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Biogeographic histories and chronologies of derived iguanodontians

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Abstract. The geographic distributions, chronology, and phylogenetic relationships of derived iguanodontians describe a biogeographic history of active intercontinental dispersal, which is tested via comparison with eustatic sea level fluctuations. A revised phylogeny of derived iguanodontians does not support a monophyletic Iguanodontidae, and produces a lineage culminating Hadrosauridae that is first recorded in the early Late Cretaceous of both Asia and North America. This distributions suggests dispersal between Asia and North America during the Late Cretaceous. Biogeographic hypotheses describing isolation of North America during the Early Cretaceous are not supported by sea level data. Dispersal patterns among Late Cretaceous taxa are corroborated by short term regressive phases in sea levels, but no distinction can be made between hypotheses of dispersal in both directions, and repeated immigration of Asian taxa into North America.

Keywords. Cretaceous. Biogeography. Dispersal. Sea levels. Iguanodontia. Hadrosauridae.

Introduction

The purpose of this analysis is to incorporate a revised phylogeny of derived iguanodontian dinosaurs (Hadrosauriformes *sensu* Sereno, 1999) into a biogeographic and chronological history, and to test this history against concurrent sea level fluctuations. Specifically, we: (1) construct a phylogeny of derived iguanodontians; (2) use that phylogeny to augment biogeographic histories, and; (3) test both previous and new hypotheses of Early and Late Cretaceous biogeography by comparison with sea levels as an indicator of potential for dispersal. Iguanodontians are Laurasian in origin, with active dispersal and local extinctions driving trans-continental distributions (Brett-Surman, 1979; Norman 1998a). Iguanodontians dispersed into North Africa at least once prior to the mid-Aptian (Taquet and Russell, 1999), but our analysis focuses on Laurasian biogeography. Timing and direction of dispersals are not well resolved for all higher order taxa, but phylogenetic relationships and first occurrences suggest both an ancestral center of origin and a minimum timing of immigration for a lineage. Currently, however, no additional test of dispersal biogeography has been proposed.

Sea level histories can be used as an independent test of biogeographic hypotheses. On a geologic timescale, trans-continental distributions of taxa are controlled by tectonic processes, including resultant sea level fluctuations, which affect areas of emergence. Eustatic transgressive and regressive events alternately prohibit and facilitate active dispersal across seaways and landbridges. All else being equal, patterns of distribution should be correlated to sea level changes. First occurrences of hypothetical immigrants should be preceded by short- or long-term regressive events, and periods of isolation should coincide with transgressions.

Materials and methods

A phylogeny of derived iguanodontians (figure 1) was constructed from 12 taxa and 24 characters (appendix 1). Critical assumptions of our phylogeny are monophyly of Hadrosaurinae and Lambeosaurinae (Weishampel and Horner, 1990). *Claosaurus* and *Tanius* are poorly known, but their geographic and temporal distributions are significant. They were manually placed in our phylogeny, and their positions are more tentative than other taxa. The phylogeny was placed in a geographic and chronological context, and the Cretaceous eustatic sea level curves of Haq *et al.*, 1987 (figure 2) were used to test the resultant biogeographic hypotheses. We use the Western Interior Seaway as the indicator of potential dispersal and isolation because: (1) transgressive

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events including initial completion of the Seaway (102 Ma) are temporally constrained, and can be correlated to global sea levels to provide a measure of sea level required to isolate dispersal routes, and; (2) it is correlated to a well-sampled terrestrial fauna (Jacobs and Winkler, 1998).

Phylogeny and biogeography

Our phylogeny is generally consistent with published studies, with two exceptions: Our study does not support a monophyletic Iguanodontidae (Norman, 1998a), and *Eolambia* forms an unresolved trichotomy with *Probactrosaurus* and more derived taxa, as opposed to being a basal lambeosaurine (Kirkland, 1998). We have achieved only limited resolution of the interrelationships among some taxa due, in part, to both the small number of characters used in our analysis and missing data. However, this lack of resolution also mirrors controversy among more exhaustive analysis (*e.g.*, Norman 1998a, Sereno, 1999). A new taxon, the Fukui form, from Japan (?Berriasian-?Aptian) is significant because it represents the first occurrence of characteristics previously considered diagnostic of more derived clades (Kobayashi and Azuma, 1999), and because it increases the diversity of Early Cretaceous iguanodontians. The low resolution of interrelationships of *Iguanodon*, *Ouranosaurus*, *Altirhinus*, and the Fukui form limit biogeographic reconstructions. However, the phylogenetic polytomy of these taxa does not significantly alter current biogeographic hypotheses. Norman (1998a) described a history of Laurasiatic dispersal of *Iguanodon* prior to the Hauterivian, followed by North American isolation and European-Asian connection by the Aptian. Isolation of North America is considered to have persisted until the latest Albian (Kirkland *et al.*, 1997), based on North American faunal endemicity.

