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INSIDE

Ruling Reptiles and Wandering Continents: A Global Look at Dinosaur Evolution

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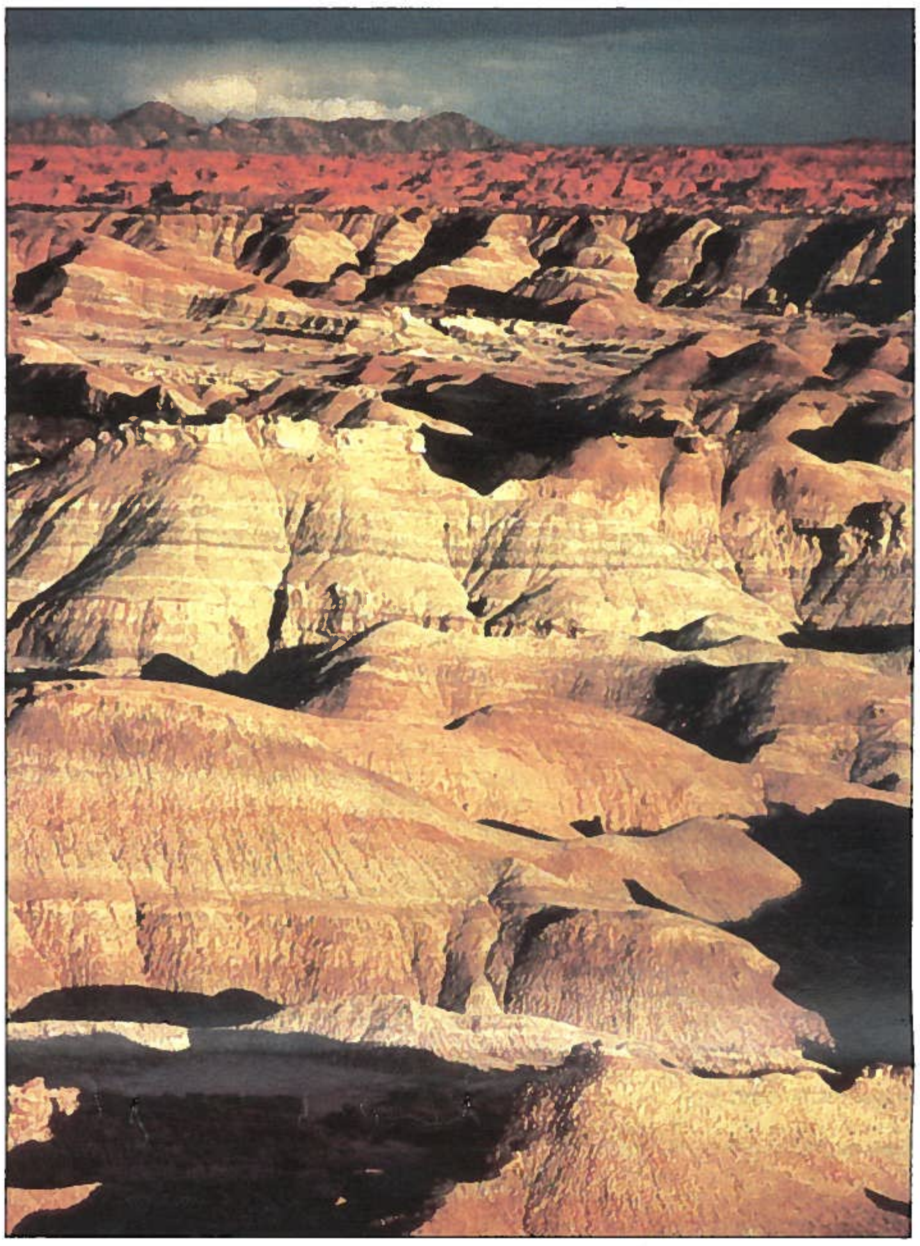
ABSTRACT

As Pangaea rifted apart during the latter half of the Mesozoic, dinosaurs dominated all land habitats and evolved into an extraordinary array of land and aerial forms. This mobile episode in Earth history provides a unique opportunity to study the evolution of animal form and diversity during a prolonged period of biogeographic fragmentation. Dinosaurs and their avian descendants belong to a larger clade of reptiles called ornithodirans that were the first vertebrates to evolve bipedal locomotor posture. Although the advent of bipedalism in the Middle Triassic may have promoted the evolution of the first vertebrate powered fliers, the pterosaurs, it cannot be invoked to explain the subsequent dinosaur radiation, which appears to have been an opportunistic, rather than competitive, faunal replacement. The aim of the current research is to provide a unified hypothesis of dinosaur descent for about 200 of the most completely known dinosaur species and temporally calibrate the branch points of this phylogeny. The calibrated phylogeny can then be used to detect missing lineages, to map major speciation events, to track parallel evolution in multiple lineages, and to investigate biogeographic history. Recent discovery of an ancient sparrow-sized fossil bird in China documents the early appearance of anatomical features associated with sustained powered flight and perching that bridge the gap between *Archaeopteryx* and the common ancestor of living birds. Much of the deep branching history that gave rise to the great diversity of living birds must have occurred before the extinction of the dinosaurs, and this ancient heritage can be reconstructed from both anatomical and genetic evidence in living birds.



