

Fossil Fishes (Arthrodira and Acanthodida) from the Upper Devonian Chadakoin Formation of Erie County, Pennsylvania¹

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ABSTRACT. Several fossil fish were discovered in 1994 in the Upper Devonian Chadakoin Formation, near Howard Falls, just outside of Edinboro, Erie County, Pennsylvania. These fossils are fragmentary in nature and have been described based on their morphology. They are identified as the median dorsal plate of the large arthrodire *Dunkleosteus terrelli* Newberry, 1873, and the spines of probable acanthodian fishes. The identification of the median dorsal plate of *Dunkleosteus* represents a new occurrence of the genus. In general, these discoveries are of scientific interest because very little is known about the composition of the fish fauna that inhabited the Devonian shallow seas of northwestern Pennsylvania.

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INTRODUCTION

This study was an outgrowth of geologic field mapping being conducted in the Howard Falls area near Edinboro, Pennsylvania. In August 1994, the first of several vertebrate fossil specimens were discovered. The first specimen was excavated, reconstructed, and identified by specialists from the Pennsylvania State Museum, Harrisburg. Since that time, four more vertebrate specimens have been collected. These specimens were excavated, reconstructed, and positive identification was attempted by the author. These include: 1) a bony, medium-sized element (30 cm in width, 15 cm in length); and 2) three specimens of bony spines (two of which are considered within). One of the latter is a slab containing approximately a dozen spines or other small, indeterminate bony elements.

The fossil fishes which are the subject of this study were collected from the Chadakoin Formation. The environment of deposition of the Chadakoin Formation is interpreted as shallow marine, subtidal but above storm wave base, on the basis of sedimentary grain size, sedimentary structures, and both body and trace fossils (Jeffrey Gryta and Dale Tshudy, 1995, personal communication). The marine invertebrate fauna of western Pennsylvania includes bivalves, gastropods, crustaceans, sponges, and, most commonly, brachiopods. The invertebrates are the subject of numerous studies which began well over a century ago. In contrast, the vertebrates, including the fish fauna, are poorly known. The lack of published reports on fishes is curious considering the diverse fish fauna known from Devonian rocks of New York and Ohio. The Ohio strata were deposited in deeper waters, where the bottom waters were little affected by waves and currents and, as a result, were oxygen deficient and inhospitable to scavengers (Hoover 1960). This lack of agitation of the bottom, coupled with the absence of scavengers, made conditions on the Ohio sea bottom especially favorable for the preservation of fossil material. By contrast, the Upper Devonian strata of

Pennsylvania were deposited in a shallow water environment. The shallower bottom sediments were oxygenated by waves and currents, and supported a variety of scavengers.

Nonetheless, reduced preservation potential alone does not explain why fossil fishes are poorly known from Pennsylvania. The Devonian rocks of southern New York were deposited in shallow waters also, but have yielded a diverse fish fauna (Eastman 1907). Therefore, it seems most reasonable to conclude that the Devonian rocks of western Pennsylvania contain a diverse fish fauna that simply has yet to be recognized. The descriptions of the fossils herein contribute to our knowledge of Pennsylvania fish fauna and provide information about a poorly known fauna.

MATERIALS AND METHODS

Vertebrate fossils were collected from bedrock exposed by stream erosion in southern Erie County, Pennsylvania. Specimens include a single bony plate, multiple spines in varying degrees of completeness, and molds of the exteriors of spines. The large bony plate fragmented into many pieces during excavation and was reconstructed in the laboratory. Latex casts were produced from spine molds. A thin section was prepared from a cross section through the carinal process of the bony plate. The prepared specimens and thin section form the material basis for the descriptive and taxonomic work. A positive identification of the bony plate was made possible when the author examined comparable fossil material at the Cleveland Museum of Natural History. The museum had no acanthodian spines that were a confident match with any of the spines described herein.

Dunkleosteus

MATERIAL The single specimen consists of one incomplete median dorsal plate. Edinboro University of Pennsylvania, catalog number 5052.

OCCURRENCE Upper Devonian Chadakoin Formation (mid-Famennian, Woodrow and Sevon 1985) of Erie County, Pennsylvania. The specimen was found in the stream channel known as Howard Run. The channel lithology consists of interbedded shale and siltstone.

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The area where the specimen was found is siltstone.

DESCRIPTION Plate subtriangular, transversely elongate, bilaterally symmetrical about axial keel on ventral surface (Fig. 1). Maximum dimensions (slightly incomplete): 30 cm transversely, 15 cm longitudinally (along axis). Plate overall is strongly, smoothly convex-up. Plate thickest (approx. 3.5 cm) over medial axis; overall, plate thins antero-laterally to only a few millimeters at the edges.

