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## FISHES FROM THE DEVONIAN OF ARIZONA

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### INTRODUCTION

During the past decade remains of Devonian fishes have been discovered at several localities in the state of Arizona, and some local geologists have collected groups of specimens. These consist mainly of single plates of small Arthrodira, fragmentary plates of larger forms and ptyctodont dental elements.

A small collection of such specimens was sent to me for study by Major L. F. Brady of the Museum of Northern Arizona and are described in this paper. They were collected by him from the Mt. Elden formation (Upper Devonian), near Flagstaff, Arizona. I am greatly indebted to Mr. Brady for the opportunity to describe these specimens, which are the first Devonian fishes to be made known from Arizona.

The materials in hand for study include: a number of small single plates representing a new species of *Coccosteus*; a few incomplete plates of *Dinichthys*; several dental elements of ptyctodonts, including an undescribed species of *Ptyctodus*; and one tooth of *Dipterus*. As appears from this list, this is a typical Devonian fish fauna.

The *Coccosteus* presents several morphologic features of interest, which are discussed in the pages following the specific description. I was able to reconstruct the ventral armor of this form from a few single plates, and several points regarding this armor are discussed.

None of the Arizona Devonian fishes has thus far been named or described. A few

small arthrodiran plates from the Mt. Elden formation were figured in a geological paper by A. A. Stoyanow (1936), but without generic or specific identification. These figures are referred to again later in the discussion of the *Coccosteus*.

Arizona is the third state in the western part of the United States in which Devonian fishes have been discovered in recent years. In 1931 Branson and Mehl described the first Devonian fishes discovered in Utah. In 1932 Bryant made known an extensive Lower Devonian fish fauna from Wyoming. The fishes of Arizona represent a different assemblage from those in these two states. They are especially different from the remarkable fauna of ostracoderms and primitive Arthrodira of the Lower Devonian of Wyoming.

They are also different from the fishes that have been recorded from Colorado, both those long known, as well as a small fish faunule from a new locality in central Colorado, described by Bryant and Johnson in 1936.

I have delayed publishing this paper for some time in the hope that additional material might become available to make it possible to elucidate the more fragmentary forms. But although a few additional specimens were found and sent to me by Mr. Brady after this paper was written, they have not added to knowledge of any of the forms.

All the specimens described in this paper are in the Museum of Northern Arizona.

### AGE OF THE FISHES

The Mt. Elden formation consists of a thick series of strata of limestone, sandstone, etc., exposed on the slopes of Mt. Elden, near Flagstaff, Arizona. A meas-

ured section of the formation, 148 feet in thickness, was described by Stoyanow (1936, p. 501). The age of the formation is stated to be Upper Devonian. This was

determined mainly on stratigraphic evidence, since invertebrate fossils are very scant.

The fishes described in the present paper indicate the age of the horizon from which they were collected to be *early* Upper Devonian. The evidence for this view is as follows.

The *Dinichthys* occurring in the Mt. Elden is a medium-sized species with plates ornamented with small tubercles, some of them showing faint stellate radiations at the base. Species of *Dinichthys* with such an ornamentation represent the earlier phase of *Dinichthys* evolution; they occur in Middle, and in early Upper, Devonian. The late Upper Devonian species of *Dinichthys* have smooth plates, without ornamental tubercles, e.g., *Dinichthys terrelli*, *D. intermedius*, *D. curtus*, of the Cleveland Shale of Ohio.

The Mt. Elden *Dinichthys*, judging by its size and ornamentation, is close to

*Dinichthys pustulosus* Eastman. This species occurs in the Middle Devonian of Iowa, Wisconsin, Illinois, and in the early Upper Devonian of Kentucky and western New York (Eastman, 1908; Hussakof and Bryant, 1918, p. 51).

Second, the ptyctodont dental elements in the Mt. Elden are forms having a very narrow tritor preceded by a trenchant edge. Species of *Ptyctodus* with this form of dental element are typical of the Middle, and the early Upper, Devonian. Species comparable with the Mt. Elden form are represented by numerous specimens in the Conodont Bed, a layer near the base of the Upper Devonian in the Buffalo, New York, area. Numerous specimens from this locality are figured by Hussakof and Bryant (1918).

On the evidence of the *Dinichthys* and the ptyctodonts, therefore, the age of the fish-bearing strata of the Mt. Elden appears to be early Upper Devonian.

