

[Original report]

Phylogenetic position of Ornithomimosauria in Coelurosauria with comments on the relationship of ornithomimosaurids and alvarezsaurids

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Abstract

The phylogenetic position of Ornithomimosauria within Coelurosauria is discussed. Most of previous phylogenetic analyses suggested that Ornithomimosauria is basal coelurosaur dinosaurs (Tyrannosauridae is the most basal taxon). One study suggested that ornithomimosaurids and alvarezsaurids form a monophyly. This study argues an ornithomimosaurids-alvarezsaurids relationship and supports the idea that they are probably not closely related. Additional information from this study are that two characters for the ornithomimosaur-alvarezsaurid monophyly from the previous study (metacarpals I-III extent of shaft-to-shaft contact 60-70% of shafts and metacarpal I length at least 60% that of metacarpal II) are not supported (roughly 20% contact between metacarpals II and III, less than 50% shaft-to shaft contact in metacarpals I and II in some taxa, and metacarpal I in *Harpymimus* roughly 50% of metacarpal II). A phylogenetic analysis in this study suggests that the features, supporting a close relationship between ornithomimosaurids and alvarezsaurids in the previous study are from derived ornithomimidids, not primitive forms.

Key words : Dinosauria, Coelurosauria, Ornithomimosauria, Alvarezsauridae, phylogeny

Introduction

Ornithomimosauria are a group of theropod dinosaurs, each of which resembles modern ground birds in having a beak-like jaw and lightly built body with long, slender limbs (Fig. 1). The members of this group are best known from the Cretaceous sediments of Laurasia (Osmólska, 1997). The first recorded ornithomimosaur is *Ornithomimus velox* by Marsh (1890), who established the family Ornithomimididae. Since the establishment of the family, six additional genera from North America (*Struthiomimus* and *Dromiceiomimus*) and Asia (*Archaeornithomimus*, *Sinornithomimus*, *Gallimimus*, and *Anserimimus*) were assigned to it. Non-ornithomimid

ornithomimosaur genera were placed in the families Harpymimidae (includes *Harpymimus*) and Garudimimididae (includes *Garudimimus*) (Barsbold, 1981; Barsbold and Perle, 1984) from Mongolia as well as unnamed taxa for *Pelecanimimus* from Spain and *Shenzhousaurus* from China (Pérez-Moreno *et al.*, 1994; Ji *et al.*, 2003). Barsbold (1976) coined Ornithomimosauria, which includes *Pelecanimimus*, *Shenzhousaurus*, Harpymimidae, Garudimimididae, and Ornithomimididae (Barsbold, 1981; Barsbold and Perle, 1984; Pérez-Moreno *et al.*, 1994) (Fig. 1). The definitions of Ornithomimididae and Ornithomimosauria have been consistent in previous literature (Russell, 1972; Barsbold and

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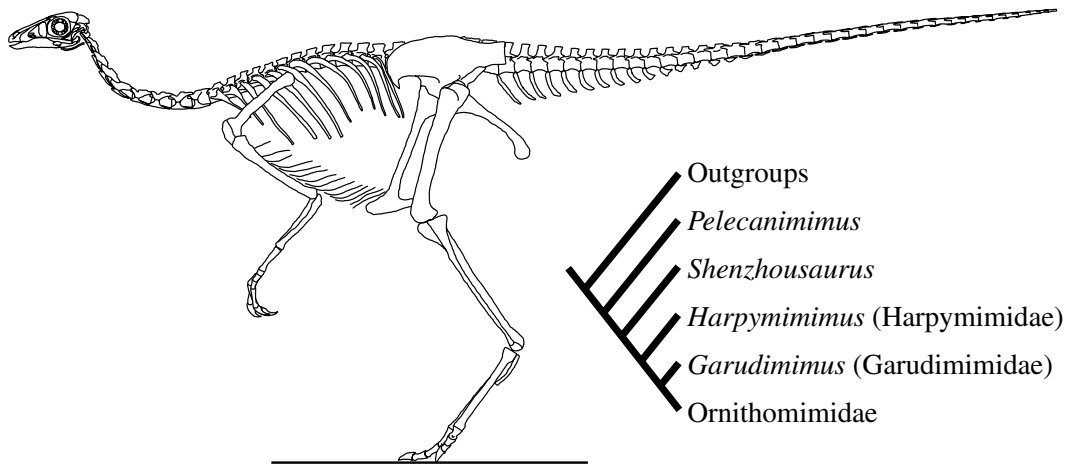


Fig. 1. Reconstruction of a Chinese ornithomimid, *Sinornithomimus dongi* (from Kobayashi and Lü, 2003) and a simplified cladogram of ornithomimosaurids (from Kobayashi and Barsbold, 2004).

