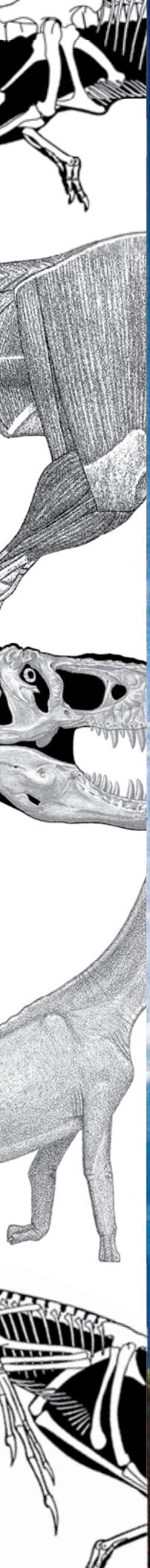
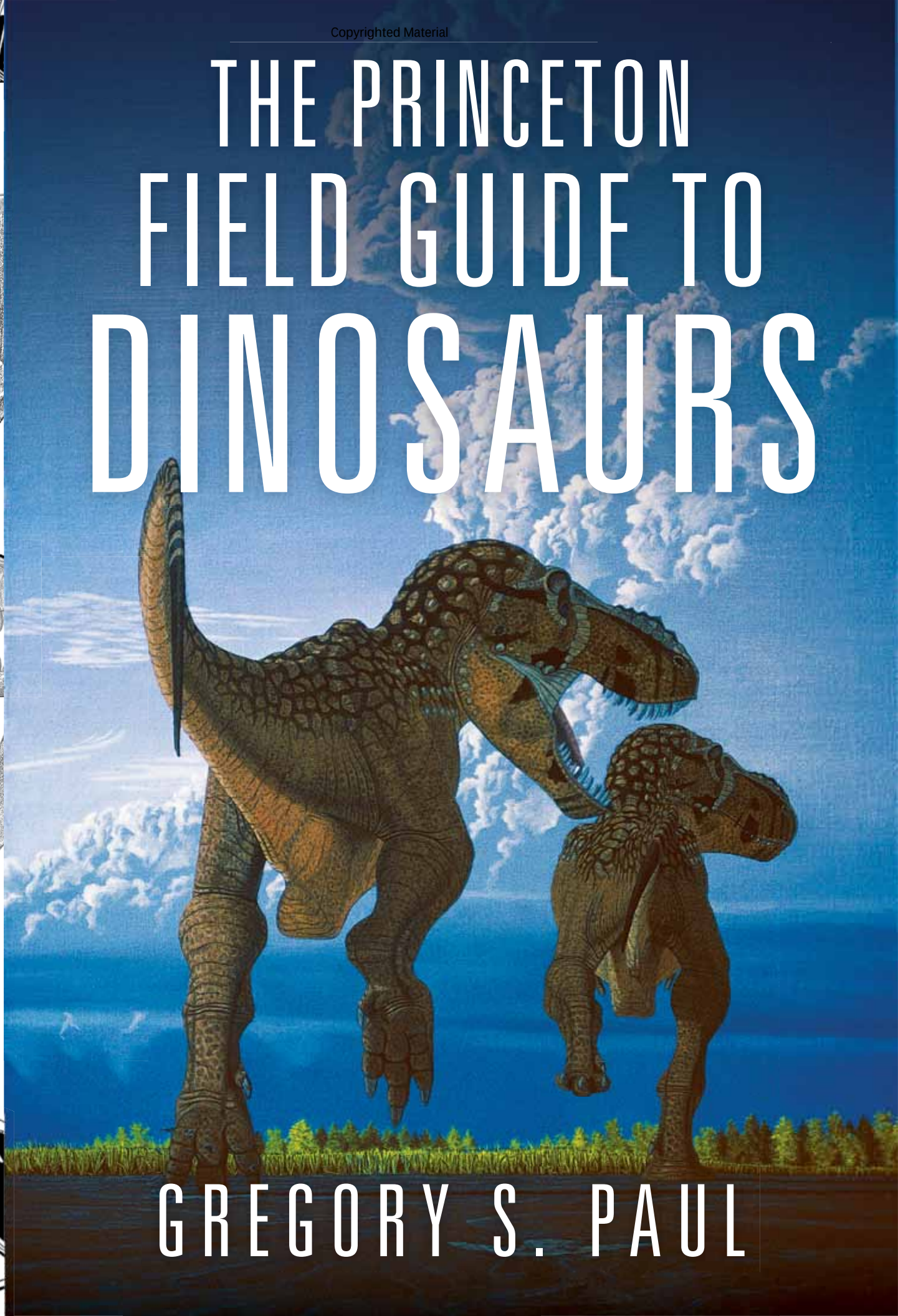