Systematic relationships of more derived taxa placed in a chronological and biogeographic framework represent a progressive transition series culminating in Hadrosauridae (*sensu* Forster, 1997). This grade begins with *Probactrosaurus* in the Early Cretaceous of Asia, and with early-middle Late Cretaceous *Eolambia* and *Protohadros* in North America, and with a series of Asian hadrosauroids (Godefroit *et al.*, 1998) approximately coeval with the first occurrences of Hadrosauridae in the Turonian of North America and Asia (Weishampel and Horner, 1990; Pasch, 1995). Ages of Asian hadrosauriods are ambiguous, but the first occurrence of Hadrosauridae minimally constrains divergence times (MDTs Weishampel *et al.*, 1993) of successive sister taxa to the base of the Turonian.

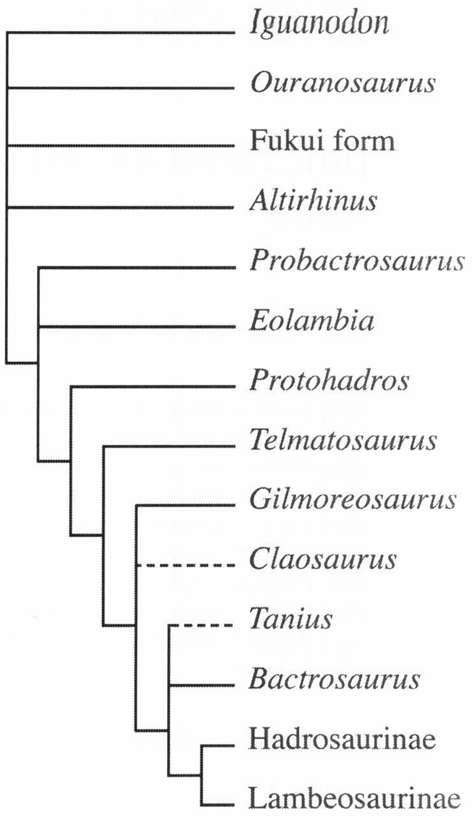

Figure 1. Strict consensus of 13 trees (tree length = 37 steps, C.I. = .70, and R.I. = .65) of ingroup relationships determined via a heuristic search in PAUP 3.1 (Swofford, 1993), exclusive of ***Tanius*** and ***Claosaurus*** (dashed lines). ***Camptosaurus***, ***Dryosaurus***, and ***Tenontosaurus*** were used as successive outgroups.

These distributions suggest a biogeographic pattern of alternating intervals of dispersal between North America and Asia from the beginning of the Late Cretaceous to the Turonian, but the directions of dispersal are not constrained. Intervals of dispersal are separated by periods of endemism and in situ evolution. Hypotheses of *in situ* evolution are supported by short phylogenetic distances that are restricted to brief periods of time, and geographic concurrence shared between *Eolambia* and *Protohadros* (and possibly *Claosaurus*) and between Gilmoreosaurus, Bactrosaurus, and *Tanius*. Geographic distributions indicate a late Early Cretaceous dispersal of *Eolambia* into North America, with subsequent divergence of *Protohadros* and *Claosaurus*, and a second migration into Asia prior to the Turonian, with subsequent divergence of hadrosauroids, followed by Hadrosauridae. The phylogenetic status of *Telmatosaurus* requires an additional dispersal back into Asia, between the first occurrences of *Protohadros* and *Claosaurus*. The systematic status of *Claosaurus* is tentative, however, and the necessity of additional dispersal into Asia can only be determined once the relative positions of *Telmatosaurus* and *Claosaurus* are resolved.

Distributions of hadrosaurids indicate Laurasian dispersals by the Turonian, followed by migration into South America by the Campanian, and Antarctica by the Maastrichtian (Brett-Surman, 1977; Case *et al.*, 1998).

Comparison with sea levels

Long- and short term trends in Cretaceous sea levels are described in figure 2. Sea levels increased during the Albian, with a maximum transgressive highstand during the Turonian. All else being equal, lowered sea levels should facilitate dispersal of terrestrial organisms, and conversely highstands should inhibit terrestrial dispersal. If these assumptions are generally true, sea level at the completion of the Western Interior Seaway, which formed a physical barrier separating eastern and western North America, can be taken as an arbitrary measure to which comparisons can be made. By this measure, sea levels prior to 102 Ma should provide access to dispersal routes, resulting in intercontinental faunal similarity. There are six intervals in the Late Cretaceous when sea levels fall below completion of the WIS, presumably reflecting intervals of greater likelihood for intercontinental dispersal, and faunas should represent alternating periods of endemicity and immigration.