#### MODE OF PRESERVATION OF THE FISHES

All the Mt. Elden specimens I have examined are isolated single plates. In no instance were two plates found sutured together in natural association. The plates are embedded in a very hard, fine-grained, impure sandstone, from which it is almost impossible for a collector in the field to extricate a specimen without some breakage or flaking.

The nature of the matrix indicates that the fishes lived in a comparatively deep sea in which fine sediment accumulated at a

very slow rate. Dead fishes, lying on the sea bottom, completely disintegrated and their plates drifted apart and became buried in sediment singly.

But the fossils underwent remarkably little subsequent deformation or flattening. The arching of the *Coccoosteus* dorsomedian plate and the surface curvature of the ventral plates are preserved in an unusual degree. These plates appear to retain about the degree of convexity they must have had in life.

#### DESCRIPTION OF THE SPECIES

##### ARTHRODIRA

##### *Coccoosteus arizonensis*, new species

Figures 1-11

Among the specimens are several single plates of *Coccoosteus*, evidently all belonging to one species. They are of corresponding size and have a similar ornamentation. Four different plates, each the best-preserved one of its kind, were selected as the types of the species.

SYNTYPES.—(1) A dorsomedian plate in matrix, shown in outer view (Fig. 1). Mus. N. Ariz. G. 531.

(2) A median ventral plate, represented by

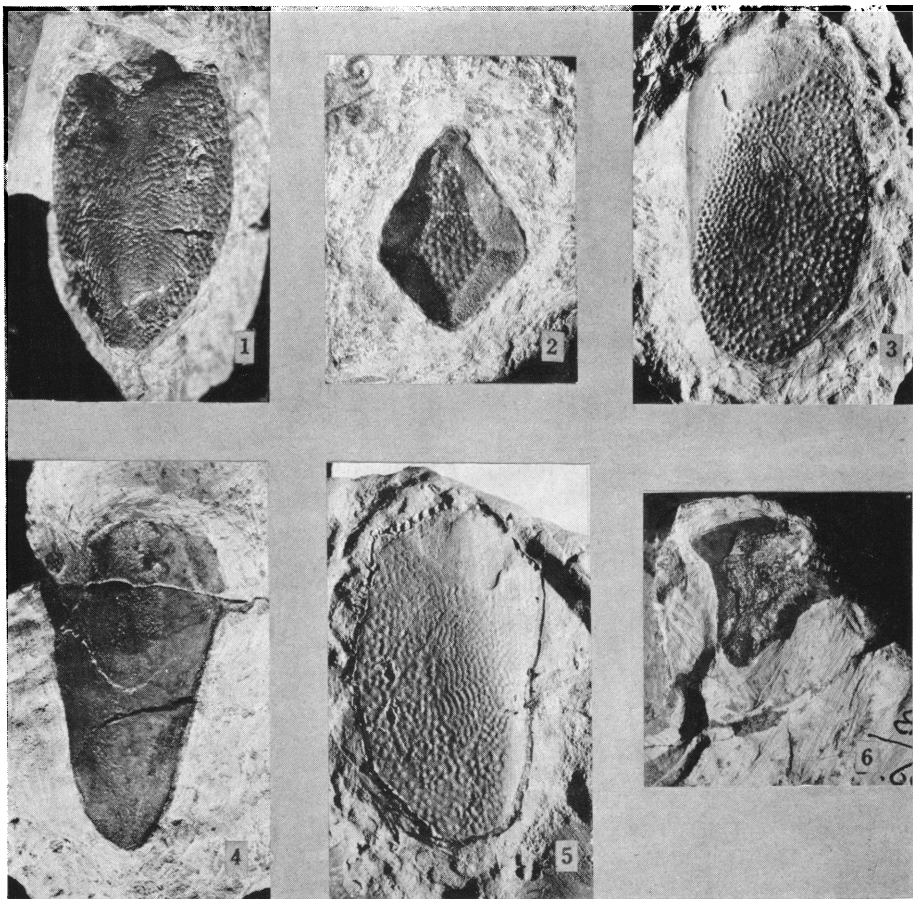
an impression of its outer face (Fig. 2). Mus. N. Ariz. G. 663.

(3) A left anterior ventrolateral, shown as an impression of its outer face (Figs. 3, 5). Mus. N. Ariz. 3155.

(4) A right posterior ventrolateral, represented by an impression of the inner face (Fig. 4). Mus. N. Ariz. G. 667.