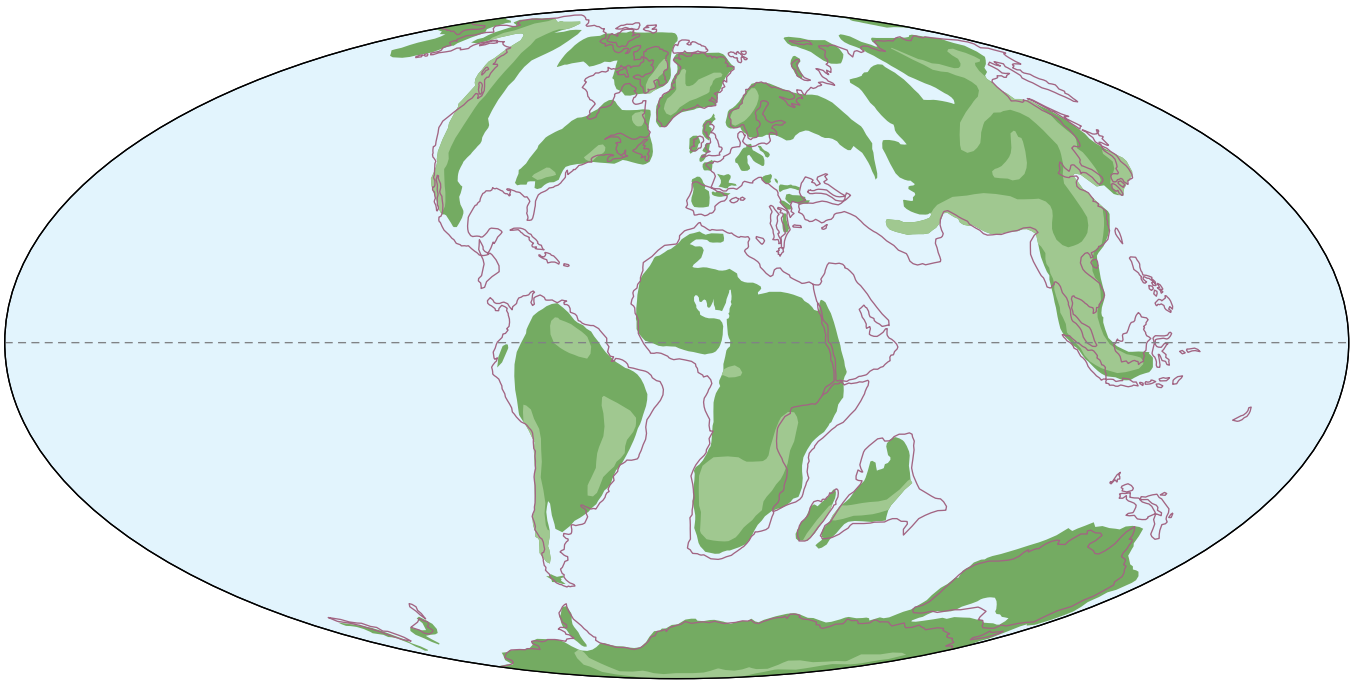
THE PRINCETON FIELD GUIDE TO DINOSAURS