Fossiliferous overbank deposits of the Ischigualasto Formation in northwestern Argentina.

INTRODUCTION

Perhaps more than the bones of ancient humans, dinosaurs stir popular interest in the fossil record. Today we are inundated with dinosaur encyclopedias and dictionaries, dinosaur lunch boxes and cups, dinosaur models and robots, and dinosaur cookies and spaghetti. Museums trumpet their newest dinosaur displays, now with groaning, lurching latex replicas. The driving force behind dinosaur appeal and the multimillion-dollar industry it has spawned may be simply our fascination—as moderate-sized mammalian endotherms—with extinct beasts of ponderous proportions that appear strangely "reptilian."

Public fanfare about dinosaurs, ironically, has cast a shadow over dinosaurs as legitimate and unique subjects for scientific inquiry. Dinosaurs are kids' stuff, after all. Do they merit serious scientific investigation beyond mere naming and description of new species? Could dinosaur skeletons in the museums of the world really help resolve any fundamental paleontological questions?

When dinosaurs first dominated land habitats in the Late Triassic about 225 Ma, most of Earth's land surfaces were joined as Pangaea. As the supercontinent rifted apart, dinosaurs evolved into an extraordinary array of land and aerial forms. This mobile, creative episode in Earth history provides a unique opportunity to study the evolution of animal form and diversity during a prolonged period of biogeographic fragmentation. Abundant dinosaur remains from every continent record a land-based vertebrate radiation from its origin and rise to dominance to its ultimate demise.

TRACING BIRD AND CROCODILE LINEAGES

Dinosaur origins have remained unnecessarily mysterious and conjectural for more than a century. Dinosaurs and their avian descendants belong to a larger clade of reptiles, the Archosauria, that also includes living crocodilians. Both dinosaur-avian and crocodilian lineages are easily traced back to the Late Triassic, where they are joined by a variety of closely related Triassic forms traditionally grouped together as "thecodonts." The key to understanding dinosaur origins lay in unraveling the "thecodont" plexus by aligning these early archosaurs with either the dinosaur-avian or crocodilian lineages (Gauthier, 1986). By application of quantitative cladistic analysis, the timing and sequence of anatomical associated functional transformations that presaged the dinosaur radiation can be evaluated (Fig. 1; Sereno and Arcucci, 1990; Sereno, 1991).

During the Middle Triassic, archosaurs split into dinosaur-avian and crocodilian clades (Sereno and Arcucci, 1991). The crocodilian clade, Crurotarsi, evolved a peculiar ball-and-socket ankle joint between the proximal tarsals (calcaneum and astragalus) which persists with little alteration in living crocodiles. The dinosaur-avian clade,

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President Curtis Dies

Doris M. Curtis, 1991 president of the Geological Society of America, died May 26, 1991. Vice-president E-an Zen made the following announcement

With a deep sense of sadness and loss, I announce the death of President Doris Curtis. Doris went into the hospital in Houston, Texas, in March for what was expected to be a routine course of medical treatment for leukemia. The treatment went well, but she developed pneumonia, and the destruction of her immune system defied medical efforts. She died peacefully in her sleep in the early morning of Sunday, May 26. She was 77 years old.

President Curtis was very much involved in the affairs of the GSA right to the end. Her last request to the headquarters was for a GSA poster with the signatures of the entire staff; she had this placed on the wall so that she could see it from her bed. She told her visitors, "They are all here with me." Doris Curtis's commitment to the Society, to the profession, and to the application of geology to the welfare of our nation was deep and active. She worked relentlessly to make geology more accessible to the users of such information, and she nurtured the Committee on Geology and Public Policy. The advocacy program is now a major part of our collaborative effort with the American Geological Institute, and Doris's last official act as President was to sign a letter, prepared by the Council, that addressed the issue of the importance of geologic mapping on a national scale.

As we face the loss of our president, let us remember what she valued in life—professional excellence and dedication to its societal applications. So, let us celebrate her life rather than mourn her death. We have been fortunate to have had Doris Curtis as our president since last October. ■

Contributions in honor of Doris M. Curtis may be made to the GSA Foundation, 3300 Penrose Place, P.O. Box 9140, Boulder, CO 80301.

