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Article



Cranial anatomy of *Jeholosaurus shangyuanensis* (Dinosauria: Ornithischia) from the Early Cretaceous of China

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Abstract

A detailed description of the skull and mandible of the Chinese cerapodan ornithischian dinosaur *Jeholosaurus shangyuanensis* (Lower Cretaceous, Yixian Formation) is presented for the first time and this information is used to reassess its phylogenetic position. *Jeholosaurus* can be distinguished from all other cerapodans on the basis of one autapomorphy (a row of small foramina on the nasal) and a character combination that is unique among ornithischians. Previously undescribed specimens add considerably to our knowledge of *Jeholosaurus*, providing new insights into its anatomy and ontogeny. Revised character scores increase the resolution of phylogenetic hypotheses and provide additional support for placement of *Jeholosaurus* within Ornithopoda.

Key words: Cerapoda, early Aptian, Jehol Biota, Marginocephalia, Ornithopoda, Yixian Formation

Introduction

The name Hypsilophodontidae has been applied to a clade or grade of small bipedal ornithischian dinosaurs, whose composition has varied from author to author depending on the phylogenetic hypothesis prevailing at the time (e.g. Thulborn 1971; Galton 1972; Sues & Norman 1990). Pre-cladistic studies viewed 'hypsilophodontids' as the nexus from which many of the major ornithischian clades arose, a conclusion based on their generalised body plan and superficial similarity to early ornithischians, such as Lesothosaurus (e.g. Thulborn 1971, 1977; Galton 1972). This view was challenged by the first (mostly non-numerical) cladistic analyses of ornithischian interrelationships, which identified 'hypsilophodontids' as members of the ornithopod radiation (Norman 1984; Cooper 1985; Sereno 1986, 1999; Sues & Norman 1990; Weishampel & Heinrich 1992). Many of these workers regarded 'hypsilophodontids' as a clade, effectively removing them from their role as 'ancestors' in ornithischian phylogeny (e.g. Maryanska & Osmólska 1985). However, more recent work has challenged this view, demonstrating that many of the taxa traditionally regarded as 'hypsilophodontid' ornithopods, such as *Hexinlusaurus* and *Othnielosaurus*, form successive outgroups to Cerapoda (Scheetz 1999; Buchholz 2002; Weishampel et al. 2003; Butler 2005; Butler et al. 2007, 2008). Moreover, these analyses indicate that other 'hypsilophodontids', such as Hypsilophodon and Thescelosaurus, form an array of ornithopod taxa that is paraphyletic with respect to iguanodontians. Consequently, 'hypsilophodontids' have regained their importance in terms of understanding the sequences of character evolution that occurred at the base of Neornithischia and in the origins of ornithopods and marginocephalians. Unfortunately, support measures for many of the nodes at the base of Cerapoda are weak (see Butler et al. 2008). In this context, description of new early cerapodan material will be essential to disentangle the relationships of these taxa and to provide more robust phylogenetic hypotheses.

Jeholosaurus shangyuanensis, from the Lower Cretaceous Yixian Formation of Liaoning Province