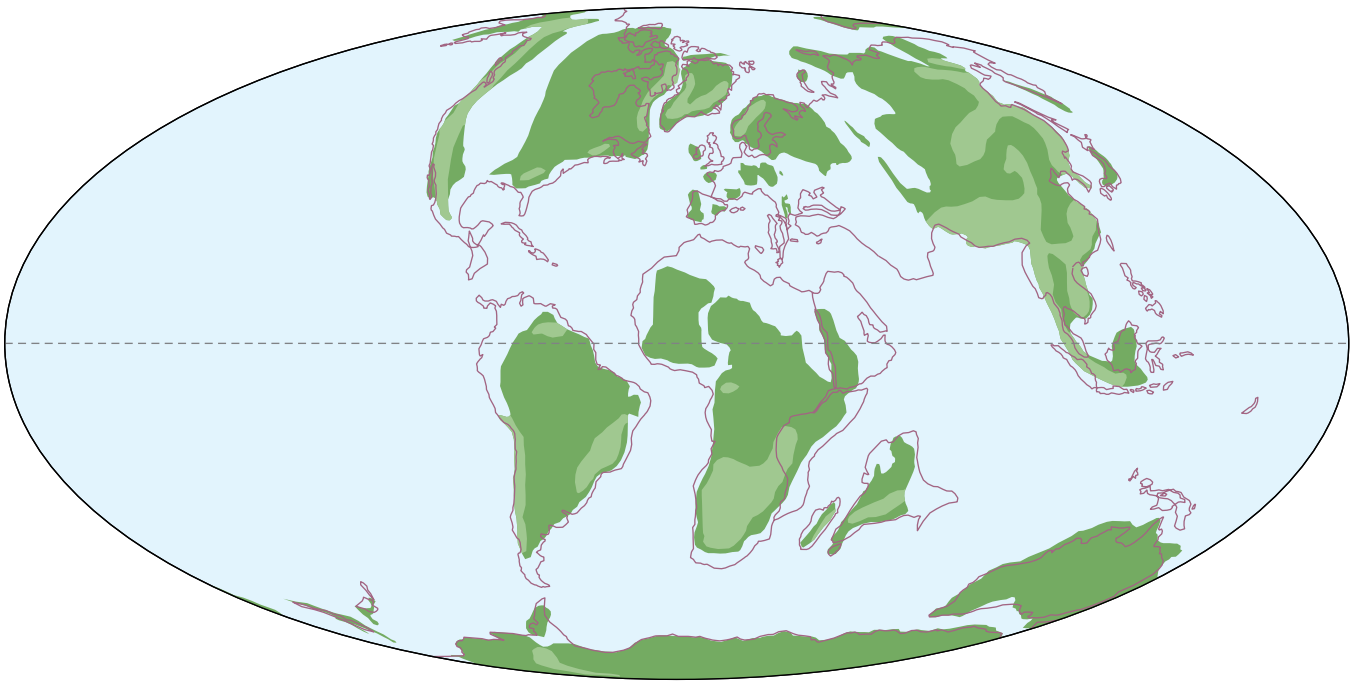




GREGORY S. PAUL



Late Cretaceous (Coniacian)



Late Cretaceous (Campanian)

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cultural revolution, Chinese paleontologists made major discoveries, including the first spectacularly long-necked mamenchisaur sauropods. As China modernized and Mongolia gained independence, Canadian and American researchers have worked with their increasingly skilled resident scientists, who have become a leading force in dinosaur research. It was finally realized that the oviraptors found associated with nests at the Flaming Cliffs were not eating the eggs but brooding them in a preavian manner. Almost all of China is productive when it comes to dinosaurs, and after many decades paleontologists started paying attention to the extraordinary fossils being dug up by local farmers from Early Cretaceous lake beds in the Northeast of the nation.

In the mid-1990s complete specimens of small compsognathid theropods labeled *Sinosauropteryx* began to show up with their bodies covered with dense coats of bristle protofeathers. It has just been realized that it is possible to determine the color of the feathers! This was just the start: the Yixian beds are so extensive and productive that they have become an inexhaustible source of beautifully preserved material as well as of strife as the locals contend with the authorities for the privilege of excavating the fossils for profit versus science. The feathered dinosaurs soon included the potentially oviraptorosaur *Caudipteryx*, the tail fan of which may be one of only two cases in which part of a dinosaur's color pattern is preserved. Even more astonishing have been the Yixian dromaeosaurs. These small sickle claws bear fully developed wings not only on their arms but on their similarly long legs as well. This indicates that dromaeosaurs not only first evolved as fliers but that they were adapted to fly in manner quite different from the avian norm. The therizinosaur *Beipiaosaurus* has a wild array of display feathers that contribute to its looking like a refugee from a Warner Brothers' cartoon. But the Yixian is not just about confirming that birds are dinosaurs and that some dinosaurs were feathered. One of the most common dinosaurs of the Early Cretaceous is the parrot-beaked *Psittacosaurus*. Although it was known from numerous skeletons across Asia found over the last eighty years, no one had a clue that its tail sported large arcing bristle spines until a complete individual with preserved skin was found in the Yixian. To top things off, the Yixian has produced the small ornithischian *Tianyulong*, which suggests that insulating fibers were widespread among small dinosaurs. There are new museums in China packed with enormous numbers of undescribed dinosaur skeletons on display and in storage.

