PY H673.15/2 No. 1 Randall, Kesler A. Dunkleosteus

## NATURAL HISTORY NOTES

of The State Museum of Pennsylvania

Number 1

February, 1996



The armored Devonian fish, Dunkleosteus. (Photo courtesy National Museum of Natural History, Smithsonian Institution, photo by Chip Clark, used by permission.)

by Kesler A. Randall, Robert M. Sullivan, and Spencer G. Lucas

Published by the Pennsylvania Historical and Museum Commission

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### **NATURAL HISTORY NOTES**

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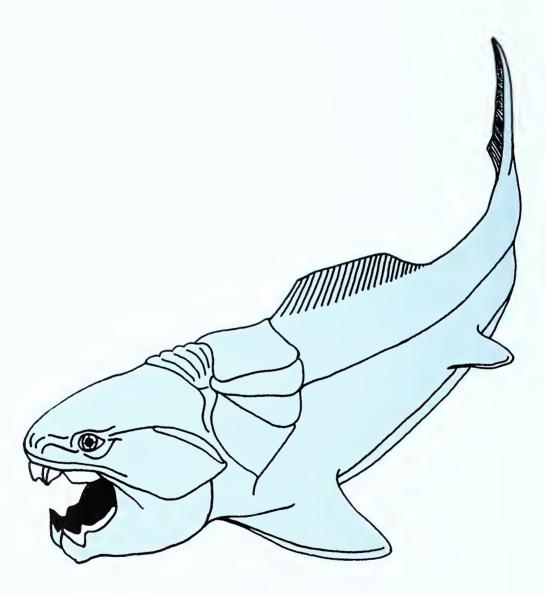


Figure 1. Reconstruction of the Devonian fish, Dunkleosteus.

# DUNKLEOSTEUS: DEVONIAN DENIZEN OF THE DEEP

by Kesler A. Randall, Robert M. Sullivan, and Spencer G. Lucas

 $m{F}$ ew, if any, fishes today would be considered truly monstrous. Only the whale shark (genus Rhincodon), the world's largest fish, which measures 12-18 m (40-60 ft.) in length (see Smithsonian Magazine, vol. 25, no. 11, pp. 94-99, February 1995), qualifies as a monster of the deep. However, the whale shark may be regarded as the giant "pussycat" of the seas because it dines only on small crustaceans and plankton as it leisurely patrols the ocean in an unthreatening way. It is interesting to note that most predaceous fishes are much smaller than the whale shark. These sharks, however, are the ones that invoke the most fear in people. But during the Devonian Period (408-362 million year ago), a time when shark evolution was in its infancy, there existed a denizen of the deep that was not only large, but unquestionably ferocious. Paleontologists call this primitive, jawed, and heavily armored fish, Dunkleosteus.

#### **DISCOVERIES**

Specimens of *Dunkleosteus*, which consisted solely of disarticulated head (cephalic) and trunk (thoracic) bony shields, were first discovered in the late 1800s in the Cleveland Shale of Ohio, and were called *Dinichthys* (Newberry 1889). Years later, in 1956, the name *Dunkleosteus* was given to some of the many species of *Dinichthys* by Jean-Pierre Lehman.

Lehman named it to honor the late David Dunkle, curator and paleoichthyologist at the National Museum of Natural History (Smithsonian Institution) in Washington, D.C. Numerous isolated occurrences of *Dunkleosteus* have been reported worldwide from such faraway places as Belgium, Morocco, Poland and Russia. In North America, specimens pertaining to *Dunkleosteus* have been discovered in California, Missouri, New York, Pennsylvania, Texas, Tennessee, and most notably, Ohio (Denison 1978).

Occurrences in Pennsylvania are very rare. Eastman (1907) noted that a specimen referred to the species *Dinichthys curtus* (now *Dunkleosteus*) had been reported by Newberry (1888) from the "Chemung" strata (Chadakoin Formation) of Warren County. This occurrence, however, was questionably documented (Eastman 1907) and the disposition of the specimen is unknown. Prior to the recent Erie County occurrence, only one documented specimen, consisting of an incomplete left anterior dorsolateral ("anterodorsal" of Murphy 1979) plate, had been discovered. This specimen (OSU-29724), from the Riceville (Shale) Formation (Late Devonian, late Famennian), near Meadville, Crawford County, Pennsylvania, is in the collection of Ohio State University's Orton Museum (Murphy 1979).