OCCURRENCE.—Mt. Elden formation (early Upper Devonian); near Flagstaff, Arizona.

DESCRIPTION.—A small species, about two-thirds the size of *Coccoosteus decipiens*. Ornamentation consisting of small, low tubercles, some showing a few short radiations at their bases; the



Figs. 1-5. *Coccosteus arizonensis*, new species. Syntypes,  $\times$  about  $1\frac{1}{4}$ . 1.—Dorsomedian, in outer view. The sensory canal does not show in this photograph. Mus. N. Ariz. G. 531. 2.—Median ventral plate, impression of outer face. Mus. N. Ariz. G. 663. 3.—Left anterior ventrolateral, impression of inner face. Mus. N. Ariz. G. 667. 4.—Right posterior ventrolateral, impression of inner face. Mus. N. Ariz. G. 667. 5.—Wax squeeze of the anterior ventrolateral shown in Fig. 3, showing detail of ornamentation and, near anterior end, imprint of the lateral plate.

Fig. 6.—Anterior median ventral, incomplete posteriorly, in inner view.  $\times$   $1\frac{1}{4}$ . Mus. N. Ariz. G. 662.

tubercles broader than high, and tending to a linear arrangement on some plates.

*Dorsomedian* of the usual coccosteoid form, well arched from side to side, rather broad in proportion to its length (as seen in a tracing made of the plate); posterior spine very short. A faintly incised lateral canal present on dorsal surface, as shown in Fig. 8.

*Median ventral* rhombic in shape, its anterior angle more elongate than the posterior one; the overlap flanges broad and well developed on all four sides. Ornamentation of central area consisting of small, rounded, discrete tubercles.

*Anterior ventrolateral* about twice as long as

wide, its posterior margin rounded; the outer surface densely ornamented with minute tubercles which coalesce into linear series in some places. Anterior part of outer margin of plate turned gently upward into a low flange which tapers backward, disappearing before reaching posterior margin of plate.

*Posterior ventrolateral* subtriangular in shape, its posterior angle rounded. Medial margin almost a straight line, without overlap flanges, the pair of plates being sutured medianly in almost a straight line. A fair-sized process at anterior outer angle of plate; this process and the margin posterior to it curved upward on the side.

## MEASUREMENTS OF THE SYNTYPES

**DORSOMEDIAN.**—Length, with the tip of spine missing, 32 mm.; with spine restored, 35. Width at middle, measured over the curved surface, 28.

**MEDIAN VENTRAL.**—Length, 19 mm.; max. width, 14.

**ANTERIOR VENTROLATERAL.**—Length, 40 mm.; width at middle, 22.

**POSTERIOR VENTROLATERAL.**—Length, 35 mm.; width at middle, 17.

This species is distinguished by its small size, by the distinctive shape of the dorsomedian and the ventral plates, and in having the posterior ventrals united in an almost straight line, apparently without overlap flanges.

It should be noted that the strong arching of the dorsomedian makes this plate appear narrower in a photograph (such as Fig. 1) than it actually is. Its true shape appears only in a tracing, as in Fig. 8.

Beside the types, two other specimens

in the collection are worth noting. One is an anterior ventromedian, lacking the slender, posterior portion, shown in Fig. 6. It has the characteristic shape of this element in *Coccosteus*. Another is a small spinelike element, evidently an inter-lateral.

A few small arthrodire plates from the Mt. Elden formation were figured in a geological paper by Stoyanow (1936, Pl.) without generic or specific names. These specimens belong to *Coccosteus arizonensis*. They were referred to in this paper as "primitive Arthrodira," a term which is not properly applicable, since the form is not an acanthaspid or a phlycteaenaspid. The specimens shown in Figs. 2 and 5 of Stoyanow's paper are incorrectly identified in his explanation of the figures as posterior ventrolaterals; both are anterior ventrolaterals.

MORPHOLOGIC NOTES ON *COCCOSTEUS ARIZONENSIS*

Several morphologic features of interest displayed by the specimens may be briefly noted.

**DORSOMEDIAN.**—The type dorsomedian plate was in two pieces when received by me. It had broken across when collected, posterior to the middle of the length, presenting smooth, clean breakage planes, as if it had been sectioned for study. This made it possible to examine the cross section of this plate.