On a global scale, the number of dinosaur trackways that have been discovered is in the many millions. This is logical in that a given dinosaur could potentially contribute only one skeleton to the fossil record but could make innumerable footprints. In a number of locations trackways are so abundant that they form what have been called "dinosaur freeways." Many of the trackways were formed in a manner that suggests their makers were moving in herds, flocks, packs, and pods. A few may record the attacks of predatory theropods on herbivorous dinosaurs.

The history of dinosaur research is not just one of new ideas and new locations; it is also one of new techniques and technologies. The turn of the twenty-first century has seen paleontology go high tech with the use of computers for processing data and high-resolution CT scanners to peer inside fossils without damaging them. Dinosaurology has also gone microscopic and molecular in order to assess the lives of dinosaurs at a more intimate level, telling us how fast they grew, how long they lived, and at what age they started to reproduce. Bone isotopes are being used to help determine dinosaur diets and to state that some dinosaurs were semiaquatic. And it turns out that feather pigments can be preserved well enough to restore original colors.

The evolution of human understanding of dinosaurs has undergone a series of dramatic transformations since they were scientifically discovered almost two hundred years ago. This is true because dinosaurs are a group of "exotic" animals whose biology was not obvious from the start, unlike fossil mammals or lizards. It has taken time to build up the knowledge base needed to resolve their true form and nature. The latest revolution is still young. When this researcher and artist was young, he learned that dinosaurs were, in general, sluggish, cold-blooded, tail-dragging, slow-growing, dim-witted reptiles that did not care for their young. The idea that some were feathered and that birds are living descendents was beyond

The flying dinosaur *Sinornithosaurus* attacking *Psittacosaurus*.

imagining. Dinosaur paleontology has matured in that it is unlikely that a reorganization of similar scale will occur in the future, but we now know enough about the inhabitants of the Mesozoic to have the basics well established. Sauropods will not return to a hippo-like lifestyle, and dinosaurs' tails will not be chronically plowing through ancient muds. Dinosaurs are no longer so mysterious. Even so, the research is nowhere near its end. To date over six hundred valid dinosaur species in about four hundred genera have been discovered and named. This probably represents at most a quarter, and perhaps a much smaller fraction, of the species that have been preserved in sediments that can be accessed. And as astonishingly strange as many of the dinosaurs uncovered so far have been, there are equally odd species waiting to unearthed. Reams of work based on as-yet-undeveloped technologies and techniques are required to further detail both dinosaur biology and the world they lived in. And although a radical new view is improbable, there will be many surprises.

WHAT IS A DINOSAUR?

To understand what a dinosaur is, we must first start higher in the scheme of animal classification. The Tetrapoda are the vertebrates adapted for life on land—amphibians, reptiles, mammals, birds, and the like. Amniota comprises those tetrapod groups that reproduce by laying hard-shelled eggs, with the proviso that some have switched to live birth. Among amniotes are two great groups. One is the Synapsidia, which includes the archaic pelycosaurs, the more advanced therapsids, and mammals, which are the only surviving synapsids. The other is the Diapsida. Surviving diapsids include the lizard-like tuaturas, true lizards and snakes, crocodilians, and birds. The Archosauria is the largest and most successful group of diapsids and includes crocodilians and dinosaurs. Birds are literally flying dinosaurs.

Archosaurs also include the basal forms informally known as thecodonts because of their socketed teeth, themselves a diverse group of terrestrial and aquatic forms that included the ancestors of crocodilians and the flying pterosaurs, which are not intimate relatives of dinosaurs and birds.

The great majority of researchers now agree that the dinosaurs were monophyletic in that they shared a common ancestor that made them distinct from all other archosaurs, much as all mammals share a single common ancestor that renders them distinct from all other synapsids. This consensus is fairly recent—before the 1970s it was widely thought that dinosaurs came in two distinct types that had evolved separately from thecodont stock, the Saurischia and Ornithischia. It was also thought that birds had evolved as yet another group independently from thecodonts. The Saurischia and Ornithischia still exist, but they are now the two major parts of the Dinosauria, much as living Mammalia is divided mainly into marsupials and placentals. Dinosauria is formally defined as the phylogenetic clade that includes the common ancestor of *Triceratops* and birds and all their descendents. Because different attempts to determine the exact relationships of the earliest dinosaurs produce somewhat different results, there is some disagreement about whether the most primitive, four-toed theropods were dinosaurs or lay just outside the group. This book includes them, as do most researchers.