Lowered Early Cretaceous sea levels are inconsistent with hypotheses of isolation and endemicity during the Early Cretaceous. We offer two alternate explanations: (1) Ecological or additional tectonic events (*e.g.*, the opening of the North Atlantic by the Hauterivian Ziegler, 1988). restricted dispersals, despite lowered sea levels; or (2) Apparent faunal endemicity is an artifact of insufficient sampling of lower Cretaceous terrestrial deposits, or comparing faunas that are not coeval. Recent discoveries of iguanodontian remains in the mid-Aptian of Texas (figure 2) (Jacobs and Winkler, 1998), as well as the range extension of the Asian ?mid-Aptian triconodont *Gobiconodon* in North America (Jenkins and Schaff,

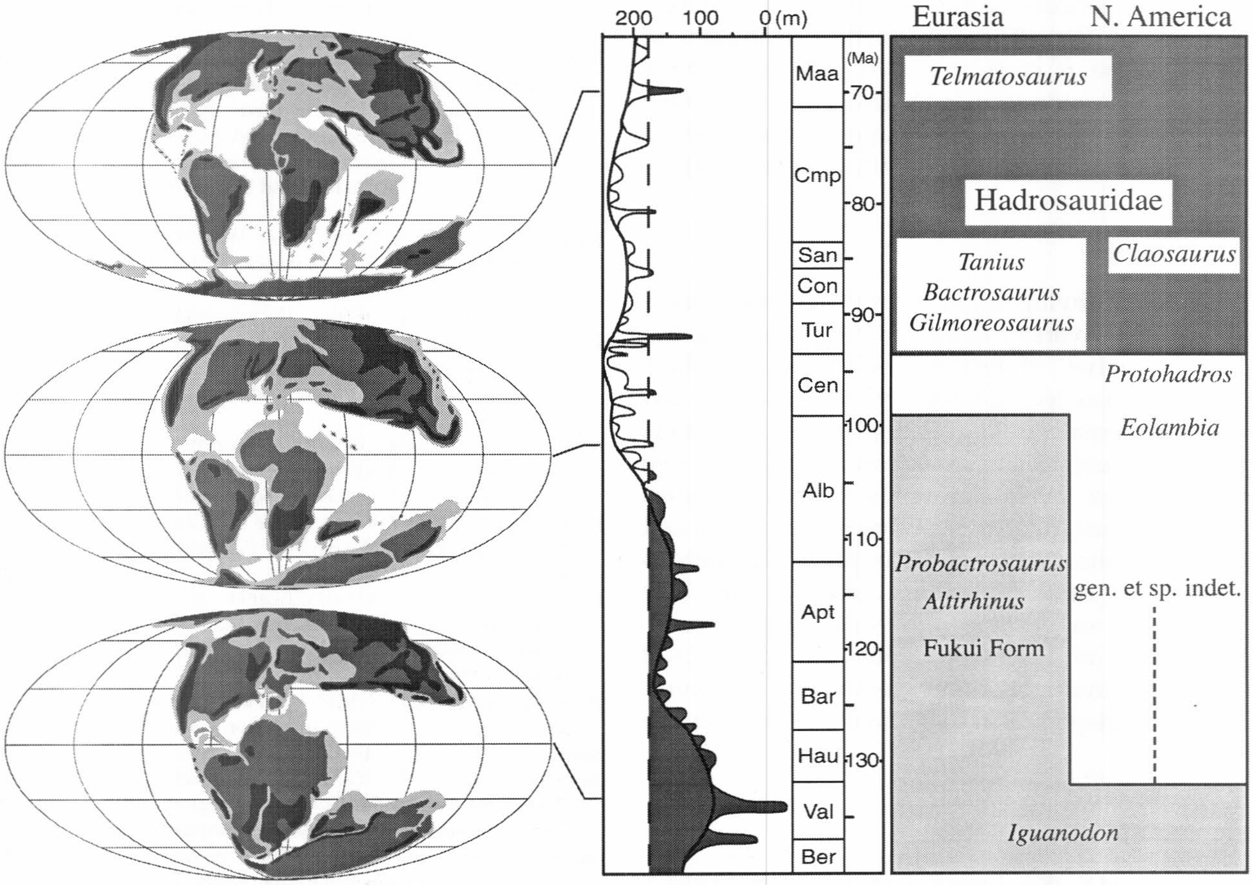

Figure 2. Temporal and geographic distributions of iguanodontians compared to PGIS (Ross, 1991) paleogeographic reconstructions and eustatic sea level curves of Haq *et al.*, 1987. Shaded regions of temporal and geographic distributions indicate known ranges for hadrosaurids (dark), and ***Iguanodon*** (light). For sea level curves, dashed line indicates sea level at completion of the Western Interior Seaway (Jacobs and Winkler, 1998), and shaded regions of short and long term curves indicate periods of open dispersal routes. For maps, darkest grey indicates highlands, medium gray indicates lowlands, lightest gray indicates continental seaways.

