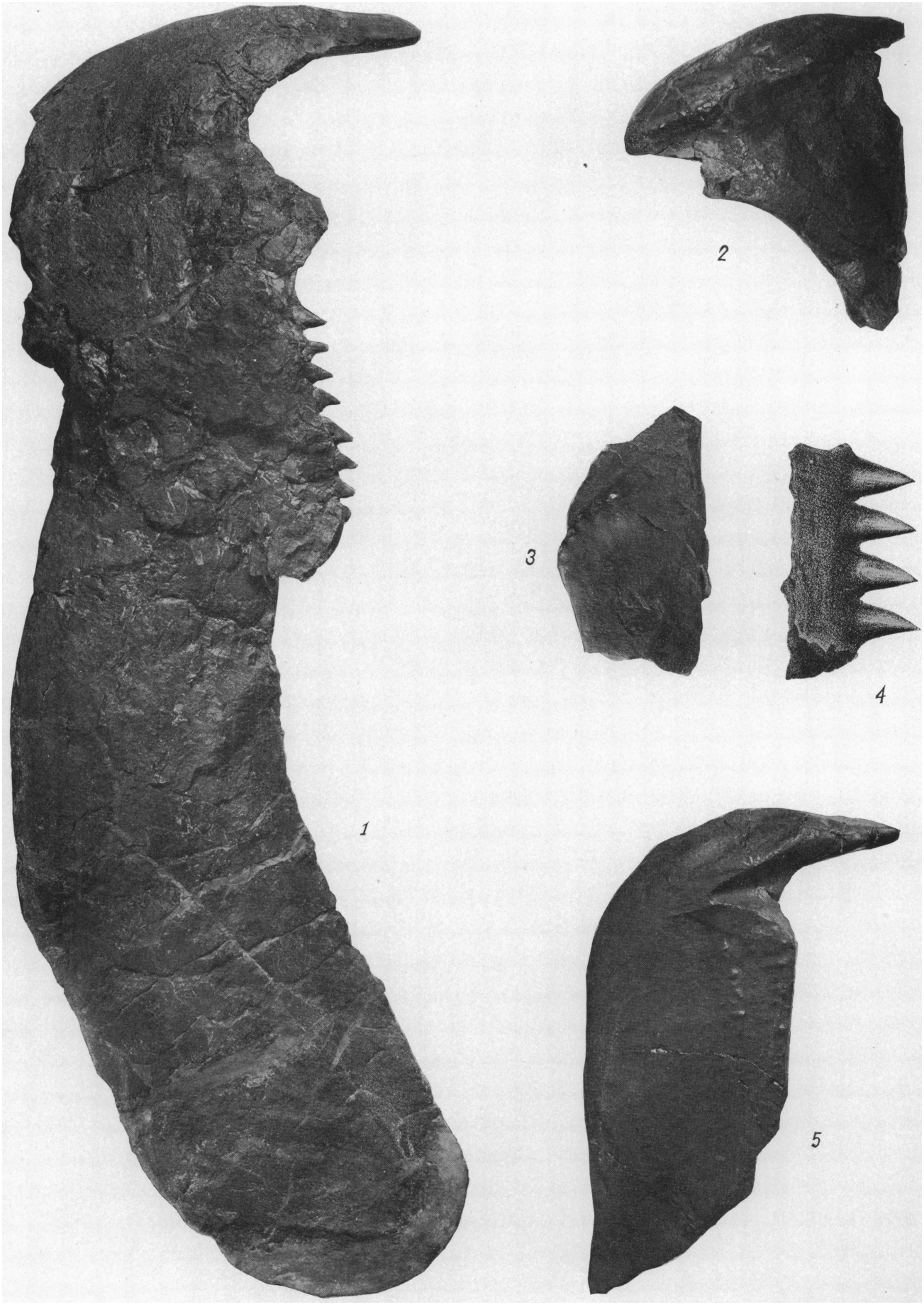
FIG. 1.—Left infero-gnathal of *Dinichthys herzeri* Newb., outer view. × ⅔. Huron shale, Ohio. (The "teeth" along the upper edge are restored.) Cat. No. 7300.

FIG. 2.—Left antero-supero-gnathal of *Dinichthys herzeri* Newb., outer view. × ⅔. Huron shale, Ohio. Note the ornamental denticles. Cat. No. 34.

FIG. 3.—Right postero-supero-gnathal of *Dinichthys herzeri* Newb. × ⅔. Huron shale, Ohio. Note two rows of "teeth." Cat. No. 33.

FIG. 4.—Four "teeth" from the cutting edge of an infero-gnathal, natural size. After Newberry.

FIG. 5.—Anterior end of left infero-gnathal of *D. intermedius* Newb. × ⅔. Note the ornamental denticles. Cat. No. 3539.



1–4, Dinichthys herzeri; 5, D. intermedius.

(*Continued from 4th page of cover.*)

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