The cross section, in a vertical plane at about the posterior third of the length of the plate is shown in Fig. 8a. The arching of the plate is well shown in the section; this cannot be far from the amount of arching in life. The bone of the plate is seen to thin out gradually from the median line toward each lateral margin.

The section of the dorsomedian keel, or ridge, is clearly shown in the section of the plate (Fig. 8a, k). It is evident from this that the longitudinal keel was low and with a sharp edge.

Heintz, in a paper on the structure of *Coccosteus* (1931, p. 303, Fig. 8), indicated a suture between the dorsomedian keel and the plate itself, as if the keel of the dorso-

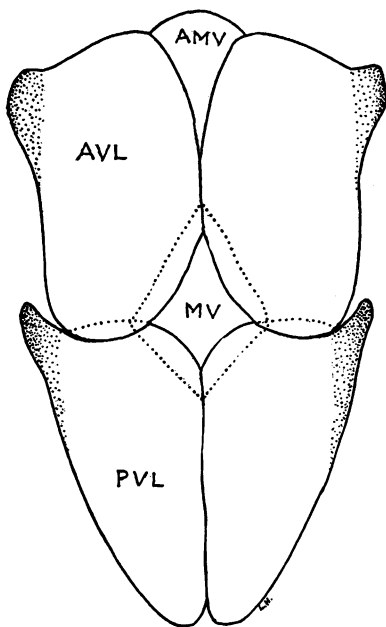
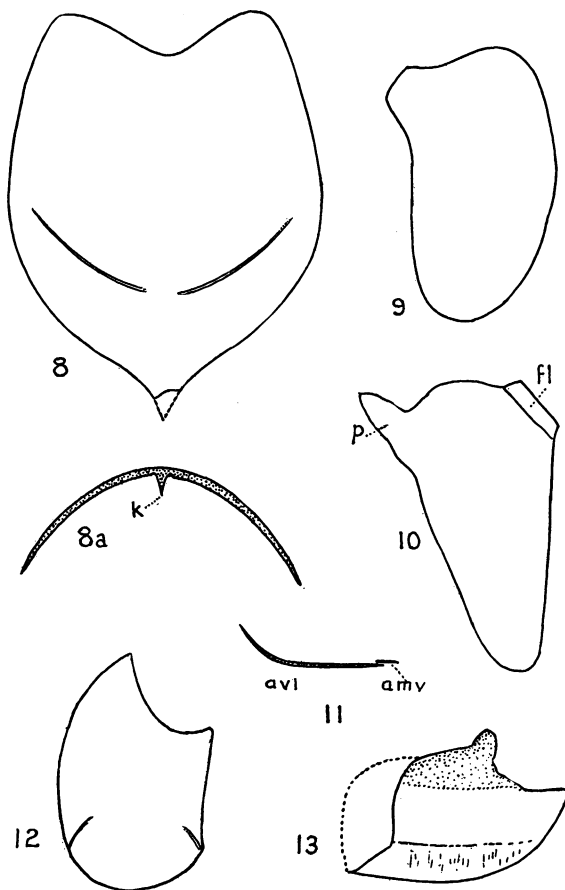


Fig. 7. *Coccosteus arizonensis*, new species. Reconstruction of ventral plates;  $\times$  about  $1\frac{1}{4}$ . AMV, Anterior median ventral; MV, median ventral; AVL, anterior ventrolateral; PVL, posterior ventrolateral.



Figs. 8-11. *Coccosteus arizonensis*, new species. 8.—Dorsomedian, from a tracing, showing the lateral canal.  $\times 1\frac{1}{2}$ . 8a.—Cross-section of dorsomedian at about its posterior third; *k*, median keel. 9.—Outline of anterior ventrolateral, restored from all available specimens.  $\times 1$ . 10.—Outline of posterior ventrolateral; *fl*, flange for overlap of corresponding flange on median ventral; *p*, anterior process. 11.—Diagrammatic cross section of left anterior ventrolateral in region of its anterior half, to show upbending of the outer margin of this plate; *avl*, anterior ventrolateral; *amv*, anterior median ventral.

Fig. 12.—Small detached arthrodire element of an unknown form. Nat. size. Mus. N. Ariz. G. 654.