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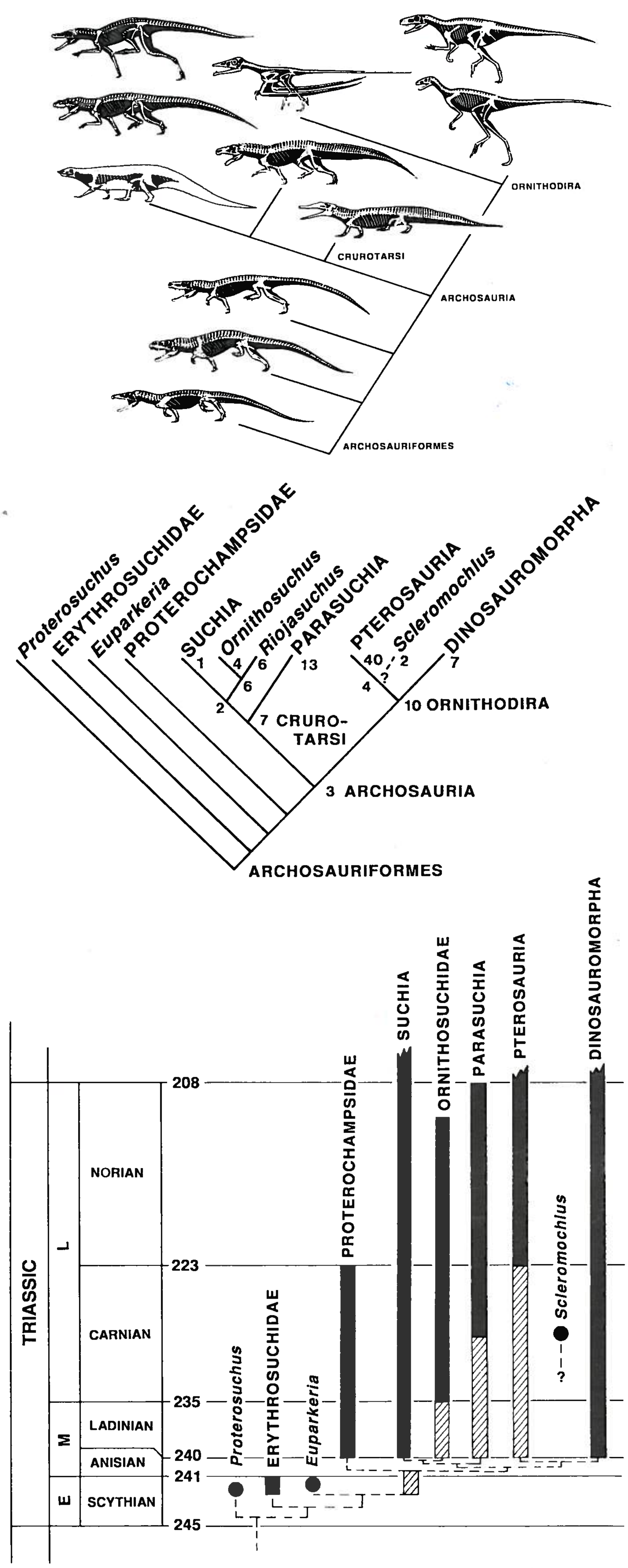

Figure 1. Cladograms (top) and corresponding calibrated tree (bottom) of extinct archosauriforms showing the divergence of the dinosaur-avian lineage (*Herrerasaurus*, top right) from the crocodilian lineage (*Pseudhesperosuchus*, top left) (from Sereno, 1991).

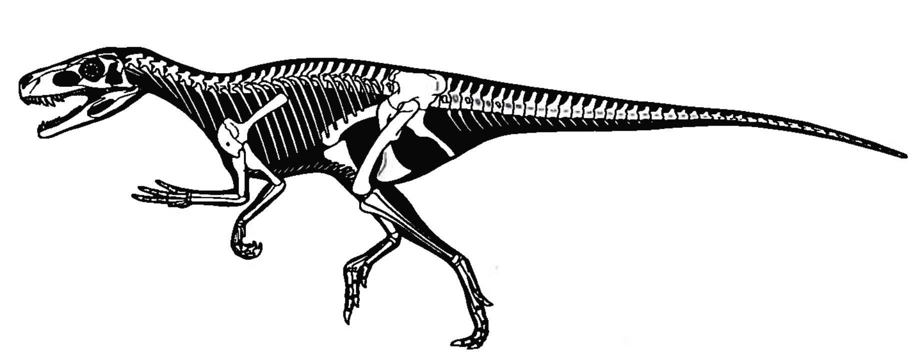

Figure 2. Reconstruction of the skeleton of the earliest dinosaur *Herrerasaurus ischigualastensis*. Overall length is about 3 m.

