DINICHTHYIDAE (PLACODERMI) : A PALEONTOLOGICAL FICTION?

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ABSTRACT

Dinichthyidae has historically been a repository for a number of large pachyosteomorph arthrodires with questions raised on several occasions concerning the validity of this family. A cladistic analysis of dinichthyid arthrodires results in a revision of basal pachyosteomorph arthrodires. We amend the families Dinichthyidae, Dunkleosteidae, and Panxiosteidae with *Dinichthys* (Dinichthyidae, in part), *Hadrosteus*, *Heintzichthys*, *Gorgonichthys*, and *Holdenius* assigned to Aspinothoracidi. *Dunkleosteus* is rediagnosed and united with *Eastmanosteus*, *Golshanichthys*, *Hussakofia*, and *Westralichthys* in Dunkleosteidae. *Janiosteus*, and possibly *Plourdosteus* are united in Panxiosteidae as sister group to Dunkleosteidae. Finally, we refer *Kiangyousteus*, formerly a dinichthyid arthrodire, to Pachyosteomorphi *incertae sedis*.

KEY-WORDS : DEVONIAN, PLACODERMI, DINICHTHYIDAE, DUNKLEOSTEIDAE, SYSTEMATICS, TAXONOMY.

RÉSUMÉ

Pour nombre de grands arthrodires pachyostéomorphes, les Dinichthyidae ont représenté un fourre-tout, ce qui n'a pas empêché de soulever des questions sur la validité de cette famille. De l'analyse cladistique des arthrodires dinichthyides résulte la révision des arthrodires pachyostéomorphes basaux. La définition des familles Dinichthyidae, Dunkleoteidae et Panxiosteidae est amendée, les genres *Dinichthys* (Dinichthyidae), *Hadrosteus*, *Heintzichthys*, *Gorgonichthys*, et *Holdenius* sont rapportés aux Aspinothoracidi. La diagnose de *Dunkleosteus* est revue et inclut celle de *Eastmanosteus*, *Golshanichthys*, *Hussakofia* et *Westralichthys*. *Janiosteus* et peut être aussi *Plourdosteus* sont placés dans les Panxiosteidae comme groupe-frère des Dunkleoteidae. *Kiangyousteus,* auparavant considéré comme un dinichthyide, est un Pachyosteomorphi *incertae sedis*.

MOTS-CLÉS : DÉVONIEN, PLACODERMES, DINICHTHYIDAE, DUNKLEOSTEIDAE, SYSTÉMATIQUE, TAXONOMIE.

INTRODUCTION

A number of dinichthyid arthrodires has been described or reviewed over the past decade along with attempts to evaluate the phylogenetic relationships among these taxa. This work again has raised a number of questions concerning the validity of the family Dinichthyidae and its relationship to other pachyosteomorph arthrodires (Miles 1969 ; Schultze 1973). Among eubrachythoracid arthrodires (pachyosteomorph and coccosteomorph arthrodires) the relationships among pachyosteomorph arthrodires have been in a state of flux. Most authors would agree that pachyosteomorph arthrodires represent those eubrachythoracid arthrodires that share a most recent common ancestor with selenosteids (*e.g.*, *Rhinosteus*) than with coccosteomorph arthrodires (a "phylogenetic definition" *sensu* de Quieroz & Gauthier 1990). Differences in opinions concerning pachyosteomorph relationships center on the position of several basal taxa and the membership of these groups. A key element of this debate is the relationship of the poorly known arthrodire *Dinichthys herzeri*. A review of the available material for this taxon and a cladistic analysis of the putative members of the family Dinichthyidae has resulted in a major revision of these pachyosteomorph arthrodires.

TAXONOMIC RESULTS

Newberry (1885) established the family Dinichthyidae. Denison (1978) modified the family to include *Dinichthys*, *Dunkleosteus*, *Eastmanosteus*, *Gorgonichthys*, *Hadrosteus*, *Heintzichthys*, *Holdenius*, *Hussakofia*, and *Kiangyousteus*. He removed *Timanosteus*, formerly assigned to Dinichthyidae by Obruchev (1964), placing this genus as Arthrodira *incertae sedis* (Denison 1978). Lelièvre *et al.* (1981) added *Golshanichthys* to the family Dinichthyidae while Long (1987) added *Westralichthys*. *Panxiosteus* and *Janiosteus* share a number of features with the dinichthyids although Wang (1979) included *Panxiosteus* in a separate family (Panxiosteidae) while Ivanov (1988) considered *Janiosteus* to be a coccosteomorph arthrodire. Vézina (1990) united *Dunkleosteus* within a revised family Dunkleosteidae with a number of taxa previously considered to be coccosteomorph arthrodires. Carr (1991) removed *Heintzichthys gouldii* and *Gorgonichthys clarkii* from the Dinichthyidae noting their close relationship with aspinothoracid arthrodires. He retained *Eastmanosteus* and *Dunkleosteus* within a monophyletic group as sister group to Aspinothoracidi. In contrast to Vézina (1990), Carr retained the systematic distinction between *Harrytoombsia* and *Dunkleosteus*. Finally, Carr & Hlavin (in press) suggest that *Holdenius holdeni,* known previously from gnathal elements only, can additionally be considered an aspinothoracid arthrodire based on the similarity of these plates with those of *Heintzichthys gouldii* (following Dunkle & Bungart 1942).