In anatomical terms one of the features that most distinguishes dinosaurs centers on the hip socket. The head of the femur is a cylinder turned in at a right angle to the shaft of the femur that fits into a cylindrical, internally open hip socket. This allows the legs to operate in the nearly vertical plane characteristic of the group, with the feet directly beneath the body. You can see this system the next time you have chicken thighs. The ankle is a simple fore-and-aft hinge joint that also favors a vertical leg posture. Dinosaurs were "hindlimb dominant" in that they were either bipedal or, even when they were quadrupedal, most of the animal's weight was borne on the legs, which were always built more strongly than the arms. The hands and feet were generally digitigrade with the wrist and ankle held clear of the ground. All dinosaurs shared a trait also widespread among archosaurs in general, the presence of large and complex sinuses and nasal passages.

Aside from the above basic features, dinosaurs, even when we exclude birds, were an extremely diverse group of animals, rivaling mammals in this regard. Dinosaurs ranged in form

A basal archosaur, *Euparkeria*.

DINOSAURS

SMALL TO GIGANTIC ARCHOSAURS FROM THE LATE TRIASSIC TO THE END OF THE MESOZOIC, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Erect leg posture achieved by cylindrical femoral head fitting into a perforated hip socket and a simple hinge-jointed ankle. All are hindlimb dominant in that legs are either sole locomotary organs in walking and running and/or are more strongly built than arms. Hands and feet digitigrade with wrist and ankle held clear of ground. Trackways show that when quadrupedal, hands always at least as far or further apart from midline as feet, never hopped, and tail normally held clear of ground. Body scales, when known and present, form a nonoverlapping mosaic pattern.
ONTOGENY Probably all laid hard-shelled eggs in pairs, nests on the ground; growth rates often moderate, sometimes rapid; usually reached sexual maturity while still growing.
HABITS AND HABITATS Strongly terrestrial; although all able to swim none were marine; otherwise highly variable.

THEROPODS

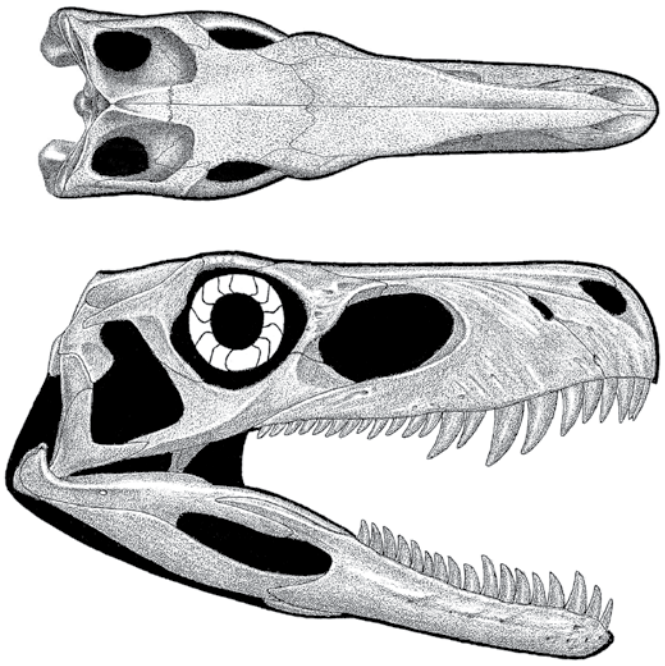
SMALL TO GIGANTIC SAURISCHIAN DINOSAURS, MOST PREDATORS, FROM THE LATE TRIASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS All obligatory bipeds, otherwise very variable. Head size and shape variable, skull bones usually somewhat loosely attached to one another, extra joint usually at middle of lower jaw, eyes large, usually if not always supported by internal bone ring, teeth from large, bladed, and serrated to absent. Neck long to fairly short, usually S-curved to greater or lesser extent, moderately flexible. Series of trunk vertebrae short and stiff. Tail from long and very flexible to very short and stiff. Arm very long to severely reduced, fingers four to one, fingers long and slender to short, sharp claws from large to reduced. Pelvis moderate in size to very large, leg flexed at all sizes, long, main toes four to three; footprints confirm that trackway gauge was very narrow. Brains vary from reptilian in size and form to similar to birds.
HABITATS Very diverse, from sea level to highlands, from tropics to polar winters, from arid to wet.
HABITS Diets ranged from classic hunting with opportunistic scavenging to full herbivory. Small and juvenile theropods with long arm and hook-clawed fingers were probably able to climb. Enormous numbers of trackways laid down along watercourses show that many theropods of all sizes spent considerable time patrolling shorelines and using them to travel.
NOTES The only dinosaur group that includes arch predators. Already somewhat bird-like at beginning, generally became increasingly so with time, especially among some advanced groups that include the direct ancestors of birds.

