



# OPPORTUNITY KNOCKED AND NO ONE WAS HOME : ASPINOTHORACID ARTHRODIRES (PLACODERMI) FROM THE OHIO SHALE FORMATION (UPPER DEVONIAN, NORTH AMERICA)

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CARR R.K. 1995. Opportunity knocked and no one was home : aspinothoracid arthrodires (Placodermi) from the Ohio Shale Formation (Upper Devonian, North America). [Une opportunité non saisie : les arthrodires aspinothoracides (Placodermi) de la Formation des Schistes de l'Ohio (Dévonien supérieur, Amérique du Nord)]. *GEOBIOS*, M.S. n° 19 : 81-83.

## ABSTRACT

The vertebrate fauna from the Ohio Shale formation is a key element to our understanding of aspinothoracid arthrodires. Many of the original descriptions for taxa from this important fauna are based on incomplete material or lack phylogenetic analyses. An ongoing study already has provided redescrptions of a number of these taxa based on a wealth of new material recovered from the Interstate 71 Paleontological Salvage Project. Continuing work centers on remaining problematic taxa from the Ohio Shale. Further analysis of this fauna will provide important information for phylogenetic studies and our understanding of the complex history of the Upper Devonian.

KEY-WORDS : DEVONIAN, PLACODERMI, ARTHRODIRA, ASPINOTHORACIDI, OHIO SHALE.

## RÉSUMÉ

La faune de vertébrés de la Formation des Schistes de l'Ohio est un élément clé de notre compréhension des arthrodires aspinothoracides. La plupart des descriptions de taxa de cette importante faune sont fondées sur du matériel incomplet et leur analyse phylogénétique fait défaut. Une étude en cours a déjà fourni une redescription d'un certain nombre de taxa d'après le matériel nouveau récolté lors du projet paléontologique de sauvegarde de l'autoroute 71. Dans le futur l'analyse de la faune des Schistes de l'Ohio constituera une information importante pour des études phylogénétiques et pour notre compréhension de l'histoire complexe du Dévonien supérieur.

MOTS-CLÉS : DÉVONIEN, PLACODERMI, ARTHRODIRA, ASPINOTHORACIDI, SCHISTES DE L'OHIO.

## INTRODUCTION

The vertebrate fauna from the Ohio Shale formation (Upper Devonian, North America) plays an important role in our understanding of pachyosteomorph arthrodires. References to taxa from this fauna are common throughout the scientific literature on placoderms. However, recent phylogenetic analyses have brought to light our true lack of knowledge concerning these fossil fishes. This is seen often in the omission of Ohio Shale taxa from many of the recent systematic studies. With the exception of *Dunkleosteus* (Heintz 1932; Dunkle & Bungart 1946; Lehman 1956; Hlavin 1976), most members of the fauna lack detailed descriptions based on a current understanding of arthrodiran anatomy. There has been a long history of study on the Ohio Shale fauna so it is

difficult to understand why this important fauna remains so poorly known.

Herman Herzer collected some of the earliest fossil fishes from northern Ohio. From this beginning, in the late Nineteenth and early Twentieth Centuries, a number of researchers provided the initial look at the members of this important fauna (e.g., Newberry 1889; Claypole 1892; Dean 1901; Hussakof 1906; Branson 1911; Heintz 1932). After this early flurry of research, Peter Bungart compiled extensive collections of Ohio Shale fossil fishes from 1923 to 1947. Dunkle's research on this material in the 1940's (e.g., Dunkle & Bungart 1942) supplied the next major published research concerning fossil fishes from the Ohio Shale (in particular, the Cleveland Shale member).

## A BRIEF REVUE OF THE OHIO SHALE ARTHRODIRE FAUNA

Since that time, phylogenetic analyses have relied on these early works although the holotype descriptions often were based on single, disarticulated, and incomplete specimens. During 1967, the Cleveland Museum of Natural History conducted the Interstate 71 Paleontological Salvage Project. This effort more than doubled the number of fossil fish specimens from the Cleveland Shale (Hlavin 1976) and represented an opportunity to revise and expand our knowledge of this North American Lagerstätten. Hlavin (1973, 1976) provided a review of the Cleveland Shale fauna, but did not include phylogenetic analyses or detailed descriptions of the vast amount of comparative or new material. An analysis of the Interstate 71 material, started by William C. Kohlberger, Yale University, ended with his untimely death. Finally, as part of an ongoing project to analyze the Ohio Shale fauna, Carr (1991, 1994, in press) and Carr & Hlavin (in press) reanalyze a number of taxa from the Ohio Shale formation. These studies form the basis of a continuing phylogenetic review of pachyosteorhynchid arthrodires. Carr (1991) reassigned *Heintzichthys* and *Gorgonichthys* to Aspinothoracidi. Following the work of Lelièvre *et al.* (1987), Carr continued their analysis of selenosteoid arthrodires by redescribing *Gymnotrachelus* (1994) and describing a new species of *Stenosteus* (in press). The latter study formed the basis of an update of Dean's (1901) original descriptions of *Selenosteus* and *Stenosteus*. Carr & Hlavin (in press) cladistically analyzed dinichthyid arthrodires and assigned *Hadrosteus*, *Holdenius*, *Hussakofia*, and *Dinichthys* (Dinichthyidae, in part) to the aspinothoracid arthrodires. The assignment of *Holdenius* (following Dunkle & Bungart 1942) was based on the similarity of its gnathal elements (the only material known at that time) to those of *Heintzichthys*. However, *Holdenius holdeni* shares with other aspinothoracid arthrodires a reduction of the lateral and occipital thickenings of the head shield and a modification of the nuchal plate double pits. These pits are rotated posteriorly and are separated by a median septum that is continuous with the posterior process of the nuchal plate (based on undescribed *Holdenius* material housed within the Cleveland Museum of Natural History, Cleveland, Ohio). A result of this recent work is the further revision of relationships among selenosteoids (see also Gardiner & Miles 1994) and the assignment of a number of taxa to Aspinothoracidi.

The relationships among the nine families and assorted individual taxa assigned to Aspinothora-

cidi (see above ; Denison 1978 ; Carr 1991) remains unclear, providing a challenge requiring continuing effort. Work is progressing on analyses of *Paramylostoma* (Dunkle & Bungart 1945) and *Bungartius* (Dunkle 1947) in light of our current knowledge of the Cleveland Shale fishes. Future endeavors include work on new material for *Holdenius* and *Dinichthys* along with undescribed taxa. *Mylostoma* remains an enigmatic taxon whose relationship may become better known as we learn more about related taxa. *Titanichthys*, for which limited new Cleveland Shale material is available, requires revision ; however, Lelièvre (personal communication) has recovered valuable material for this purpose from Morocco.

Similar to the necessity for continuing work on the Ohio Shale fauna, there is a need to review the vast amount of arthrodiran material recovered from Wildungen (*e.g.*, Gross 1932 ; Stensiö 1963). Continued work on the Cleveland Shale fauna and a review of European aspinothoracid arthrodires should prove to be valuable efforts and will provide important information for future phylogenetic studies and our understanding of the complex history of the Upper Devonian.

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