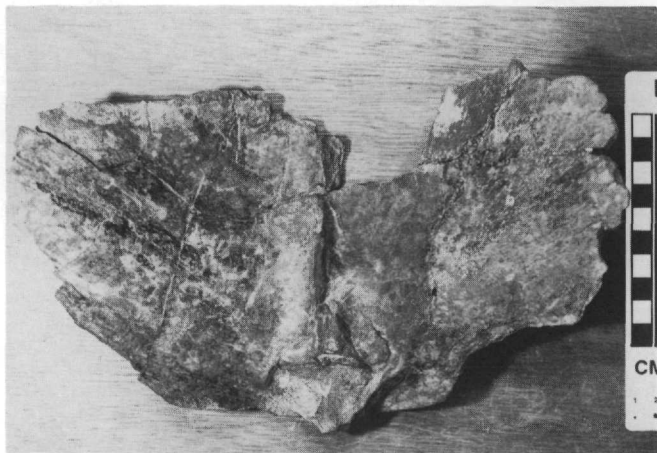


FIGURE 1. *Dunkleosteus terrelli*. Median dorsal plate in ventral view (specimen catalog # 5052). The posterior end of the plate is at the bottom of the photo. The carinal process is shown at the base of the plate along the center axis.

Dorsal surface is unornamented (Fig. 2). Ventral surface with very prominent, sharp, axial keel. Keel triangular in cross section; thickens posteriorly. The keel extends posteriorly from plate as robust carinal process. Base of process subovate in cross section; maximum dimension 3.0 cm (transverse) by 5.0 cm (dorsoventral). Extending antero-laterally from the posterior end of the axial keel are broadly rounded, elevated regions. Maximum thickness of plate over this region is 1.5 cm. Ventral surface finely striated, especially away from axis.



FIGURE 2. *Dunkleosteus terrelli*. Median dorsal plate in dorsal view (specimen catalog # 5052). Note the featureless surface.

Acanthodians

Specimen One

MATERIAL The specimen consists of one slab of siltstone containing the exterior molds of numerous spines (Fig. 3). The spines are distributed over a surface measuring approximately 20 cm by 15 cm. Edinboro University of Pennsylvania, catalog number 5050.

OCCURRENCE Upper Devonian Chadakoin Formation (mid-Famennian, Woodrow and Sevon 1985) of Erie County, Pennsylvania. The specimen was found in the stream channel known as Howard Run. The channel lithology consists of interbedded shale and siltstone. The area where the specimen was found is siltstone.

DESCRIPTION The siltstone contains approximately 20 spine molds of various sizes. Most of the imprints have a darker color than the host rock (Fig. 3). The spines are exposed in one bedding plane, and most are arranged with their long axes near parallel. It appears that the molds are oriented at a slight angle with respect to the bedding plane, resulting in an incomplete preservation of the spines' length. The molds are elongate. Cross-sectional shape is also uncertain due to the shallowness of the impressions. Molds range from 3.0 to 5.0 cm in length and from 0.3 to 0.5 cm in width. In several cases, it is uncertain whether two or more spines are preserved overlapping, or that a multi-element spine is preserved. Some molds are straight; others are slightly curved. Most spines are straight and taper symmetrically to a point. Others taper asymmetrically to a point, with the presumed anterior margin more curved than the posterior one. No surface ornamentation is evident in the spine molds.



FIGURE 3. Acanthodida *incertae sedis*. Close-up of specimen one showing the exterior molds of the spines (specimen catalog # 5050). Note the much darker imprints (carbon impression) as compared to the host rock. (Scale in cm)

Specimen Two

MATERIAL A single bony spine, 2.0 cm in length (incomplete proximally), 0.43 mm in width at broken, proximal termination. Spine preserved as a bony element over distal 1.5 cm and as exterior mold over the remainder. Edinboro University of Pennsylvania, catalog number 5051.

OCCURRENCE Upper Devonian Chadakoin Formation (mid-Famennian, Woodrow and Sevon 1985) of Erie County, Pennsylvania. The specimen was found in the stream channel known as Howard Run. The channel lithology consists of interbedded shale and siltstone. The area where the specimen was found is siltstone.

DESCRIPTION The spine is triangular in cross section. The spine is black, appears laterally flattened, and thins gradually distally. The point tapers asymmetrically with the presumed anterior margin more strongly curved than the posterior one (Fig. 4).



FIGURE 4. *Acanthodida incertae sedis*. Specimen two; the tip of a bony spine shown next to the imprint from which it was removed to better examine it (specimen catalog # 5051).