HERRERASAURS

SMALL TO MODERATELY LARGE PREDATORY THEROPODS, LIMITED TO THE LATE TRIASSIC.

ANATOMICAL CHARACTERISTICS Fairly uniform. Generally lightly built. Head moderately large, long and shallow, subrectangular, fairly robustly constructed, fairly narrow, teeth serrated, blades. Neck moderately long, only gently S-curved. Tail long. Arm and four-fingered hand moderately long, claws well developed. Pelvis short but deep. Four load-bearing toes. Beginnings of bird-like respiratory system possibly present. Brains reptilian.
HABITS Pursuit predators. Head and arms primary weapons. Jaws and teeth probably delivered slashing wounds to disable muscles and cause bleeding, shock, and infection. Arms used to hold onto and control prey, possibly delivered slashing wounds. Prey items include prosauropods, possibly sauropods, especially juveniles, small ornithischians, herbivorous thecodonts, small game.
ENERGETICS Thermophysiology probably intermediate, energy levels and food consumption probably low compared to more derived dinosaurs.
NOTES The most primitive dinosaurs, the briefly existing baso-theropods were apparently not able to compete with the more sophisticated avepods.



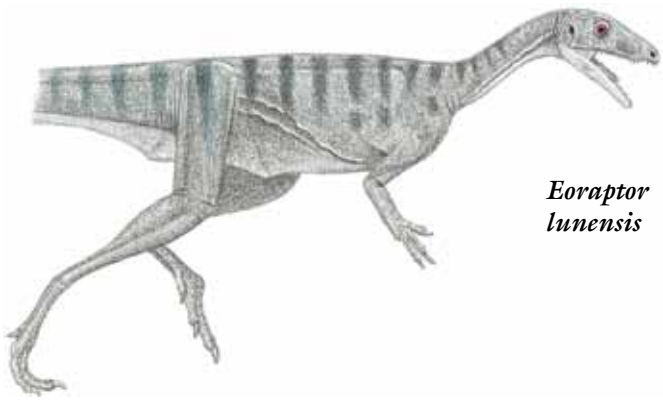
Herrerasaurus skull

Eoraptor lunensis
1.7 m (5.5 ft) TL, 2 kg (4 lb)

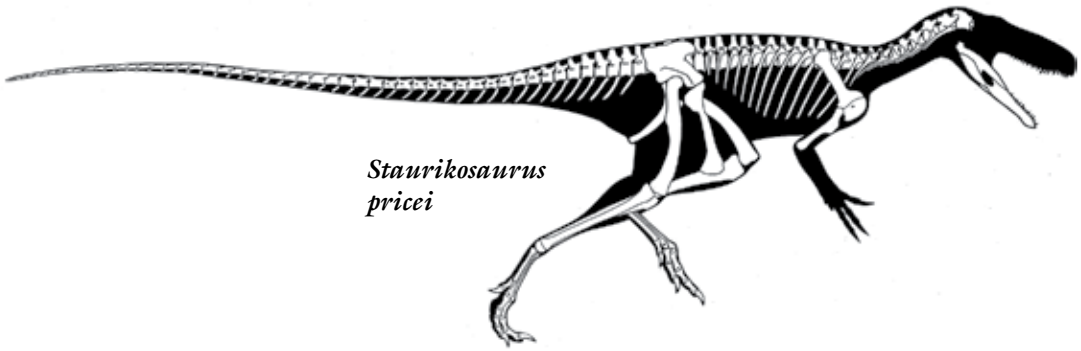
FOSSIL REMAINS: Two nearly complete skulls and skeletons, almost completely known.
ANATOMICAL CHARACTERISTICS: Back teeth are bladed, front teeth are more leaf shaped.
AGE: Late Triassic, Carnian.
DISTRIBUTION AND FORMATION: Northern Argentina; Ischigualasto.
HABITAT: Seasonally well-watered forests, including dense stands of giant conifers.
HABITS: Probably omnivorous, hunted smaller game and consumed some easily digested plant material.
NOTES: One of the most (if not the most) primitive dinosaurs. The prey of larger *Herrerasaurus.* Prey included *Panphagia* and *Pisanosaurus.*

Alwalkeria maleriensis
1.5 m (5 ft) TL, 2 kg (4 lb)

FOSSIL REMAINS: Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS: Appears to be standard for baso-theropods.
AGE: Late Triassic, Carnian.
DISTRIBUTION AND FORMATION: Southeast India; Lower Maleri.