Two new Pennsylvania specimens of *Dunkleosteus*, each represented by a median dorsal plate, were discovered by Drs. Jeff Gryta and Dale Tsudy while mapping the geology of the Edinboro North quadrangle in 1994 for the Pennsylvania Geological Survey. The specimens were collected from the gray siltstones exposed in the creek beds of Porter and Falk runs, Erie County, Pennsylvania. Both specimens came from the Chadakoin Formation, which is Late Devonian (mid-Famennian) age (approximately 370 million years ago). The

first specimen came from the unnamed "lower coarser member" of the formation in Porter Run, and the second from the unnamed "upper coarser member" in Falk Run (Tsudy, personal communication, 1995). At this latter site, fin spines of acanthodians, primitive shark-like fishes, were also discovered. These new discoveries of *Dunkleosteus* in north-western Pennsylvania are not surprising. The rocks that contain this Devonian armored fish are lateral extensions of the same stratigraphic sequence that is well known for producing many of the fabulous specimens from the greater Cleveland, Ohio, area.

#### PLACODERMS - PALEOZOIC ARMORED FISHES

Placoderms are a group of primitive, heavily armored, jawed fishes that lived primarily during the Devonian Period. This group, formally called the Placodermi, consists of a number of subgroups that underwent an explosive evolutionary diversification during Devonian times. Paleontologists recognize seven placoderm groups: the antiarchs and arthrodires (which include *Dunkleosteus*) comprise 80 percent of the known placoderm species; the remaining 20 percent include acanthothoracids, petalichthyids, phyllolepids, ptyctodontids and stensioellids (Long 1993). All placoderm remains are known solely by fossilized bony plates, which in life formed an external, armored body covering. In some forms, like Dunkleosteus, this armature was restricted to the front of the animal, encasing the head and upper trunk region. In other forms, like the antiarch Pterichthyodes (which is known from the Middle Devonian of Europe), the entire head and torso (including the pectoral appendages) were heavily armored and the tail was covered by large bony scales.

The origin of the bony plates in placoderms is uncertain. Some paleontologists believe that these bony fishes arose from an unarmored ancestor, or from a precursor that had small bony denticles (tooth-like scales) embedded in the skin. Other paleontologists believe that placoderms evolved from a heavily armored ancestor and that the reduction of bony plates, exemplified in many placoderms from the Late Devonian, occurred independently (Carroll 1988).

#### ARTHRODIRES

The arthrodires were an extremely diverse group of placoderms. In general, they are characterized by a complement of bony plates that cover only the head and upper trunk regions (Moy-Thomas and Miles 1971). The nature of the posterior covering of these fishes is not known, but may have consisted of a dermal covering composed of discrete, unconnected, bony ossicles (tesserae) or may have been completely devoid of any bony material. Primitive arthrodires retained an extensive covering of bony plates. Their jaws were relatively short, which resulted in a small jaw gape that restricted the size of their prey. Advanced arthrodires, which consisted mostly of larger forms, had less armature and a wider jaw gape, allowing for the capture and ingestion of larger fishes. The reason for the lack of armor covering the rear portions of these fishes is evident. Armor plates would severely restrict locomotion, thus the absence of armor enabled predatory (advanced) arthrodires to move swiftly and capture their prey. Furthermore, advanced arthrodires had no need for a posterior protective covering because they were atop the Devonian food chain. Their smaller, more primitive, counterparts needed a more complete armature to protect them from predators.

#### **DUNKLEOSTEUS**

Dunkleosteus was the giant of all advanced arthrodires. Its head and anterior shield region measured up to 140 cm (55 in.), with a skull height of 102 cm (40 in.). The total body may have reached a length of 10 m (30 ft.). It is difficult to estimate accurately the overall body length because we know nothing of its anatomy posterior to the trunk region. Presumably this region was totally devoid of any armor (Fig. 1, page 2).

Dunkleosteus belongs to the arthrodire family
Dinichthyidae, which includes ten other genera that had
collectively a widespread paleobiogeographic distribution that
included North America, Australia, eastern Europe, Iran, North
Africa and eastern Asia (Carroll 1988; Lelièvre et al. 1993;
Schultze 1973). These dinichthyids can be characterized, in part,
by a decrease in ossification of the bony armature. The bony
plates were probably embedded in the skin of these fishes
and were juxtaposed to one another without being firmly
sutured. Growth of these plates was confined to their margins
(Carroll, 1988).

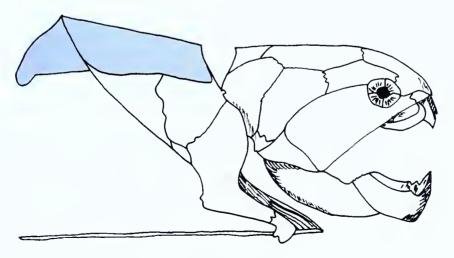


Figure 2. Reconstruction of Dunkleosteus terrelli showing the plates that comprise the armature of the head and trunk region. Colored plate is the median dorsal plate. Modified from Heintz (1932) and reprinted by special permission.