RESULTS

Dunkleosteus

SYSTEMATIC PALEONTOLOGY

Superclass Pisces

Class Placodermi M'Coy, 1848

Order Arthrodira Woodward, 1898

Suborder Pachyosteina Stensiö, 1944

Superfamily Dinichthyoidea Denison, 1978

Family Dinichthyidae Newberry, 1885

Genus *Dunkleosteus*

Type species: *Dinichthys terrelli* Newberry, 1873

Dunkleosteus terrelli (Newberry), 1873

(Figs. 1, 2, 5)

The specimen is identified as a median dorsal plate of a large arthrodire placoderm. The plate is referred to *Dunkleosteus terrelli*, a species of arthrodire known worldwide from the Upper Devonian. Generic and species identification is based primarily on overall geometry, including the plate's strong convexity, and also the prominent axial keel and oblique thickenings on the ventral surface (Figs. 1, 2).

The plate was compared directly to median dorsal

plates from several arthrodire genera at the Cleveland Museum of Natural History. Of the Family Dinichthyidae (*sensu* Denison 1978), the specimen was compared to *Dunkleosteus* Lehman, 1956, *Gorgonichthys* Clappole, 1892, and *Hussakofia* Kossmann, 1910. *Gorgonichthys* has a much thinner median dorsal plate, a much smaller axial keel, and no oblique thickenings. The same plate on *Hussakofia* is also much thinner than that of *Dunkleosteus* and is marked externally by an irregular wrinkling (Denison 1978).

The specimen is very similar to the median dorsal plate of *Dunkleosteus terrelli* Newberry, 1873. The specimen is much smaller than the same plate on the larger reconstructed specimens at the Cleveland Museum. Adult individuals are thought to have been approximately 20 feet in length (Denison 1978). However, it is comparable in size to a smaller individual of *D. terrelli* examined at the museum.

It is interesting to note that, on the smaller individual, the boundaries of the plates comprising the head shield and shoulder girdle are distinct. By contrast, on larger individuals (such as the larger specimens at the Cleveland Museum), the plate boundaries are indistinct due to fusing and intergrowth. This fusing of plates is interpreted as an ontogenetic feature, one analogous to the ontogenetic fusing of the cranial elements in humans. The fact that the specimen is a single and nearly complete plate, with margins approximating the true plate boundaries, combined with its small size, strongly suggests that the individual died as a juvenile or young adult.

Acanthodians

The molds from specimens one and two have been tentatively identified as acanthodian fish spines. Acanthodian fish were abundant in Late Devonian seas, and their spines, which functioned for protection and as fin supports, are known world wide (Denison 1979).

The great and overlapping range of variation in spines within acanthodian taxa, from the ordinal through

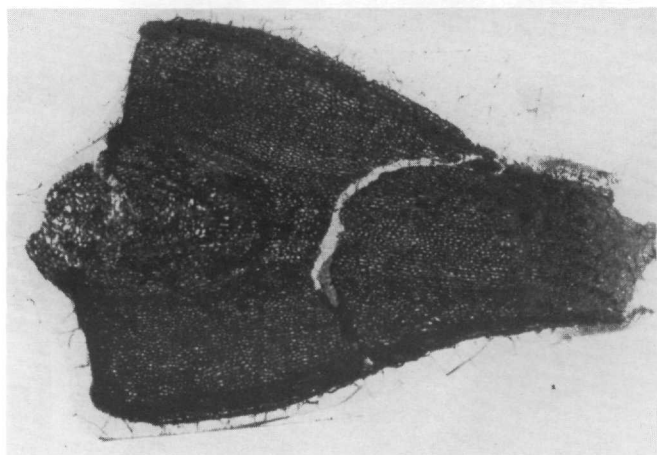


FIGURE 5. *Dunkleosteus terrelli*. A transverse thin section taken from the posterior base of the plate, at the origin of the carinal process (specimen catalog # 5053). The section has been rotated 90° in the counter-clockwise direction relative to the correct anatomical orientation. Maximum dimensions are 5.0 cm by 3.0 cm.

generic levels, coupled with the ambiguous nature of the specimens in question, precludes identification with any certainty at even the ordinal level. Based on the information available, the collected specimens are referred to *Acanthodida incertae sedis*.

DISCUSSION

Dunkleosteus

Dunkleosteus has been found in Upper Devonian (Upper Frasnian to upper Famennian) rocks worldwide (Denison 1979). The type species, *D. terrelli*, is reported from: 1) the Huron and Cleveland Shale members of the Ohio Shale, Ohio; 2) the Riceville Shale, northwestern Pennsylvania; 3) the Chattanooga Shale, Tennessee; 4) the Lost Burro Formation, California; and, "doubtfully," 5) the Ives Breccia, Texas (Denison 1979). Other species of *Dunkleosteus* are described from the Rhinestreet Shale and Genesee Group of New York (both Frasnian), and from Belgium (Famennian), the Holy Cross Mountains of Poland (Lower Famennian), and Tafilalet, south Morocco (Lower Famennian) (Denison 1979).