1988), suggests connection between Asia and North America during the Aptian, and supports the second explanation.

Application of sea level histories to Late Cretaceous iguanodontian biogeography provides temporal constraint to patterns of dispersal, indicates multiple episodes immigration, but does not necessarily support hypotheses of in situ evolution. Short term regressions preceded the first occurrences of *Eolambia*, *Protohadros*, *Claosaurus*, and Hadrosauridae (figure 2). Based on the youngest ages for *Eolambia* (98.3 Ma, Kirkland, 1998), immigration from Asia occurred prior to the 102 Ma transgression. The first occurrence of *Protohadros* (≈ 95.5 Ma) after a short term regression implies dispersal. Currently, however, there is no Asian equivalent to *Protohadros*. The occurrence and timing of *Claosaurus* is ambiguous: if basal to *Telmatosaurus*, it may be a represent a continuation of the North American record, which requires a dispersal into Asia prior to the divergence of more derived hadrosauroids. If more derived than *Telmatosaurus*, it may represent a late-surviving, immigrant hadrosauroid from Asia, with potential dispersal either concurrent with Hadrosauridae or during the Coniacian. The Laurasiatic distribution of Hadrosauridae is correlated with the pronounced Turonian regression (figure 2). This phase may have also provided dispersal routes into Central America for North American *iguanodon*tians (Horne, 1994).

Conclusions

A revised phylogeny of derived iguanodontians increases the diversity of Early Cretaceous taxa, but cannot resolve their interrelationships. Late Cretaceous taxa include both North American and Asian representatives, suggesting alternating periods of dispersal and in situ evolution between the two continents. Sea levels during the Early Cretaceous permit dispersal, despite hypotheses of isolation and endemicity. Short term regressive phases correlate to patterns of first occurrence during the Late Cretaceous, suggesting intervals of dispersal. Distributions of Late Cretaceous taxa may result from either multiple Asian dispersals into North America, or dispersals in both directions between the continents.

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APPENDIX 1

Characters and data matrix used in phylogenetic analysis. Characters and states 1- 16 are from Head (1998- minus characters 4, 7, 12, and 20). Additional states are from sources in Appendix 1 of Head (1998), and the following: Fukui form (Kobayashi and Azuma, 1999); *Altirhinus* (Norman, 1998a); *Probactrosaurus* (Norman, 1998b); *Eolambia* (Head, 1999); *Bactrosaurus* (Godefroit *et al.*, 1998). *Claosaurus* and *Tanius* (Fig. 1) are based on Carpenter *et al.* (1995), and Wiman (1929), respectively. Characters 17-24 are from Weishampel and Horner, 1990; Norman, 1998a; Sereno, 1999; and Kobayashi and Azuma, 1999. They are: 17) Secondary surangular foramen (Present=0, Absent=1); 18) Dental battery extends posteriorly beyond coronoid (A=0, P=1); 19) Eight or more sacral vertebrae (A=0, P=1); 20) Prominent iliac antitrochanter (A=0, P=1); 21) Femoral anterior intercondylar groove fully enclosed (A=0, P=1); 22) Conical pollex spike (A=0, P=1); 23) Well-developed, discrete iliac postpubic process (A=0, P=1); 24) Elongate "finger-like" jugal process of the maxilla (A=0; P=1).

			10	20	
Iguanodon	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 1 0 0 0	0 1 0 1
Ouranosaurus	1 0 0 1 0	0 0 0 0 1	0 0 0 0 0	0 0 0 0 0	0 1 0 1
Fukui form	0 0 1 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 ? ?	0 ? ? 0
Altirhinus	0 0 0/?00	0 0 0 0 1	1 0 0 0 0	0 0 0 0 1	? 1 0 1
Probactrosaurus	0 0 0 0 ?	? ? ? ? 0	1 1 1 0 0	0 ? 0 0 ?	0 1 ? 0
Eolambia	0 0 0 0 0	0 ? 0 0 0	1 1 1 0 0	0 0 0 0 0	0 ? 0 0
Protohadros	1 0 1 0 0	0 1 0 0 1	1 1 1 0 0	0 1 0 0 ?	? ? ? 0
Telmatosaurus	0 0 1 0 1	0 1 1 1 0	1 1 1 0 0	0 1 0 0 ?	1 ? ? 0
Gilmoreosaurus	? ? 1 ? ?	0 ? ? ? 0	1 1 1 0 1	0 ? 0 0 1	1 ? 1 0
Bactrosaurus	0 1 1 0 1	0 ? 1 1 0	1 1 1 0 1	0 1 1 0 1	1 0 1 0
Hadrosaurinae	1 0 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 0 1 0
Lambeosaurinae	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 0 1 0