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Ornithodira, includes as basal offshoots the pterosaurs and small-bodied dinosaur precursors. Ornithodirans were the first vertebrates to evolve a bipedal locomotor posture, which utilizes only the hind limbs for propulsion. Bipedal locomotion appears to have loosened functional constraints on the forelimbs, which were rapidly modified as wing supports in pterosaurs, the first vertebrate powered fliers.

The earliest dinosaurs were erect bipeds characterized by a suite of modifications in the hand, hip, and ankle, some of which have been invoked as causal factors for the subsequent dinosaur radiation (Bakker, 1971; Charig, 1972; Carrier, 1987). But these small postcranial adjustments do not support a model of superior performance. Living animals with erect locomotor posture, high metabolic rates and the capacity for stamina, such as most birds and mammals, do not perform more efficiently at slow speeds than quadrupedal sprawlers such as lizards (Bennett, 1985). During the Late Triassic, erect dinosaurs coexisted for millions of years alongside more abundant sprawling or semi-erect reptiles, such as rhynchosaurs and early synapsids. The dinosaur radiation at the end of the Triassic postdates the extinction of rhynchosaurs and synapsids and thus appears to be an opportunistic, rather than competitive, replacement (Benton, 1983, 1987).

TRACKING THE FIRST DINOSAUR

Evidence of the earliest dinosaurs was based on two fragmentary postcranial skeletons discovered more than 30 years ago, one in the Ischigualasto Formation of northwestern Argentina (photo, p. 141) and the other in the Santa Maria Formation of southeastern Brazil (Reig, 1963; Colbert, 1970). These dinosaurs, *Herrerasaurus* and *Staurikosaurus*, respectively, did not fit well with either of the two major dinosaur clades, Saurischia and Ornithischia. Rather, they represent a short-lived radiation at the base of Dinosauria. Recent work in the Ischigualasto Formation has uncovered the first complete remains of *Herrerasaurus*, a 12–15-foot-long bipedal predator (Fig. 2). The lightly constructed skull has a well-developed joint at mid-length along the lower jaw designed for flexing around struggling prey (Fig. 3). The forelimbs are short and the manus (hand) is characterized by a partially opposable pollex and large unguals on the inner three digits for subduing prey.

The new material from Argentina provides the first complete picture of an early dinosaur. The succession of vertebrate horizons in the fossiliferous Ischigualasto Formation and overlying Los Colorados Formation document the transition from Carnian rhynchosaur-synapsid–dominated faunas to Norian faunas with prosauropods, theropods, and the first mammals (Bonaparte, 1982).

RECONSTRUCTING DINOSAUR DESCENT

Although nearly half of currently known dinosaur species have been described in the past 20 years (Weishampel et al., 1990), a more important development has been the recent emergence of cladistic hypothe-

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Figure 3. Skull of the early dinosaur *Herrerasaurus ischigualastensis* discovered in the Carnian Ischigualasto Formation in 1988 by a joint American-Argentine team.

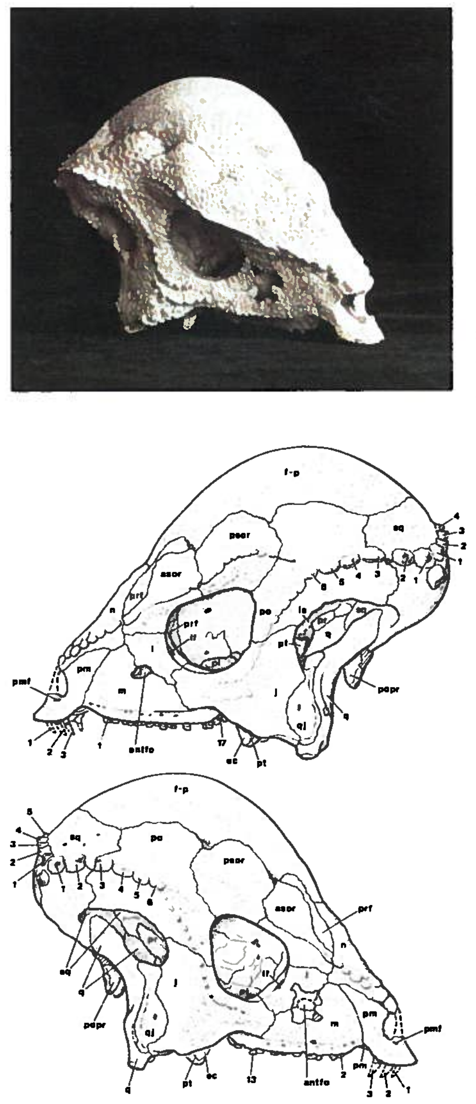

Figure 4. Skull of the Maastrichtian pachycephalosaur *Prenocephale prenes* from the Gobi Desert of Outer Mongolia. *Prenocephale* shows the linear cranial ornamentation that characterizes all pachycephalosaurs and the extreme doming of the skull roof that characterizes a subset of advanced pachycephalosaurs. Character information from specimens like this is analyzed to reconstruct dinosaur descent.