Arthrodire remains, including those of *Dunkleosteus*, are well known from the dark shales of Ohio, but have been less commonly reported from correlative, shallower facies of New York and Pennsylvania. Most of what is known is based on discoveries made around the turn of the century. Since that time, few discoveries of identifiable arthrodire remains in New York and Pennsylvania have been reported in the literature.

In 1907, Charles R. Eastman presented a monograph on the *Devonic Fishes of New York Formations*, in which he described the occurrence of a variety of primitive, long extinct fish from southern New York and northern Pennsylvania. Eastman's magnificent work described the occurrence in Pennsylvania of the arthrodire genera *Coccosteus*, *Holonema*, *Phyllolepis*, *Sphenophorus*, and a species of *Dinichthys* now considered (Denison 1979) to be *Dunkleosteus*. The latter, the first published report of *Dunkleosteus* from the state, was Newberry's account of *Dinichthys curtus* Newberry 1888 from the Chemung Formation of Pennsylvania (Eastman 1907). Eastman indicated that *D. curtus* (synonym to *D. terrelli*) is known from the Cleveland Shale, but that its occurrence in Pennsylvania is poorly documented.

Subsequent to Eastman's (1907) work, there were three published reports of arthrodires from Pennsylvania, and a few from New York. Two of the former are specimens from southwestern Pennsylvania and were referred to *Eastmanosteus* (Hlavin 1976, Kressel 1994). The third report is that of *Dunkleosteus* by Murphy (1979), who described an incomplete left anterodorsal (anterior dorsolateral) plate from the Riceville Shale near Meadville, Pennsylvania, approximately 32 km south of the new localities reported herein. The *Dunkleosteus* plate reported herein is only the fourth report of arthrodire fish from Pennsylvania since 1907, and only the third report of the arthrodire genus *Dunkleosteus* ever published from the state.

The genus is well known from the Ohio Shale of Ohio. The Ohio Shale is divided into three members.

From oldest to youngest, these include the Huron Shale, Chagrin Shale, and Cleveland Shale members (Hoover 1960). The Cleveland Shale Member is particularly well known for its *Dunkleosteus* specimens, but the older Huron Shale is also known to contain the genus (Denison 1978). In Pennsylvania, the Riceville Shale (Murphy 1979) is considered uppermost Famennian in age, while the Chadakoin Formation is considered mid-Famennian (Woodrow and Sevon 1985, Fig. 3). The Chadakoin Formation of Pennsylvania is the time equivalent of both the Chagrin and Huron Shale members of the Ohio Shale formation (American Association of Petroleum Geologists 1985) and, thus, the new discoveries require no extension of stratigraphic range.

All arthrodires had skeletons ossified to some degree, both internally and externally. The usual superficial tissue of dermal bones and teeth is not dentine, as in most fishes, but a tissue characteristic of Placodermi, semidentine (Denison 1978, Fig. 9C, H). The microstructure of *Dunkleosteus* bone is very similar to that of modern bone. The bone is cancellous, forming a spongiosa, in the middle layer of dermal bones such as the median dorsal plate (Denison 1978) (Fig. 5).

It is very likely that *Dunkleosteus* was at the top of the marine food chain during the Late Devonian Epoch. The worldwide distribution of this genus seems to indicate that *Dunkleosteus* was well adapted and successful on a large scale. It is possible that this genus lived and hunted in the open oceans and the shallow marine environments of the time. The interpretation of *Dunkleosteus* as a vigorous swimmer with powerful jaws (relative to other arthrodires) also supports this hypothesis (Denison 1978).

Acanthodians

The earliest known acanthodians are Silurian in age and are known only from marine sediments. Geologically younger acanthodians are known from both marine and fresh water sediments. They have also been found in marginal marine sediments formed on deltas, tidal flats, estuaries, and lagoons, consistent with the interpreted depositional environment of the Chadakoin Formation (Denison 1979).

The acanthodians are believed to have been an important part of the late Paleozoic food chain. They have been preserved in the guts and coprolites of the arthrodires, sharks, iniopterygian fish, and paleoniscoid fish (Denison 1979).

This paper provides information concerning the occurrence of Devonian-age fish in Pennsylvania strata. This is important due to the lack of such information in the literature. In addition, this paper contributes to the understanding of a poorly known fauna. Continued collecting in the future will serve to increase our knowledge of these fish, and our knowledge of how they may have interacted with their environment so long ago.

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