Osmólska, 1990; Pérez-Moreno *et al.*, 1994; Holtz, 1994; Osmólska, 1997; Holtz, 1998; Norell *et al.*, 2002; Clark *et al.*, 2002; Hwang *et al.*, 2002; Kobayashi and Lü, 2003; Makovicky *et al.*, 2004) except for Sereno (1997; 1998; 1999).

Padian *et al.* (1999) used a node-based definition of Ornithomimosauria: *Pelecanimimus* and *Ornithomimus* and all descendants of their most recent common ancestor, which is similar to “Ornithomimidae” of Sereno (1998). Based on this definition, Ornithomimosauria includes *Pelecanimimus*, *Shenzhousaurus*, *Harpymimus*, *Garudimimus*, *Archaeornithomimus*, *Sinornithomimus*, *Gallimimus*, *Anserimimus*, *Struthiomimus*, *Dromiceiomimus*, and *Ornithomimus*. “Ornithomimosauria” of Sereno (1998) is different from this and is a stem-based definition (all maniraptoriforms closer to *Ornithomimus* than Neornithes), consisting of Therizinosauridae, Alvarezsauridae, and “Ornithomimidae” (Sereno, 1999). This inconsistency in terminology is caused by a disagreement in the phylogenetic position of Ornithomimosauria/Ornithomimidae within Coelurosauria. This study compares the difference in the phylogenetic position of Ornithomimosauria/Ornithomimidae within Coelurosauria in previous studies and discusses the relationships of Ornithomimosauria and Alvarezsauridae.

This study follows the definition of Padian *et al.* (1999) for Ornithomimosauria because it is concordant with the traditional usage of Ornithomimosauria. Ornithomimidae traditionally

includes all ornithomimosaurids from the Late Cretaceous of North America and Asia except *Garudimimus brevipes* of Mongolia (*Archaeornithomimus*, *Sinornithomimus*, *Gallimimus*, *Anserimimus*, *Struthiomimus*, *Dromiceiomimus*, and *Ornithomimus*) (Barsbold and Osmólska, 1990; Osmólska, 1997). In this study, Ornithomimidae is based on a stem-based definition as all ornithomimosaurids closer to *Ornithomimus* than to *Garudimimus*.

Phylogenetic status of Ornithomimosauria/Ornithomimidae in previous studies

Main phylogenetic analyses on Coelurosauria are Holtz (1998), Sereno (1999), Maryanska *et al.* (2002), and the Theropod Working Group (Norell *et al.*, 2002; Clark *et al.*, 2002; Hwang *et al.*, 2002; Makovicky *et al.*, 2005; Norell *et al.*, 2006; Turner *et al.*, 2007) and suggested that Ornithomimosauria/Ornithomimidae are maniraptoriforms, basal to Oviraptoridae, Dromaeosauridae, and Aves. Although their relationships with other maniraptoriforms (e.g., Troodontidae, Tyrannosauridae, Therizinosauridae, and Alvarezsauridae) are inconsistent, the phylogenetic status of Ornithomimosauria/Ornithomimidae is consistent in Maryanska *et al.* (2002) and the Theropod Working Group, which differs from Holtz (1998) and Sereno (1999) (Fig. 2).

In Maryanska *et al.* (2002) and the Theropod Working Group, Ornithomimosauria is placed higher than Tyrannosauridae but more basal to the rest of