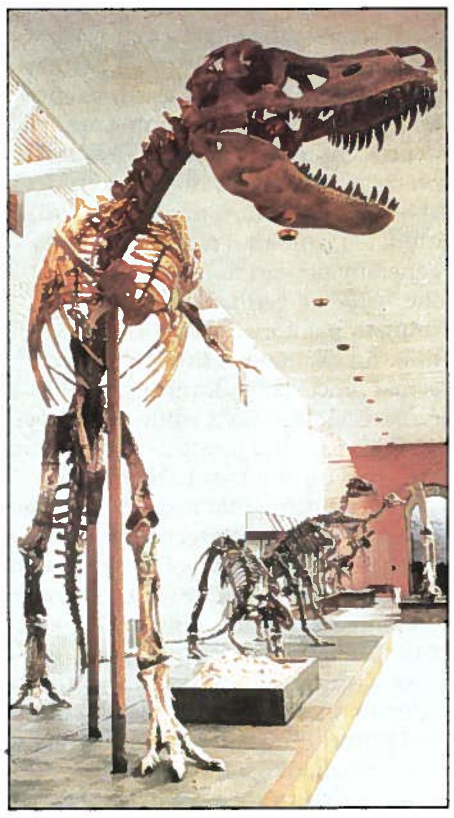

Figure 5. Large tyrannosaurid theropod *Tarbosaurus bataar* at the Paleontological Institute in Moscow. *Tarbosaurus*, a close relative of the North American *Tyrannosaurus*, is exemplary of the large-skulled predators that were restricted to the northern continents during the Late Cretaceous.

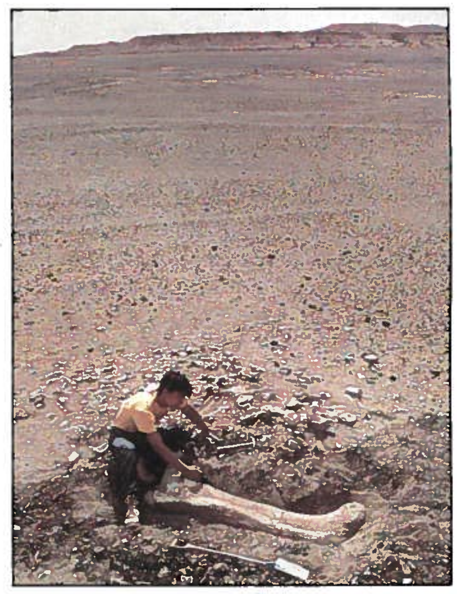

Figure 6. Author Sereno uncovering the femur from a skeleton of a new sauropod dinosaur in Neocomian beds in Niger during a joint British-American expedition in December 1990. Little is known about the sauropods of Africa and the biogeographic history of sauropods on the southern continents.

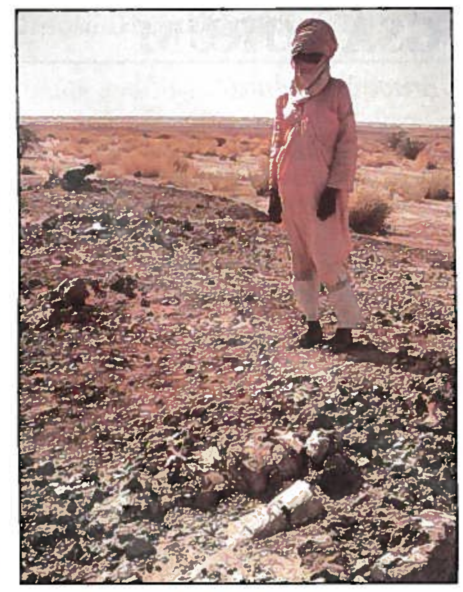

Figure 7. Tuareg tribesman standing over the partially exhumed skeleton of a large sauropod dinosaur in Neocomian beds in Niger during a joint British-American expedition in December 1990.