Eoraptor lunensis



Staurikosaurus pricei

Chindesaurus bryansmalli
2.4 m (8 ft) TL, 15 kg (30 lb)

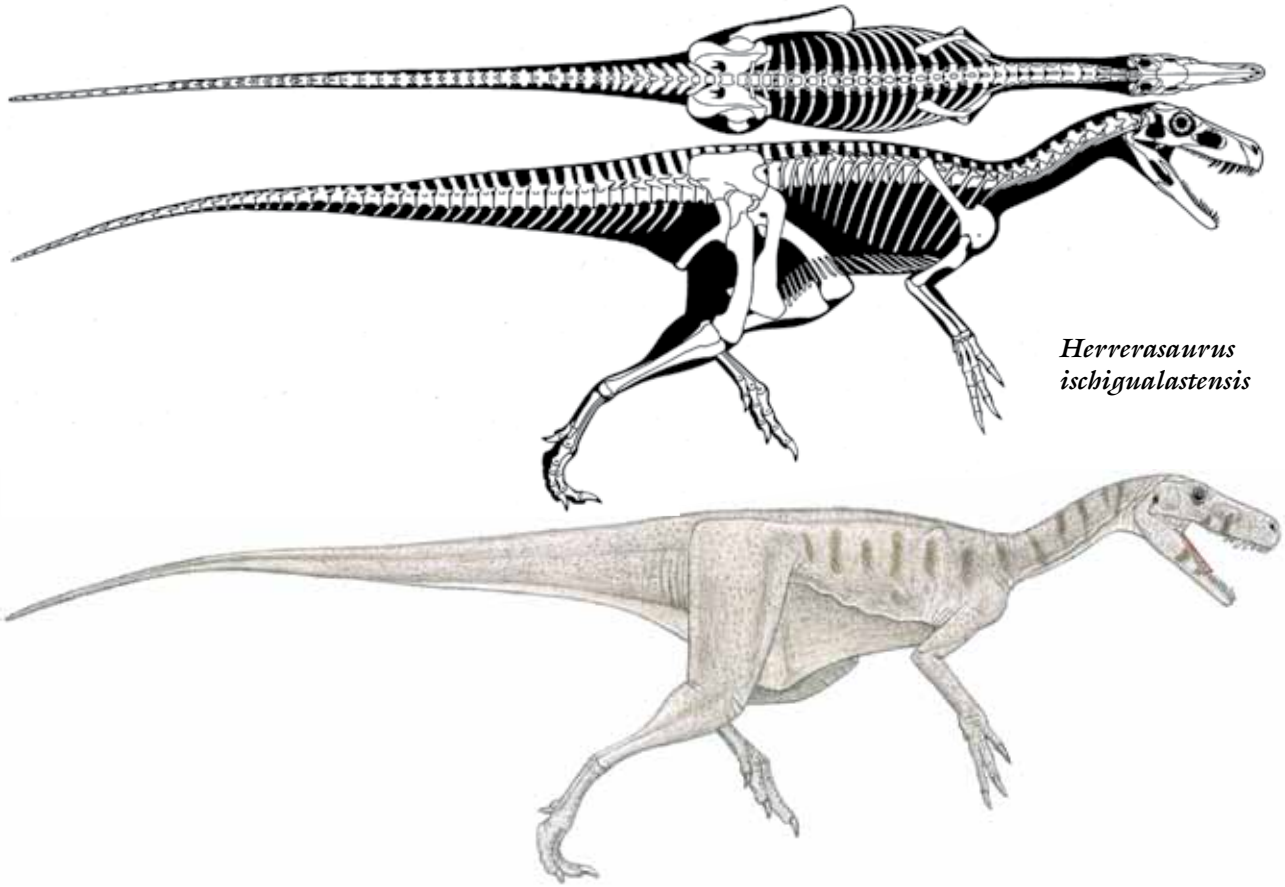
FOSSIL REMAINS: Minority of skeleton, isolated bones.
ANATOMICAL CHARACTERISTICS: Appears to be standard for baso-theropods.
AGE: Late Triassic, late Carnian and/or Norian.
DISTRIBUTION AND FORMATIONS: Arizona, New Mexico, Texas; Petrified Forest, Chinle, Bull Canyon, Tecovas.
HABITAT: Well-watered forests, including dense stands of giant conifers.

Staurikosaurus pricei
2.1 m (7 ft) TL, 12 kg (26 lb)

FOSSIL REMAINS: Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS: Standard for baso-theropods.
AGE: Late Triassic, early Carnian.
DISTRIBUTION AND FORMATION: Southeast Brazil; Santa Maria.
NOTE: Prey included *Saturnalia*.