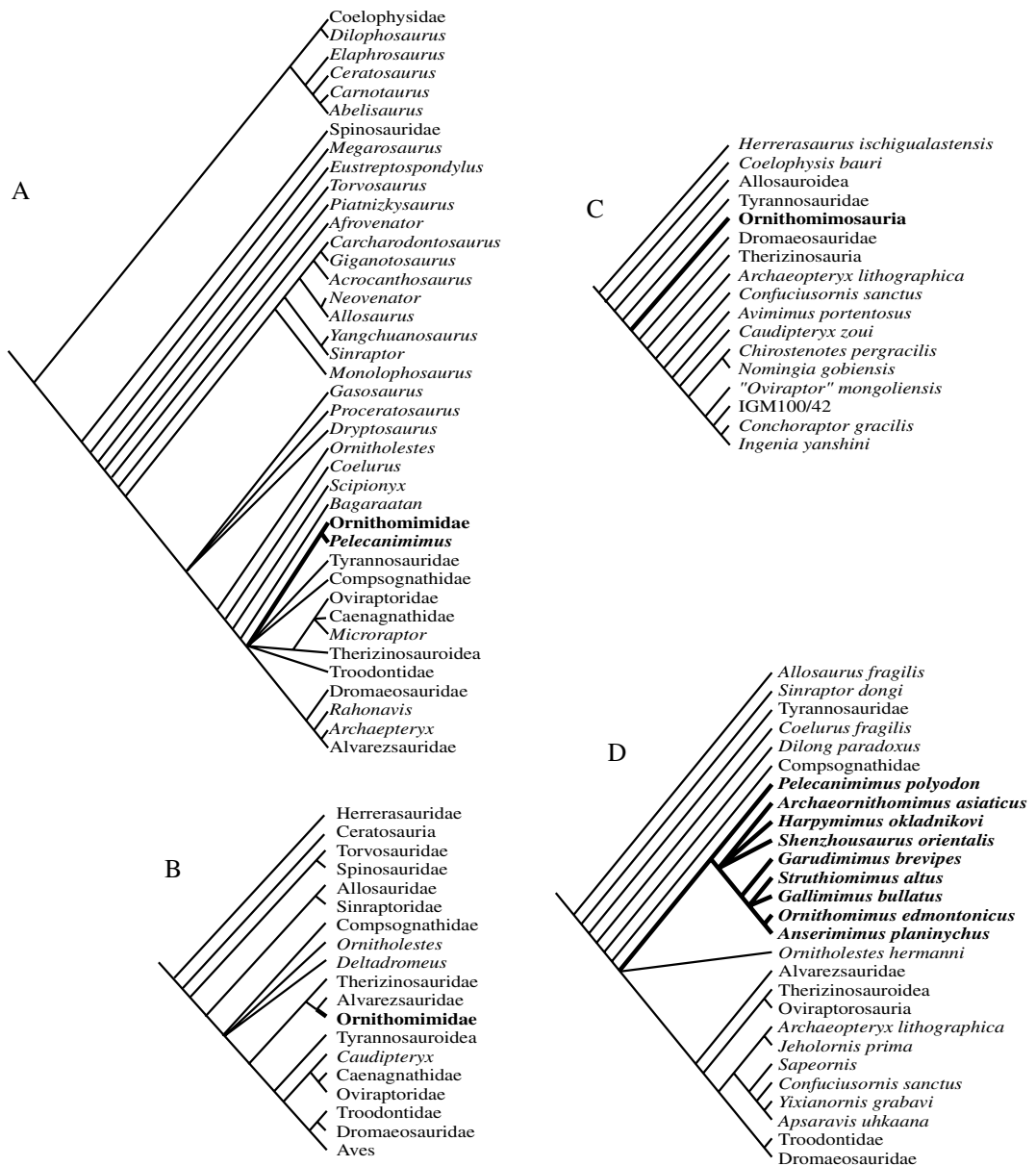


Fig. 2. Cladograms of theropods from previous phylogenetic analyses : Holtz (1998) (A), Sereno (1999) (B), Maryanska *et al.* (2002) (C), and Turner *et al.* (2007) (D).

members of Coelurosauria (Turner *et al.* (2007) suggested that Compsognathidae is more basal to Ornithomimosauria). Their analyses indicate that the differences in interrelationships for higher taxa (especially the position of Oviraptoridae/Oviraptorosauria) do not effect on the phylogenetic position of Ornithomimosauria. Holtz's study shows unresolved polytomy among Troodontidae, Compsognathidae,

Tyrannosauridae, Ornithomimosauria, the clade of Oviraptorosauria and Therizinosauroidae, and the clade of Dromaeosauridae and higher taxa. Although the relationships of these clades are not resolved, it leaves a possibility of the phylogenetic status of Ornithomimosauria as suggested by Maryanska *et al.* (2002) and the Theropod Working Group. Sereno's study is completely different from

the other studies. Ornithomimidae is nested within a clade with Therizinosauridae and Alvarezsauridae, where this clade is called “Ornithomimosauria” by Sereno, and Tyrannosauridae is placed higher than Ornithomimosauria.