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ses that outline dinosaur phylogeny (Gauthier, 1986; Sereno, 1986). One aim of the current research is to provide a unified hypothesis of dinosaur descent for about 200 of the most completely known dinosaur species. The branching pattern and sequence of anatomical transformations is calculated by computer-assisted cladistic analysis of an extensive character/taxon database (Fig. 4). The phylogeny is calibrated temporally by determining the minimum age of divergence for each branch point in the tree. Most evolutionary interpretations depend on a calibrated phylogeny, if only acknowledged implicitly. The phylogeny can be used to detect missing lineages, to calculate the completeness of the fossil record, to date major speciation events, to track parallel evolution in multiple lineages, and to investigate biogeographic history.

The evolution of body size is an interesting example. When body size is mapped onto dinosaur phylogeny, a strong trend toward increasing body size is apparent in many lineages. Although there are several instances when body size must have decreased rapidly, there is only one subgroup (ceratosaurian theropods) that shows a trend (more than a single step) toward smaller body size. In this way the timing of body size increase and its relation to skeletal transformation can be studied in more detail.

Coevolution between feeding mechanisms in dinosaurian herbivores and plants is particularly interesting in light of the mid-Cretaceous transition to angiosperm-dominated floras. Unconstrained by a rigid replacement scheme as occurs in mammalian tooth rows, dinosaur dentitions were free to increase the length of the tooth row and speed of tooth replacement in response to increased tooth wear. Three groups of dinosaurian herbivores (diplodocids, hadrosaurids, ceratopsids) independently evolved rapid tooth replacement, several new crowns being stacked beneath each functioning crown. Hadrosaurids and ceratopsids independently evolved tooth batteries that have a single continuous wear surface on each jaw formed by a patchwork of interlocking crowns. The simultaneous appearance at the beginning of the Late Cretaceous of tooth batteries in large-bodied herbivores and of angiosperm-dominated floras strongly suggests plant-herbivore coevolution (Wing and Tiffney, 1987; Weishampel and Norman, 1989; Lidgard and Crane, 1990).

DINOSAURS AND ISLAND CONTINENTS

Tectonic fragmentation of Pangaea during the latter half of the Mesozoic offers a unique opportunity to compare vicariant and dispersal models of biogeographic differentiation on a continental scale. Are plate dynamics reflected in the phylogenesis of major dinosaur clades in the latter half of the Mesozoic? Where and when did intercontinental land connections permit dinosaur dispersal? And how did continental differentiation or climate influence dinosaur diversity?

The initial split of Pangaea into Laurasia and Gondwana resulted in the evolution of distinct ornithischian and saurischian faunas on each landmass during the Cretaceous, with hadrosaurs, ceratopsids, and tyrannosaurids (Fig. 5) predominating on Laurasia and titanosaurid sauropods and ceratosaurs occupying Gondwana (Figs. 6, 7; Bonaparte and Kielan-Jaworowska, 1987). Continental fragmentation during the Early Cretaceous (Fig. 8) isolated dinosaur faunas on each major land mass. The biogeographic relations among taxa within various dinosaur clades should show either replicate patterns corresponding to continental fragmentation or evidence of dispersal across transitory land bridges or oceanic barriers.

Evidence for dispersal between land masses in the Late Cretaceous abounds when dinosaur phylogenesis is carried to the generic or species level. Asian and North American dinosaur faunas of the Late Cretaceous do not share a single species in common, despite broad similarities in faunal composition at higher taxonomic levels. A cladogram depicting the relations of pachycephalosaurs and ceratopsians (Fig. 9) shows an alternating pattern of biogeographic relations that can only be explained by multiple dispersal events across Beringia with subsequent differentiation on the opposing land mass. The same pattern of dispersal is supported by several other contemporaneous ornithischian and saurischian clades.

EARLY EVOLUTION OF AVIAN FLIGHT AND THE DEEP BRANCHING HISTORY OF LIVING BIRDS

The past 15 years have witnessed two principal conceptual advances in the understanding of the origin and early evolution of birds. First, birds were placed in proper phylogenetic context as dinosaurian descendants with close affinity to advanced theropod dinosaurs (Ostrom, 1976; Cracraft, 1986; Gauthier, 1986), a realignment with a remarkable historical precedent (Huxley, 1868). Second, the best known Mesozoic birds—*Archaeopteryx, Hesperornis*, and *Ichthyornis*—have been reviewed and positioned as successive sister taxa to living birds, or Neornithes (Martin, 1983; Cracraft, 1986). Thus, a framework for the early evolution of Aves has emerged.

The avian fossil record is almost barren during the first third of avian history—a 50 m.y. interval between *Archaeopteryx* (Fig. 10) in the latest Jurassic and *Hesperornis* and *Ichthyornis* in the Late Cretaceous. The recent discovery of an articulated fossil bird about 10 to 15 m.y. younger than *Archaeopteryx*, has opened a new window on early avian evolution (Fig. 11). The sparrow-sized skeleton is preserved in the fine-grained sediment of a freshwater lake, with associated plant, insect, and fish remains.