Fig. 13.—*Dinichthys* species. Juvenile. Right posterior upper tooth (posterior superognathal), incomplete anteriorly; shown in inner view. Nat. size. Mus. N. Ariz. G. 665.

median plate were a separate bone sutured on. This may have been merely an error in Heintz's drawing, for it seems obvious that the keel is a part of the dorsomedian plate itself, not a separate element. This can be seen readily in *Dinichthys*, where the large size makes examination easy; or in phlyctaenaspids, where the keel appears as a mere sharpened ridge along the median line of the dorsomedian plate.

A second specimen of the dorsomedian of *C. arizonensis* is among the materials in

hand. It is incomplete, with most of the bone flaked off. It is noted here merely because it shows a similar degree of convexity to the type dorsomedian, thus strengthening the evidence that this was near the natural arching of the plate.

The type dorsomedian shows a faint lateral canal, situated on the hinder portion of the plate, as shown in Fig. 8. The canal is very faintly incised and might easily be overlooked; it can be seen only when the specimen is held at an angle to

the light. The canal is in two halves, separated from each other by a short hiatus on the middle of the plate.

A similar interruption in the DM canal is sometimes found in species of *Coccosteus* which normally have a continuous canal. I have a tracing of such a specimen of *C. decipiens* which I examined years ago in the British Museum. In this specimen (Brit. Mus. P. 695a) the canal consists of two segments separated on the middle of the plate by a space of about a quarter of an inch.

It does not seem to have been noted previously by any writer on Arthrodira that the dorsomedian canal may sometimes be entirely lacking in *Coccosteus*, as an individual variation. I found it lacking in one (or perhaps two) specimens in the British Museum collection, of which I have notes. In the *Antiarcha*, also, a part of the dorsal canal system is sometimes lacking, as an individual variation. An instance of this in *Bothriolepis canadensis* was recently discussed by Robertson (1938). He showed that the supposed new species *Bothriolepis stensiöi* Sohn, based on a head shield, was merely a specimen of *B. canadensis* in which the V portion of the sensory canal, posterior to the eye region, was lacking.

**VENTRAL ARMOR.**—A reconstruction of the ventral armor of *C. arizonensis* is shown in Fig. 7. This reconstruction was made possible by the fortunate presence in the collection of a median ventral plate showing the overlap flanges clearly (Fig. 2), and specimens of the other ventral plates. The type postero-ventrolateral has a flange (Fig. 10, *fl*) which in size and contour almost exactly fitted the corresponding flange on the median ventral. The posterior margin of the anterior ventral also fitted well against the corresponding concave line of the median ventral. By using tracings of these elements and making a slight allowance for difference in size, the reconstruction shown in Fig. 7 was drawn.

A special feature of the ventral armor in *C. arizonensis* is the union of the pair of posterior ventrals medianly in almost a straight line, not by overlap flanges as is usual in *Coccosteus*. This recalls the con-

dition in the primitive Arthrodira of the Lower Devonian, e.g., acanthaspids and phlyctaenaspids. It may therefore be regarded as a primitive character retained in this species.

Ventral plates of *Coccosteus* are generally found almost flattened out. In *C. arizonensis*, however, due to favorable preservation, some of the original curvature is retained. The anterior ventrolateral shows the following condition. The anterior part of the outer margin of the plate is curved gently upward, as shown in the cross section in Fig. 11. The upturned flange is highest anteriorly, diminishing backward. The portion of the plate that was upturned is indicated by the stippled area of the *avl* plate in the reconstruction in Fig. 7.

This upcurving of the anterior ventrolateral is shown in the type specimen of this plate and in a second, slightly smaller specimen in the collection.

A somewhat similar upcurving exists also in the posterior ventrolateral. The front portion of the outer margin of this plate and the adjacent thin anterior process were turned up on the side of the animal. The area of this plate that was upturned is shown by the stippled part of the *pvl* in Fig. 7. A similar upturning of the posterior ventrolateral has been noted in *Coccosteus decipiens* by Heintz (1931, p. 306, Fig. 10) but in a lesser degree.

In the light of the Arizona species, a reëxamination of well-preserved specimens of anterior ventral plates in *Coccosteus decipiens* would probably show that in this species also these elements were upturned a little on the side.

The demonstration that the ventral armor of *Coccosteus* was bent up in low flanges along the sides is a point of much theoretic interest. The writer as well as others has long maintained that the Arthrodira and the *Antiarcha* are related. To the other structural resemblances between these two groups may now be added the upturning of the ventrolateral plates on the sides.