Relationships of Ornithomimidae and Alvarezsauridae

Sereno (2001) re-evaluated the previous phylogenetic studies on Alvarezsauridae (e.g., Perle *et al.*, 1993; Novas, 1996; Chiappe *et al.*, 1996; Forster *et al.*, 1998). He argued that bird-like characters in Alvarezsauridae are synapomorphies with Ornithomimidae and proposed that Ornithomimidae and Alvarezsauridae are monophyletic, named as Ornithomimoidea, and the clade for Ornithomimoidea and Therizinosauridae is called “Ornithomimosauria” (Fig. 2).

Suzuki *et al.* (2002) discussed the validity of Ornithomimidae-Alvarezsauridae synapomorphies proposed by Sereno (1999; 2001). Among 19 putative synapomorphies, they re-evaluated 15 synapomorphies (dorsoventrally flattened premaxillary internarial bar, prefrontal exposure on the skull roof larger than the lacrimal, prefrontal orbital flange, teeth along maxillary and dentary rows uniform in size, chevron height four to five times height of corresponding neural spines, dentary length up to 80% of the lower jaw length, presence of a dorsomedial tubercle on the proximal phalanx of manual digit I, ventral surface of manual ungual flattened and broad, distally placed flexor tubercle of manual ungulas, iliac blades deflected toward midline and having partial contact along their dorsal margin, maxillary and dentary teeth implanted in a groove, presence of paired flexor process of manual proximal phalanges, metacarpal-phalangeal joint with approximately 15 degrees maximum extension, metacarpal III midshaft width 75% or more than that of metacarpal II, and presence of a marked flexor depression proximal to the distal condyles on the manual proximal phalanges).

Dorsoventrally flattened premaxillary internarial bar is certainly seen in both Ornithomimidae and Alvarezsauridae, but Suzuki *et al.* (2002) pointed out that this feature is more widely distributed in Coelurosauria such as troodontids. They also discussed that some characters are misinterpreted by Sereno. Prefrontal exposure on the skull roof is

subequal to that of the lacrimal ornithomimids. Prefrontal orbital flange is absent in *Struthiomimus altus* (AMNH 5339). Anterior teeth are smaller than posterior ones in the maxilla in *Pelecanimimus*. Chevron height is no greater than twice height of corresponding neural spines in ornithomimids. Dentary length relative to the lower jaw length varies in both groups (no more than 77% in *Shuvuuia* and 70% in *Garudimimus*). A dorsal tubercle on the proximal phalanx of manual digit I is on lateral side not medial side in *Mononykus* and is absent in *Patagonykus*. Ventral surface of manual ungual is rounded in digit III of a Mongolian alvarezsaurid and flat in digit I of *Mononykus* and *Shuvuuia*, convex in *Patagonykus*. Flexor tubercle of manual ungulas is faint in alvarezsaurids. Iliac blades along their dorsal margin are separated in *Alvarezsaurus* and not clear in basal alvarezsaurids.

Suzuki *et al.* (2002) also argued that some other characters are ambiguous. Maxillary and dentary teeth implanted in a groove in *Pelecanimimus* but not well preserved in other toothed ornithomimosaur (all teeth in tooth sockets in *Harpymimus* and *Shenzhousaurus*: Ji *et al.*, 2003; Kobayashi and Barsbold, 2005). Both ornithomimids and alvarezsaurids have paired flexor process of manual proximal phalanges but their structures are too different to consider that as a homology. Because the degree of maximum extension of metacarpal-phalangeal joint is a functional character, it is difficult to interpret. Also this character as well as another one (metacarpal III midshaft width 75% or more than that of metacarpal II) were not included in Sereno’s cladistic analysis. Presence of a marked flexor depression proximal to the distal condyles on the manual proximal phalanges could be informative but it should be restricted to digit I because of the condition of alvarezsaurids.

Four of 19 characters were not discussed by Suzuki *et al.* (2002) (paired flexor processes in manual proximal phalanges; posteriormost tooth of maxillary teeth significantly anterior to posteriormost dentary tooth; metacarpals I-III extent of shaft-to-shaft contact 60-70% of shafts; metacarpal I length at least 60% that of metacarpal II). Ornithomimosaurids have paired flexor processes in manual proximal phalanges as suggested by Sereno (2001). In *Pelecanimimus*, the posteriormost tooth of maxillary teeth is