The head of *Dunkleosteus* was composed of 17 loosely connected plates that encased the entire skull. The plates that made up the biting apparatus, the upper and lower "jaws" (the supra- and infragnathals), were particularly sinister in appearance, having a jagged, pointed, razor-like cutting edge that could have easily sliced through any human-sized prey. Even the eyes of this predatory beast were made up of bony plates, called sclerotic rings. These rings, in turn, consisted of four distinct plates that served to support, and perhaps protect, the eyeball.

The ventral armor consisted of four medium-sized plates and two smaller plates which protected the underside of the fish and attached muscles needed for downward movement of the lower jaw.

The trunk (thoracic) armor consisted of nine plates which surrounded the sides and upper back of *Dunkleosteus*. The most conspicuous and largest of these plates was the median

dorsal plate, which in life was situated directly behind the head and was the principal plate of the thoracic shield (Fig. 2, page 7). The two specimens (which represent two separate individuals), recently collected in Erie County, are median dorsal plates.

The first specimen (SMP VP-448), the larger of the two, is

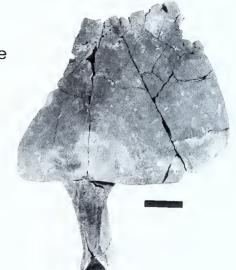


Figure 3. Dunkleosteus sp. (SMP VP-448), dorsal view of median dorsal plate. Anterior direction is up. (Bar scale = 5 cm)

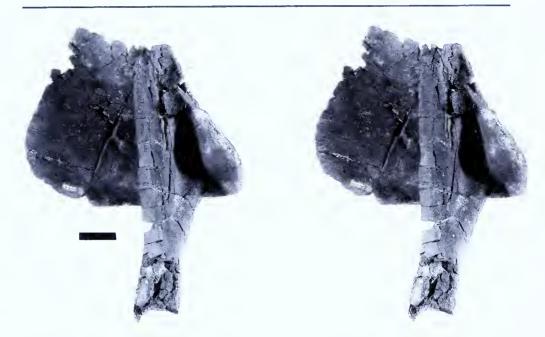


Figure 4. Dunkleosteus sp. (SMP VP-448), ventral view of median dorsal plate (stereo pair); note prominent carinal process. Anterior direction is up. (Bar scale = 5 cm)

incomplete (Figs. 3 and 4). The plate is roughly shovel-like and is characterized by a prominent (posteriorly directed) carinal (keel-shaped ridge) process that extends from the ventral keel. The well-developed carinal process is the feature that is diagnostic (characteristic) of *Dunkleosteus*. This process, and the associated ventral keel, served (in life) for the attachment of the muscle called the "musculus levator capitis." This muscle is believed to have been responsible for the upward movement of the head, which allowed for the opening of the mouth (Heintz 1931, 1932). The second specimen (not figured), an uncataloged median dorsal plate, is smaller, less complete, and lacks most of the distinct carinal process and ventral keel (underside bony ridge) present in SMP VP-448. This specimen is questionably referred to *Dunkleosteus* because of its incomplete nature.

A number of specimens (median dorsal plates) that we have observed, in the collections at the Carnegie Museum of

Natural History and the National Museum of Natural History, display wide variation in robusticity and size. The taxonomic implications (naming of specimens) of this variability are not understood. Differences in growth stage, and or sexual dimorphism (different form for each sex), may account for this variability.

Numerous species of *Dunkleosteus* have been named (Denison 1978). The type species, *Dunkleosteus terrelli*, is the species frequently cited for occurrences in the Devonian of Ohio and Pennsylvania. However, the new material offers little in the way of specific characters needed for a reliable species assignment. Futhermore, the genus *Dunkleosteus* (and the genus *Dinichthys*, in which some species of *Dunkleosteus* were once included) is in need of a rigorous taxonomic revision. Therefore, we can refer to these specimens, at this time only, as *Dunkleosteus* sp.

We thank Joseph Lichtinger and Jeff Gryta (Edinboro University of Pennsylvania) for helping Robert Sullivan and Kesler Randall with collecting SMP VP-448. Special thanks are extended to Dale Tsudy (Edinboro University of Pennsylvania), who, with Jeff Gryta, discovered the specimens, brought them to our attention, and provided us with pertinent stratigraphic and geographic data. We also thank Ed Landing (New York State Geological Survey) for information concerning *Dunkleosteus* material in the collections of the New York State Museum, Mary Dawson and Elizabeth Hill (Carnegie Museum of Natural History, Pittsburgh), and Robert Purdy (United States National Museum, Washington, D. C.) for access to the *Dunkleosteus* material under their care. Claire Messimer took the photos.

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ISBN 0-89271-068-3