

The North American avisaurids (Aves: Enantiornithes): new data on biostratigraphy and biogeography

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Abstract. In addition to the two described *Avisaurus* species (*A. archibaldi* Brett-Surman and Paul and *A. gloriae* Varrichio and Chiappe), undescribed material from the Maastrichtian contributes important morphologic, biostratigraphic, and biogeographic data on North American avisaurids. A juvenile *Avisaurus* specimen of an undescribed species from the Maastrichtian Hell Creek Formation of Montana reveals the presence of distal tarsals in enantiornithines and an ontogenetic stage shared with non-avian dinosaurs. All known *Avisaurus* fossils were deposited in a variety of habitats along the Western Interior Seaway of North America and areas more interior. The presence of other clades of birds in the Hell Creek Formation indicate that avisaurids formed only part of a diverse avifauna at the close of the Cretaceous in North America. Phylogenetic analysis of the new Maastrichtian material places these new specimens as the sister to the other known *Avisaurus* species within Avisauridae. This hypothesis of avisaurid relationships points to a South American origin of this clade with a dispersal or vicariant event to North America before or early in the Campanian. This event was penecontemporaneous with the Laurasian movement of alvarezsaurids and sauropods. These Montanan enantiornithine specimens represent the northern-most record of this bird clade in North America. These Maastrichtian species and specimens are from very late in the Maastrichtian and are probably the youngest known enantiornithines. The stratigraphic position of these birds with respect to the rest of the fauna indicate that their extinction was nearly synchronous with the extinction of other toothed bird clades and other vertebrates at the end of the Cretaceous.

Key words. Aves. Enantiornithes. *Avisaurus*. biogeography

Introduction

Enantiornithes is the most diverse Mesozoic avian clade known, and their fossilized remains have been collected from all continents except Antarctica. Avisauridae, currently known only from the New World (North and South America), is among the best known clades of enantiornithines. Several studies support its monophyly (Chiappe, 1993; Chiappe and Calvo, 1994; Sanz *et al.*, 1995), although this conclusion was not reached by Kurochkin (1996). Avisauridae comprises two Argentine species (*Neuquenornis volans* Chiappe and Calvo and *Soroavisaurus australis* Chiappe) and two named North American species (*Avisaurus archibaldi* and *A. gloriae*), as well as undescribed *Avisaurus* material (Stidham, 1998).

The origin of Avisauridae appears to have been before the middle Campanian in South America. The North American record begins in the Campanian of Montana and continues into the Maastrichtian of Montana. The sole described Campanian North

American record is the type specimen *Avisaurus gloriae*. The fauna of the Two Medicine Formation, including *A. gloriae*, is part of the Campanian Judithian North American Land Mammal Age and is thought to be time equivalent with the Judith River Formation deposited about 78 million years ago (Goodwin and Deino, 1989). Therefore, the age of the earliest record of North American avisaurids (middle Campanian) appears to be at least slightly younger than the early Campanian or older age of oldest South American avisaurid species (Dingus *et al.*, 2000). This stratigraphic and geographic distribution of *Avisaurus* parallels that of the water ferns, *Hydropteris* (Erwin, 1998), and other vertebrates (McCord, 1998) in North America.

New material

Undescribed avisaurid fossils from the Hell Creek Formation of Montana includes tarsometatarsal fragments representing one or two undescribed taxa, as well as a large distal tibiotarsus attributable to *A. archibaldi*. Additional currently indeterminate Hell Creek enantiornithine material (Stidham, 1998) may represent additional avisaurid material.

The presence of three distal tarsals in enantiornithines is confirmed by analysis of x-rays of *A.*

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archibaldi and the other Hell Creek material. The juvenile avisaurid material demonstrates an ontogenetic pattern of tarsometatarsal fusions quite different from ornithuran birds, but similar to many non-avian dinosaurs. The avisaurid tarsometatarsus did not pass through a stage in which it had a free distal tarsal cap as in ornithuran birds, and therefore avisaurid (and possibly all enantiornithine) tarsometatarsi likely represent a condition not homologous with the ornithuran tarsometatarsus.