The fossil bird documents the very early appearance of anatomical features associated with sustained powered flight and perching that are absent in Archaeopteryx (Rao and Sereno, 1990; Ruben, 1991). Modifications for sustained flight include a strut-shaped coracoid that braces the shoulder joint against an ossified sternum during flight, a modified V-shaped wrist bone (ulnare) that allows tight folding of the wing during the flight stroke, and a reduced, coossified tail bone (pygostyle) that holds tail feathers for flight stability and landing (Fig. 11). The Chinese bird was arboreal, with extremely slender recurved unguals and a fully reversed hallux for perching (Fig. 12). Other characters establish the fossil avian as the second most primitive bird next to *Archaeopteryx*, such as the presence of toothed jaws, ossified stomach ribs (gastralia), and a pelvis with a footed pubis reminiscent of the ancestral theropod condition.

The principal groups of living birds, such as ratites, loons, pelicans, penguins, and songbirds, to name a few, must have diverged before the end of the Mesozoic (Olson, 1985) in

Dinosaurs *continued on p. 145*

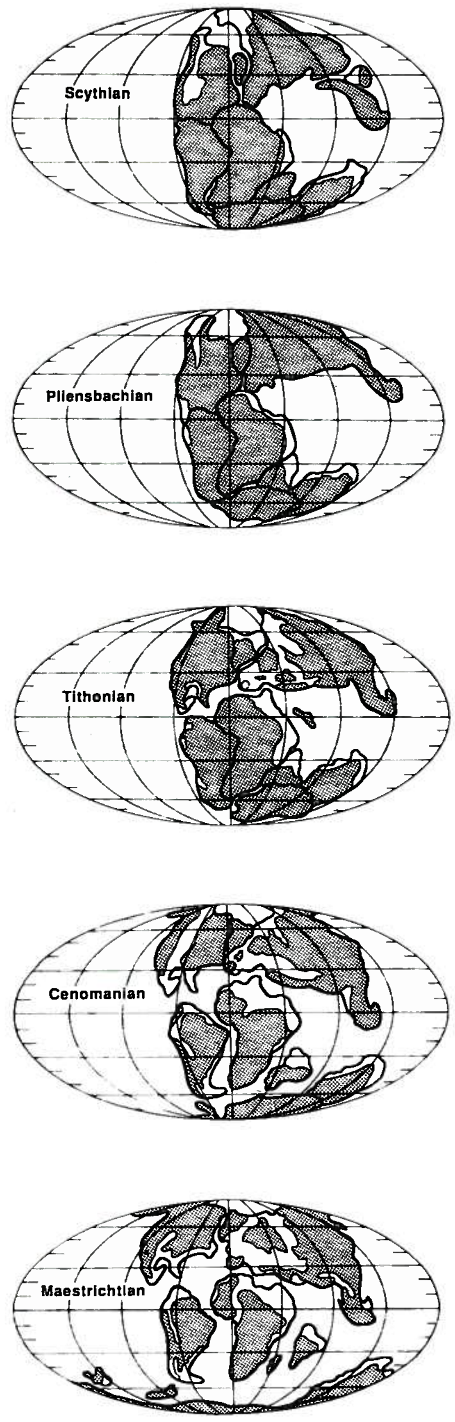

Figure 8. Paleogeographic maps showing exposed land surfaces (stipple) for several Mesozoic stages that span the origin and evolution of dinosaurs (after Zeigler et al., 1983).

