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New basal hadrosauroid (Dinosauria: Ornithopoda) from the Lower Cretaceous Kitadani Formation, Fukui, central Japan

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Abstract

A new basal hadrosauroid, *Koshisaurus katsuyama*, from the Lower Cretaceous Kitadani Formation in Fukui, central Japan, is reported. The new taxon is distinguished by an autapomorphy and a unique combination of maxillary, vertebral, pubic and femoral characters. A phylogenetic analysis indicates that *Koshisaurus* is positioned as a basal member of Hadrosauroidea and is more derived than the contemporaneous *Fukuisaurus*, which is a non-hadrosauroid hadrosauriform. The presence of the antorbital fossa on the maxilla and at least three subsidiary ridges on the labial side of maxillary tooth crown implies that *Koshisaurus* was among the most basal hadrosauroids. This discovery indicates a higher diversity of hadrosauroids along the eastern margin of the Asian continent in the Early Cretaceous.

Key words: Early Cretaceous, Hadrosauroidea, Kitadani Formation, Totori group, Japan

Introduction

Recent discoveries and descriptions of styracosternal iguanodonts indicate the great diversity of this group throughout the Early Cretaceous (You & Li 2009; McDonald *et al.* 2010a, b; Wu *et al.* 2010; You *et al.* 2011; McDonald *et al.* 2012; Wu & Godefroit 2012). In Asia, the fossil record of this group is extensive. However, discoveries in Asia are largely restricted to dinosaur-rich formations in China and Mongolia. Until recently, *Fukuisaurus tetoriensis* from the Lower Cretaceous (Barremian–lower Aptian) Kitadani Formation of Japan was the only named Asian styracosternal recognized from outside of this region (Kobayashi & Azuma 2003). The recent reports of two species of styracosternans in Thailand extended their diversity and distribution into Southeast Asia in the late Early Cretaceous (Buffetaut & Suteethorn 2011; Shibata *et al.* 2011). In Japan, styracosernan iguanodont discoveries in addition to *Fukuisaurus* include a maxillary tooth from the Tatsukawa Formation (Hauterivian) in Tokushima, several well-preserved teeth from the Kuwajima Formation (Barremian) in Ishikawa (Morozumi *et al.* 1995; Manabe & Barrett 2000), and shed teeth from the “Lower Formation” (lower Albian) of the Sasayama Group in Hyogo (Saegusa & Ikeda 2014).

The Kitadani Formation, the uppermost unit of the Totori Group, is the most productive dinosaur-bearing unit in Japan, having yielded *Fukuiraptor kitadaniensis*, *Fukuisaurus tetoriensis* and *Fukuititan nipponensis* (Azuma & Currie 2000; Kobayashi & Azuma 2003; Azuma & Shibata 2010). Additionally, ornithopod dentaries, which do not pertain to *Fukuisaurus*, have also been reported (Shibata & Azuma 2011). All of these dinosaurian specimens were found in one locality, the Kitadani Quarry in Katsuyama City (Fig. 1). At least four bonebeds are recognized at this locality (Fig. 2A); the definition of “bonebed” in this study follows Behrensmeyer (2007). The lowermost one, the Bonebed I (BB I), has yielded *Fukuiraptor*, *Fukuisaurus*, other dinosaur bones and teeth, and other vertebrates including crocodilians, turtles and fishes (Shibata & Goto 2008). Most of the BB I vertebrate assemblage consists of disarticulated or associated skeletons of dinosaurs and other vertebrates. Other horizons (BB II and III), which are approximately 10 m above BB I, yielded *Fukuititan* elements and a well-preserved small theropod skeleton (Shibata & Goto 2008), respectively. The iguanodontian bones described in this paper came from the fourth bone

In all consensus trees the two Fukui taxa are not particularly closely related. In the Adams consensus tree, for example, *Koshisaurus* is positioned at the base of Hadrosauroidea. In contrast, the other Fukui iguanodontian, *Fukuisaurus*, falls out as a basal hadrosauriform and closely related to *Proa*, *Iguanodon* and *Oouranosaurus*. Consequently, our analysis corroborates that *Koshisaurus* and *Fukuisaurus* are phylogenetically distinct; *Koshisaurus* is more derived than *Fukuisaurus*. Coexistence of at least two taxa of styracosternans occurred repeatedly during the Early Cretaceous. Examples include *Barilium* and *Hypselospinus* in the Wadhurst Clay Formation of England, *Cedrorestes*, *Iguanocolossus* and *Hippodraco* in the Cedar Mountain Formation of Utah, *Iguanodon* and *Mantellisaurus* in the Wessex Formation of England and Sainte-Barbe Clays Formation of Belgium, *Bolong* and *Jinzhousaurus* in the Yixian Formation of China, and *Lurdusaurus* and *Oouranosaurus* in the El Rhaz Formation of Niger (Taquet 1976; Norman 1980, 1986; Taquet & Russell 1999; Wang & Xu 2001; You and Ji *et al.* 2003; McDonald *et al.* 2010b; Wu & Godefroit 2012).

Koshisaurus was one of the most primitive forms of Hadrosauroidea because it possesses an antorbital fossa and three subsidiary ridges on the maxillary teeth, similar to *Equijubus* (You *et al.* 2003). The subsidiary ridges of the maxillary teeth are also present in *Xuwulong*, *Jinzhousaurus* and *Altirhinus* among basal hadrosauroids, but these taxa lack the antorbital fossa on the maxilla (Norman 1998; You *et al.* 2003; Barrett *et al.* 2009).

Conclusions

A new hadrosauroid, *Koshisaurus katsuyama* from the Early Cretaceous Kitadani Formation, is a distinct new genus and species and distinguishable from the contemporaneous hadrosauriform *Fukuisaurus tetoriensis*. Due to its possession of an antorbital fossa and at least three subsidiary ridges on the crown of the maxillary teeth, *Koshisaurus* is found to be one of the most primitive hadrosauroids in our phylogenetic analysis. The occurrence of numerous basal hadrosauroids in Asia suggests a diversification of this group in Asia during the Early Cretaceous period.

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