A series might be arranged showing progressive stages in the reduction of the upturned side portion of the lateroventral

plates, starting with the maximum amount of upbending in the *Antiarcha* (e.g., *Bothriolepis*). The next stage would be a primitive arthrodire, such as a phlyctaenaspid; in this the height of the upturned part of the ventrals is less. The next stage is *Coccosteus*, in which the upturning is still

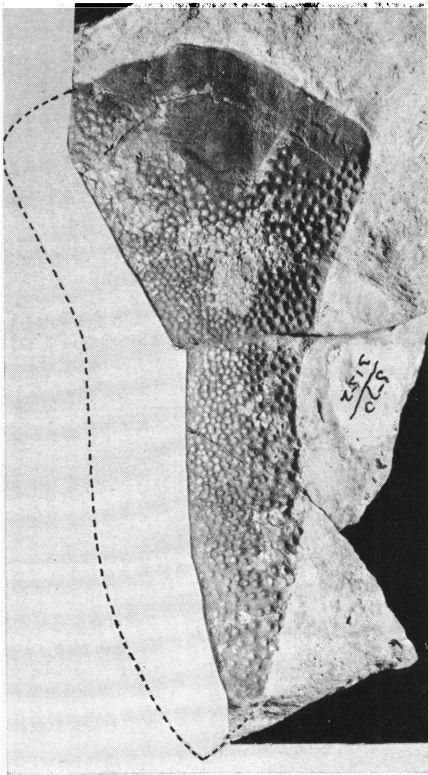


Fig. 14. *Dinichthys* species. Incomplete anterior median ventral plate; impression of outer, ornamented face.  $\times \frac{3}{4}$ .

less (as shown in *C. arizonensis* and to a less degree in *C. decipiens*). Finally, in late Devonian Arthrodira, as, for example, in *Dinichthys* of the Cleveland Shale of Ohio, the upturned flanges on the sides have entirely disappeared.

#### *Dinichthys* species

Among the specimens in the collection are two plates and some fragments of a

medium-sized *Dinichthys*. They are ornamented with small tubercles, some showing stellate radiations at the base. These specimens prove the presence of *Dinichthys* in the Mt. Elden formation along with *Coccosteus*; but the material in hand is insufficient for complete comparison of this species with others. In size and ornamentation the species is close to *Dinichthys pustulosus* Eastman.

One of the plates is an incomplete anterior median ventral (Mus. N. Ariz. 3152), shown in Fig. 14. The specimen is an impression in matrix of the outer, ornamented face, except at the anterior end where some of the thin bone of this part of the plate is present. The plate is 11 cm. long and is estimated to have been about 4 cm. in width at the middle when complete.

The specimen resembles a median ventral plate of *Dinichthys pustulosus* Eastman, figured by Hussakof and Bryant (1918, Pl. XII, fig. 2). It is a little larger, and its entire outer surface is densely covered with tubercles, whereas in the figured *pustulosus* specimen the tubercles are present mainly on the central part of the plate and are more widely spaced. Further material is necessary to determine whether this species is distinct from *D. pustulosus*.

There is also among the specimens a posterior dorsolateral plate of *Dinichthys*, probably of the same species as the preceding plate, but from a small, immature individual. The specimen is an impression in matrix of the outer face. It is of the usual subtriangular form, with broad overlap flanges. The central area is ornamented with small tubercles similar to those of the median ventral plate. There is no lateral canal on the outer face.

#### *Dinichthys* species

One of the specimens from the Mt. Elden formation is a very small, incomplete posterior upper tooth (posterior superognathal) of the right side of the jaw (Mus. N. Ariz. G. 665). It lacks the anterior end (Fig. 13).

The specimen is an impression in matrix of the inner face of the element, with a

little of the bone of the cutting edge present. Its length, as preserved, is 23 mm.; when complete it was about 28; width, posterior to the process, 14 mm.

The specimen is probably juvenile, but it may perhaps indicate a second, very small species of *Dinichthys* to be present in this formation. Comparison of this specimen may be made with the small *Dinichthys* jaw elements figured by Hussakof and

I have compared it. A specimen of one of these small plates in association with some other element is needed to determine its relationship.

#### PTYCTODONTIDAE

A few ptyctodont dental elements and isolated tritors are among the specimens. Ptyctodonts are comparatively numerous in the Mt. Elden formation. Among the specimens are some representing a new species.