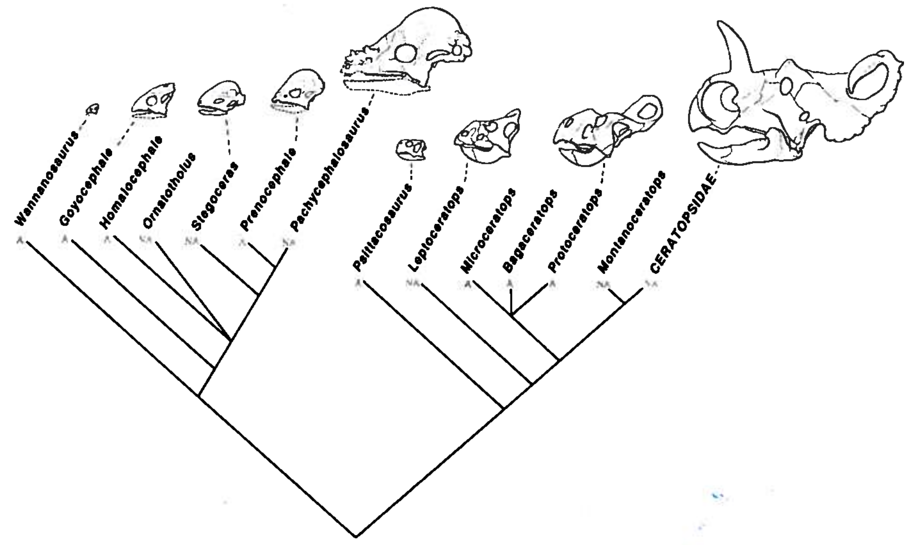

Figure 9. Cladogram showing the relations among pachycephalosaur and ceratopsian dinosaurs; known paleogeographic ranges are indicated below scaled skull profiles (A = central Asia; NA = western North America). A dispersal route across Beringia could account for the alternating biogeographic areas for the species in each group. The scaled skull profiles show the increase in body size that characterizes many dinosaurian subgroups.

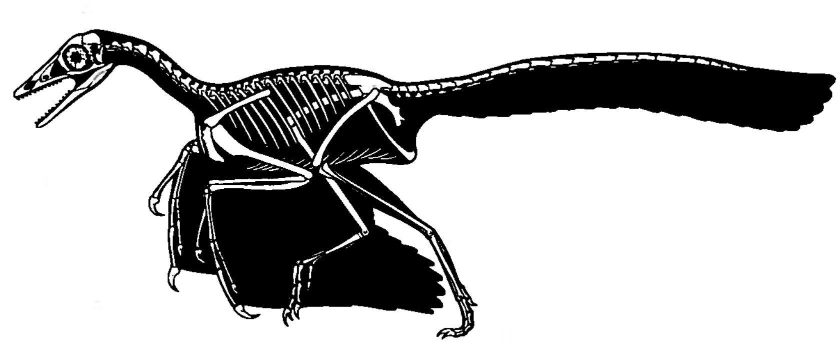

Figure 10. Reconstruction of the ancient dinosaur-bird *Archaeopteryx lithographica*, running. Archaeopteryx was capable of powered flight, as evidenced by aerodynamic flight feathers, but it apparently could not fold its forelimb during flight or resting as modern birds do.

Figure 11. Reconstruction of a newly discovered 125 million-year-old fossil bird, in flight, from Liaoning Province in northeastern China. The presence of an elongate coracoid buttress to an ossified sternum suggests the presence of significant flight musculature. The wrist joint is capable of tight folding as occurs in the flight stroke of modern birds. The shortened tail bone (pygostyle) provides attachment for stabilizing tail feathers and shifts the center of balance from the pelvic girdle to the pectoral girdle for sustained flight.

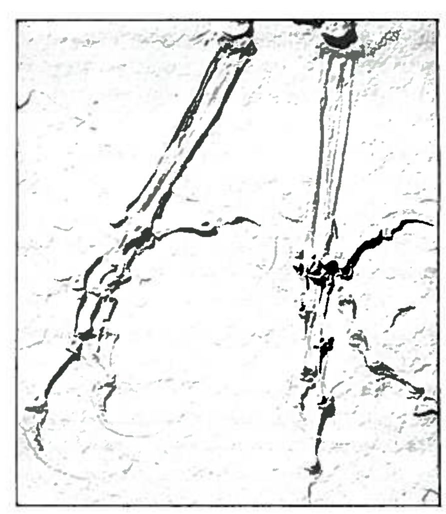

Figure 12. Epoxy cast of perching feet of the new Chinese bird, showing the reversed position of the hallux and the extremely slender, recurved unguals.

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the last great radiation of the dinosaur-avian clade. Most Cretaceous and Paleogene avian fossils, although usually quite fragmentary, can be aligned with extant subgroups, suggesting that the principal skeletal variation among major groups of living birds arose, perhaps during a relatively short interval, before the end of the Mesozoic. Cladistic surveys of anatomical variation among living birds is very preliminary (Cracraft, 1988). Molecular techniques that measure overall sequence similarity of genomic components between species, such as DNA-DNA hybridization (Sibley and Ahlquist, 1991), have been used to construct composite phylogenies (phenograms), but this technique may not be able to resolve the deep branching history of living birds. My laboratory is currently obtaining DNA sequences from the mitochondrial genome of species from disparate avian subgroups. Sequence information, in combination with new DNA hybridization studies and cladistic evaluation of anatomical characters, will shed light on these early branching events.

ACKNOWLEDGMENTS

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Editor's Note:
This article is the second of several that we will publish in which Packard Fellows in earth science report on research in their field. See p. 117 of the June 1991 issue of *GSA Today* for more information.

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