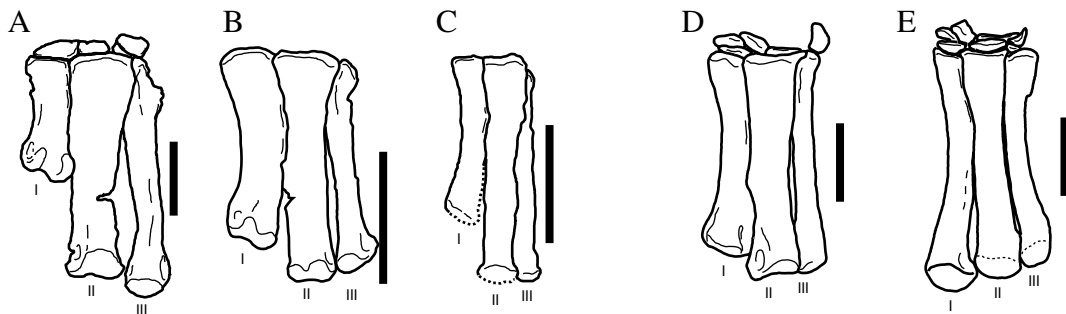


Fig. 3. Left metacarpals of ornithomimosaur ; *Harpymimus okladnikovi* (A), *Archaeornithomimus asiaticus* (B), *Sinornithomimus dongi* (C), *Struthiomimus altus* (D), and *Ornithomimus edmontonicus* (E).

positioned anterior to posteriormost dentary tooth as seen in *Shuvuuia* (Sereno, 2001). Other toothed forms (*Harpymimus* and *Shenzhousaurus*) lack maxillary teeth and have dentary teeth at the anterior end of the lower jaw (Barsbold and Perle, 1984; Ji *et al.*, 2003; Kobayashi and Barsbold, 2005). The other two characters proposed by Sereno are not true for all ornithomimosaur. The attachment of metacarpals II and III is small (roughly 20% of metacarpal II length), and that of metacarpals I and II vary among taxa (Fig. 3). Primitive forms tend to have shorter contact between metacarpals I and II (50% or less). Re-description of *Harpymimus okladnikovi* by Kobayashi and Barsbold (2005) shows that metacarpal I is roughly half of metacarpal II. Re-evaluation of Sereno's study (2001) by Suzuki *et al.* (2002) and this study infer that the affinities between Ornithomimidae and Alvarezsauridae are weaker than Sereno indicated.

Additional phylogenetic approach to test the preferable phylogenetic status of Ornithomimosauria

Among previous phylogenetic analyses of Theropoda or Coelurosauria, such as Holtz (1998), Sereno (1999), Maryanska *et al.* (2002), and the Theropod Working Group, only the Theropod Working Group utilized specific-level terminal taxa, whereas the other analyses, including Sereno (1999), used Ornithomimosauria or Ornithomimidae as a terminal taxon. Kobayashi (2004) demonstrated phylogenetic analyses on coelurosaurs using specific-level terminal taxa for Ornithomimosauria based on data matrices of these previous studies. For a phylogenetic analysis based on the data

matrix of Sereno (1999), Ornithomimidae from the original matrix is replaced with eleven individual ornithomimosaur taxa, producing a new data matrix with 27 ingroups. This analysis produced 290,382 most parsimonious trees.

A strict consensus tree shows an unresolved polytomy of Alvarezsauridae and all member of Ornithomimosauria, caused by three alternative placements of *Pelecanimimus polyodon* (Fig. 4). *Pelecanimimus* is shown as a sister taxon to the other members of Ornithomimosauria, in a position as a derived ornithomimosaur with *Harpymimus okladnikovi* and a Mongolian taxon (GIN 960910 KD) (Fig. 4 C), and a sister taxon to Alvarezsauridae (Fig. 4B and D), which is probably caused by the large amount of missing data for *Pelecanimimus polyodon* (89% is missing). The monophyly of all ornithomimosaur is supported in the first and second alternative positions of *Pelecanimimus polyodon* and is supported by one unambiguous character (sub-equal metacarpals I and II) in the first alternative, and by one unambiguous character (absence of dentary teeth) in the second alternative placement. One unambiguous synapomorphy unites *Pelecanimimus polyodon* and Alvarezsauridae (posteriormost maxillary tooth is anterior to posteriormost dentary tooth) because the maxillary teeth are present only in *Pelecanimimus polyodon* among ornithomimosaur. With or without inclusion of *Pelecanimimus polyodon* in a monophyly of ornithomimosaur, *Harpymimus okladnikovi* and GIN 960910KD (both are from Lower Cretaceous sediments) are more derived in their phylogenetic positions than Late Cretaceous forms (Fig. 4B-D). This result is discordant with

