

A three-dimensional skull of a primitive clupeomorph from the Cenomanian English Chalk, and implications for the evolution of the clupeomorph *acusticolateralis* system

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Abstract

A three-dimensional skull of a †paraclupeid is described and referred to the genus †*Diplomystus* based on the shape of the dorsal scutes. All other †paraclupeids are known only from flattened or nearly flattened specimens. Therefore, this skull provides hitherto unavailable data on delicate braincase structures. This study allows a more complete assessment of primitive clupeomorph conditions and contributes to our understanding of how the complex specialisations of the acusticolateralis system in Recent clupeiform fishes developed. All are absent from †paraclupeids. A phylogeny is proposed (†Paraclupeidae (†*Spratticeps* (†*Santanaclupea*, †*Denticeps*, clupeids))) which acknowledges a sequential acquisition of acusticolateralis specialisations. Additionally, some derived characters are identified within the †paraclupeids such as excavated parietals and enlarged entopterygoid teeth occluding with enlarged teeth upon a consolidated basibranchial toothplate.

Introduction

The family †Paraclupeidae CHANG & CHOU 1977 (= †Ellimmichthyidae GRANDE, 1982 after CHANG & GRANDE 1997) is a group of Lower Cretaceous to Middle Eocene clupeomorph fishes consisting of at least six genera (†*Ellimmichthys*, †*Paraclupea*, †*Triplomystus*, †*Sorbinichthys*, †*Ezkutubrezi* and †*Diplomystus*) and at least ten species (see below). They are characterised by laterally expanded and subrectangular dorsal scutes each of which bears a median keel. Our current view on the phylogenetic placement of these fishes GRANDE (1982) suggests that †paraclupeids, the only family within the order †Ellimmichthyiformes, with the genus †*Armigatus*, form an unresolved trichotomy with the crown group clupeiforms. †*Spratticeps gaultinus* PATTERSON, 1970, currently known only by isolated partial braincases, may be a stem species to Recent clupeiforms. A phylogenetic framework current in the literature is shown in Figure 1 together with some of the characters listed in the legend. †Paraclupeids and †*Armigatus* are regarded as plesiomorphic clupeomorphs because they lack a recessus lateralis (a convergence of sensory canals in the temporal region separated from the perilymphatic cavity of the inner ear by a membrane). Some of these characters mentioned in Figure 1, such as the presence of pre-epiotic fossae, prootic and pterotic bullae, are difficult to see in material that has been flattened during fossilisation. Most currently described †paraclupeids are preserved flattened and therefore the systematic distribution of some of these features is unknown. The importance of the specimen described in this paper is that it is preserved in perfect three-dimensions and therefore many cranial details can be seen undistorted. Furthermore, it can be identified as belonging to the genus †*Diplomystus* by virtue of the fact that the dorsal scutes are pectinated along their posterior borders (GRANDE 1982) and the supraoccipital crest is enlarged. It is therefore possible to answer some uncertainties concerning the more delicate structures. Additionally this specimen shows a very well-preserved palate and copula and this adds considerable information to our knowledge of the visceral skeleton which is currently very scanty in other †paraclupeids. In nearly all areas of the skull which can be directly compared, this †*Diplomystus* specimen is similar to other †paraclupeids. Therefore, it may be legitimate to extrapolate

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