Based on a cladistic analysis employing PAUP (v. 3.1, Swofford 1993), we have attempted to evaluate the current state of knowledge for basal pachyosteomorph arthrodires (Carr & Hlavin in press). This study includes two new dunkleosteid taxa, *Dunkleosteus raveri* nov. sp. from the Huron Shale (Frasnian) of northern Ohio, U.S.A., and *Dunkleosteus* sp. from the Kettle Point Shale (Upper Devonian), Ontario, Canada. The analysis suggests that *Dinichthys herzeri* is more closely related to aspinothoracid arthrodires than to former members of Dinichthyidae. *Dinichthys herzeri* and its family (Dinichthyidae, in part) are considered here to be Aspinothoracidi *incertae sedis*. This leaves the former dinichthyid arthrodires in an unnamed group (*Dunkleosteus*, *Eastmanosteus*, *Gorgonichthys*, *Hadrosteus*, *Heintzichthys*, *Holdenius*, *Hussakofia*, and *Kiangyousteus*). As noted previously, *Heintzichthys*, *Gorgonichthys*, and *Holdenius* are members of Aspinothoracidi. *Hadrosteus rapax* additionally is assigned to Aspinothoracidi and provisionally united with *Gorgonichthys clarki.*, *Dunkleosteus*, *Eastmanosteus calliaspis*, *Eastmanosteus pustulosus*, *Golshanichthys*, *Hussakofia*, and *Westralichthys* are placed within the family Dunkleosteidae. *Hussakofia*, known from inferognathal and nuchal plates, is included in this family based on the presence of two cusps along the inferognathal occlusal surface similar to the condition seen in *Dunkleosteus* and *Golshanichthys*. *Eastmanosteus* represents a paraphyletic group suggesting the need for further work. *Dunkleosteus* is a monophyletic taxon characterized by the presence of articular surfaces on the anterior portion of the parasphenoid that contact the posterior processes of the anterior superognathal plates. *Panxiosteus* and *Janiosteus*, united in the family Panxiosteidae, are the sister group to Dunkleosteidae. A preliminary analysis of *Plourdosteus* suggests that it too may be a member of Panxiosteidae in contrast to interpretations by Vézina (1990) and Gardiner & Miles (1994). Finally, we refer *Kiangyousteus* to Pachyosteomorphi *incertae sedis*. Our proposed changes are summarized below :

PACHYOSTEOMORPHI Stensiö, 1944
DUNKLEOSTEOIDEA Vézina, 1990

DUNKLEOSTEIDAE Stensiö, 1963
Dunkleosteus LEHMAN, 1956
Eastmanosteus OBRUCHEV, 1964
Golshanichthys LELIÈVRE, 1981
Hussakofia COSSMAN, 1910
Westralichthys LONG, 1987

PANXIOSTEIDAE Wang, 1979
Panxiosteus WANG, 1979
Janiosteus IVANOV, 1988
?*Plourdosteus* ØRVIG, 1951

ASPINOTHORACIDI *sensu* Miles & Dennis, 1979

DINICHTHYIDAE Newberry, 1885
Dinichthys herzeri NEWBERRY, 1868
Gorgonichthys CLAYPOLE, 1892
Gymnotrachelus DUNKLE & BUNGART, 1939
Hadrosteus GROSS, 1932
Heintzichthys WHITLEY, 1933
Rhinosteus JAEKEL, 1911

PACHYOSTEOMORPHI *incertae sedis*
Kiangyousteus LIU, 1955

From the current cladistic analysis, we have revised the relationships of Dunkleosteidae and its members (Carr & Hlavin in press). However, this study has raised a number of new questions concerning the relationships of *Plourdosteus* and the

relationships among the many taxa united within Aspinothoracidi (these questions are beyond the scope of our current study). Continued work on North American taxa, in particular the Cleveland Shale and Huron Shale faunas, is fundamental to our further understanding of pachyosteomorph arthrodires. *Dinichthys herzeri* remains an enigmatic species requiring the preparation and study of new fossil material. The aspinothoracid arthrodires from the Cleveland Shale are an important aspect of future studies since many of the previously described taxa were based on limited material and lacked phylogenetic analyses.

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