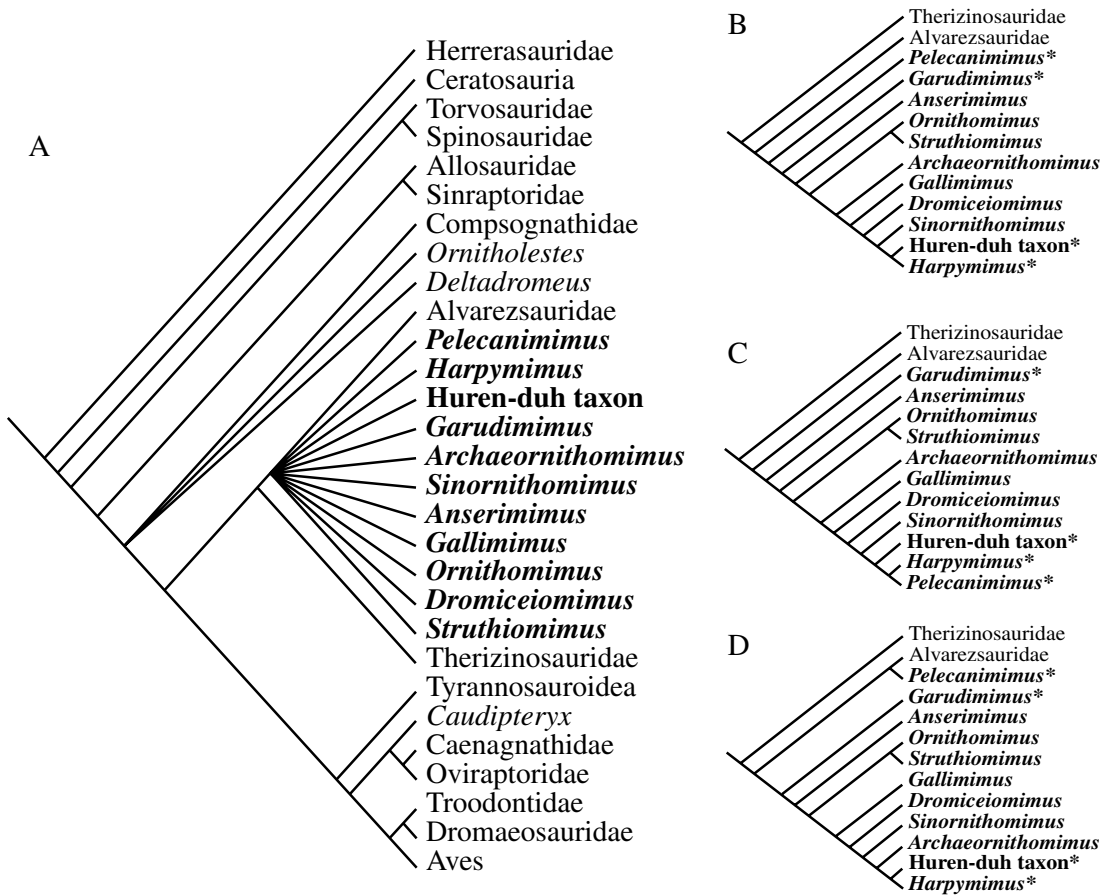


Fig. 4. A strict consensus tree of 290,382 most parsimonious trees from the phylogenetic analysis based on data matrix by Kobayashi (2004), modified from Sereno (1999) (A); three possible placements of *Pelecanimimus* in most parsimonious trees (B-D).

previous studies and the temporal occurrences of ornithomimosaurs, indicating that the close relationship of Ornithomimidae and Alvarezsauridae may be supported by derived conditions in Ornithomimidae. This indicates that Sereno's data matrix may not be useful for resolving ornithomimosaur relationships in Coelurosauria.

Conclusions

Sereno (1999) suggested that the affinities between ornithomimosaurs and alvarezsaurids and bird-like features in both groups, forming a monophyletic group. However, many of putative synapomorphies for the clade, proposed by Sereno, were evaluated by Suzuki *et al.* (2002) and they suggested that most were misinterpreted. This study also supports Suzuki *et al.*'s study by

pointing out some interpretations by Sereno were unlikely and a phylogenetic analysis suggests that the monophyly of Ornithomimidae and Alvarezsauridae is probably caused by derived characters, at least, of ornithomimids.

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