Phylogenetic analysis of the new avisaurid material indicates monophyly of the North American material within a monophyletic Avisauridae. These results do not support Kurochkin's (1996) phylogenetic hypothesis of enantiornithine interrelationships. The Hell Creek material appears to be the sister group to *A. archibaldi* and *A. gloriae*. *Soroavisaurus* is the sister taxon to the North American avisaurids, with *Neuquenornis* as the sister to all other avisaurids. These are the same results reported by Chiappe (1993) and Varrichio and Chiappe (1995). At this point, we cannot determine if this new Hell Creek material represents two or three undescribed species of different sizes or is a growth series of one species.

Biogeography

The paraphyly of the Argentine sister taxa with respect to the monophyletic North American *Avisaurus* species points to a dispersal or vicariant event from South to North America, resolving the biogeographic ambiguity cited by Gayet *et al.* (1992). The stratigraphic data from these avian fossils suggests that this event likely occurred before the middle Campanian. This phylogeographic pattern is seen in other vertebrate clades. Within Alvarezsauridae, the Argentine *Alvarezsaurus* and *Patagonykus* are the sister taxa to the Mononykinae in North America and Asia (Chiappe *et al.*, 1996). In both of these cases, the North American members of these clades appear to have dispersed to North America (or the northern hemisphere) before the middle Campanian. The presence of mononykines in North America (Hutchinson and Chiappe, 1998), possibly even belonging to the same species as described Asian taxa may indicate that alvarezsaurids dispersed to Asia from South America by way of North America (Novas, 1996). In addition, South American titanosaurs are probably the sister taxa to the Campanian and Maastrichtian North American sauropods (Salgado *et al.*, 1997). On the other hand, hadrosaurs, ceratopsians, and ankylosaurs apparently took the opposite route (North to South America) during the Campanian (Gayet *et al.*, 1992; Salgado and Coria, 1996). This conclusion will need to be revised if the South American members of these clades

are found to belong to other clades as their phylogenetic positions with respect to North American taxa become better known. Overall, these groups and many others support the presence of a land bridge (Gayet *et al.*, 1992) between North and South America starting before the middle Campanian, since volant, ground-dwelling, and aquatic taxa of various sizes dispersed in both directions within the same interval of time before the late Campanian. This hypothesized land bridge coincides with a drop in global sea level after a late Turonian highstand and before a highstand in the middle Campanian (Haq *et al.*, 1987), possibly exposing previously submerged portions of Central America. Even with these data, the apparent absence of dispersal of other clades, notably multituberculates, eutherians, and most theropod clades, during this same interval raises questions about the selectivity of dispersal between these continents.

Environment

All currently described *Avisaurus* material is from the Hell Creek Formation and the Two Medicine Formation in Montana. The Hell Creek Formation was deposited along the western coastal plain of the Western Interior Seaway in North America. This coastal plain was forested with rivers and streams dissecting it. Other birds known from the Hell Creek Formation include hesperornithiforms and neornithines (Stidham, 1998), and they indicate that avisaurids were only a minor part of a very diverse avifauna. In contrast, the Two Medicine Formation was deposited further interior, away from the coast, with *Avisaurus gloriae* the only bird known from the formation (Varrichio and Chiappe, 1995).

Extinction

The Hell Creek enantiornithine material is latest Cretaceous in age, and is probably the youngest known enantiornithine material. Contrary to the idea of a gradual extinction of toothed bird clades through the Maastrichtian (Tokaryk, 1992), the presence of enantiornithines and other toothed bird clades (Stidham, 1998) near the K-T boundary in North America supports the possibility that they perished along with most dinosaurs in the Cretaceous mass extinction. No enantiornithines or other toothed bird clades are known from the overlying Paleocene Tullock Formation or even the Paleocene parts of the Hell Creek Formation. The presence of a relatively modern flight mechanism in avisaurids (Chiappe and Calvo, 1994) seems to eliminate poor flight capability as a possible reason for their extinction. However, as noted above, differences between

avisaurids and neornithines in their development and other aspects of their biology (Chinsamy *et al.*, 1994) may have contributed to the avisaurid and enantiornithine vulnerability to extinction. The extinction of the aquatic and terrestrial toothed sister taxa to *Neornithes* at the end of the Cretaceous points to a selectivity of extinction that did not follow strict body size, ecologic, or morphologic rules.

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