#### *Ptyctodus bradyi*, new species

Figures 15, 16

**HOLOTYPE.**—A small dental element in limestone (Fig. 15). Mus. N. Ariz. 2851.

**OCCURRENCE.**—Mt. Elden formation (early Upper Devonian); near Flagstaff, Arizona.

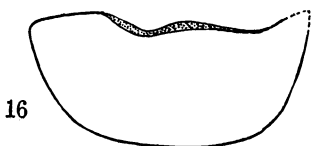
**DESCRIPTION.**—A small dental element, 20 mm. long by 9 mm. deep at its middle, with a low, gently upturned beak. The element is deep in proportion to its length, the depth being contained more than twice in the length. Posterior part of oral margin with a very narrow tritor, about 1 mm. wide, narrowing anteriorward into a trenchant edge in the region near the beak; a depression, or step, in the tritor at its posterior third, worn by tritor of opposing element. Tritoral surface with fine pittings visible under a magnifier, which tend to an arrangement in transverse oblique rows.

Posterior to the tritor, the upper margin of the element is continued backward in a short, straight line, sloping a little downward, which forms an acute angle with the upcurving lower margin of the element. Lower margin subparallel to tritoral margin, gently convex downward.

The species is named for Major L. F. Brady, geologist of the Museum of Northern Arizona, who collected these specimens.

This is a small species, distinguished by its comparatively deep form and the character of the tritoral margin. In shape this species is somewhat intermediate between *Ptyctodus* and *Palaeomylus*, but the character of the tritor leaves no doubt that it belongs to *Ptyctodus*.

The species resembles *Ptyctodus compressus* Eastman, which also has a narrow tritor preceded by a cutting edge. *P. bradyi* differs from this in its narrower tritor and in the greater depth of the entire element in proportion to its length. This difference may be clearly seen on comparison with a series of specimens of *P. com-*



Figs. 15, 16. *Ptyctodus bradyi*, new species. Holotype,  $\times$  about  $1\frac{1}{2}$ . Mus. N. Ariz. 2851. 16.—Outline of the same.

Bryant (1918, Pl. xvi) from the Conodont Bed (basal Upper Devonian) of western New York, but it does not agree with any of these forms.

#### AN ARTHRODIRAN PLATE

There is among the specimens from the Mt. Elden a very small arthrodiran plate of an unusual form which cannot at present be identified in its isolated condition. The specimen (Mus. N. Ariz. G. 654) is shown in outline in Fig. 12.

The surface of this small plate is gently convex and covered with extremely fine tubercles. Two short, curved, lateral canals are present on the plate, appearing like the end portions of one curving canal with a large interruption in the center, as shown in the figure.

This element does not agree in shape with any ventral or other plate of various acanthaspids and related forms with which



*pressus* figured by Hussakof and Bryant (1918, Pls. xxxvi, xxxvii) from the Conodont Bed (basal Upper Devonian), near Buffalo, New York.

The holotype, although small, shows signs of wear and is probably from an adult form. But the species attained a larger size as is shown by a detached tritor, which is larger than the one of the holotype, being about 2 mm. wide.

Another specimen of this species (Mus. N. Ariz. G. 674), lacking the beak, is not so deep as the type. This may be due to the loss of some of the very thin bone of the lower margin, but more probably this element belongs to the opposing jaw. The oral margin in this specimen has a somewhat different formation from that of the holotype; the outer and the inner margins of the tritor are each elevated into a trenchant edge, the inner one slightly higher than the outer. This formation of the tritor and the shallow form of the entire dental element indicate that this specimen is from the opposite jaw to that of the holotype.

Besides the preceding specimens, there is a very small element from a young individual. This is more triangular in outline than the adult form.

## DIPNEUSTA

### *Dipterus* species

A small dipterine tooth among the specimens gives definite evidence of the occurrence of dipnoan fishes in the Mt. Elden formation in association with the *Arthrodira*.

The tooth (Mus. N. Ariz. G. 673) is poorly preserved, being embedded in matrix which fills the valleys between the ridges so that some of the features are obscured.

The outline of the tooth is elongate triangular; it is about 10 mm. in length by 6 mm. in width at the narrower side. Seven or eight ridges can be distinguished, which decrease progressively in size. Each ridge is compressed into a sharp cutting edge along which are a few faint, irregular crenulations.

The species resembles *Dipterus nelsoni* Newberry, but owing to the small size and obscurity of the specimen, specific identification cannot be positive. A well-preserved specimen may prove it to be a distinct species.

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