Herrerasaurus ischigualastensis
4.5 m (15 ft) TL, 200 kg (250 lbs)

FOSSIL REMAINS: Two complete skulls and several partial skeletons.
ANATOMICAL CHARACTERISTICS: Standard for baso-theropods.
AGE: Late Triassic, Carnian.
DISTRIBUTION AND FORMATION: Northern Argentina; Ischigualasto.



Herrerasaurus ischigualastensis

Barapasaurus tagorei
12 m (40 ft) TL, 7 tonnes

FOSSIL REMAINS Majority of skeleton from bone beds.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Early Jurassic.
DISTRIBUTION AND FORMATIONS Southeast India; Kota.
NOTE Shared its habitat with *Kotasaurus*.

Chuanjiesaurus anaensis
Size not certain

FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Middle Jurassic.
DISTRIBUTION AND FORMATION Southwest China; Chuanjie.

Dystrophaeus viaemalae
13 m (43 ft) TL, 7 tonnes

FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle and/or Late Jurassic, Callovian and/or Oxfordian.
DISTRIBUTION AND FORMATION Utah; Summerville.
NOTE The relationships of *Dystrophaeus* are not certain.

Rhoetosaurus brownie
15 m (50 ft) TL, 9 tonnes

FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Bajocian.
DISTRIBUTION AND FORMATIONS Northeast Australia; Hutton.
HABITAT Polar forests with warm, daylight-dominated summers and cold, dark winters.

Volkheimeria chubutensis
Adult size not certain

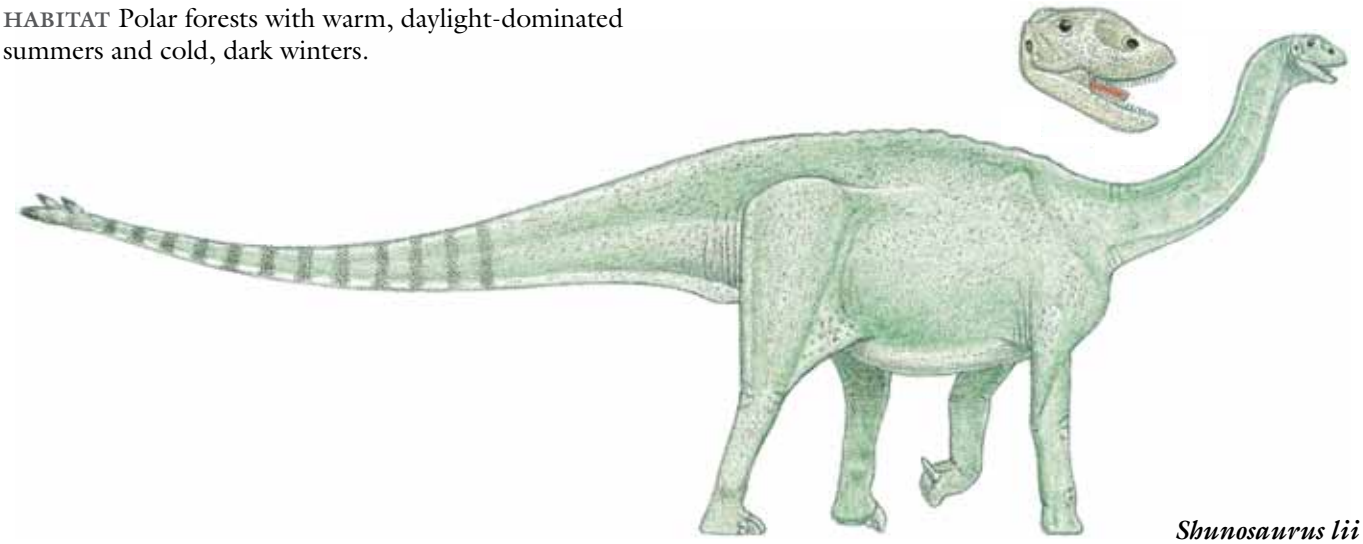
FOSSIL REMAINS Minority of skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Callovian.
DISTRIBUTION AND FORMATION Southern Argentina; Canadon Asfalto.
NOTE Shared its habitat with *Patagosaurus*, *Tehuelchesaurus*, and *Brachytrachelopan*.

Spinophorosaurus nigerensis
13 m (45 ft) TL, 7 tonnes

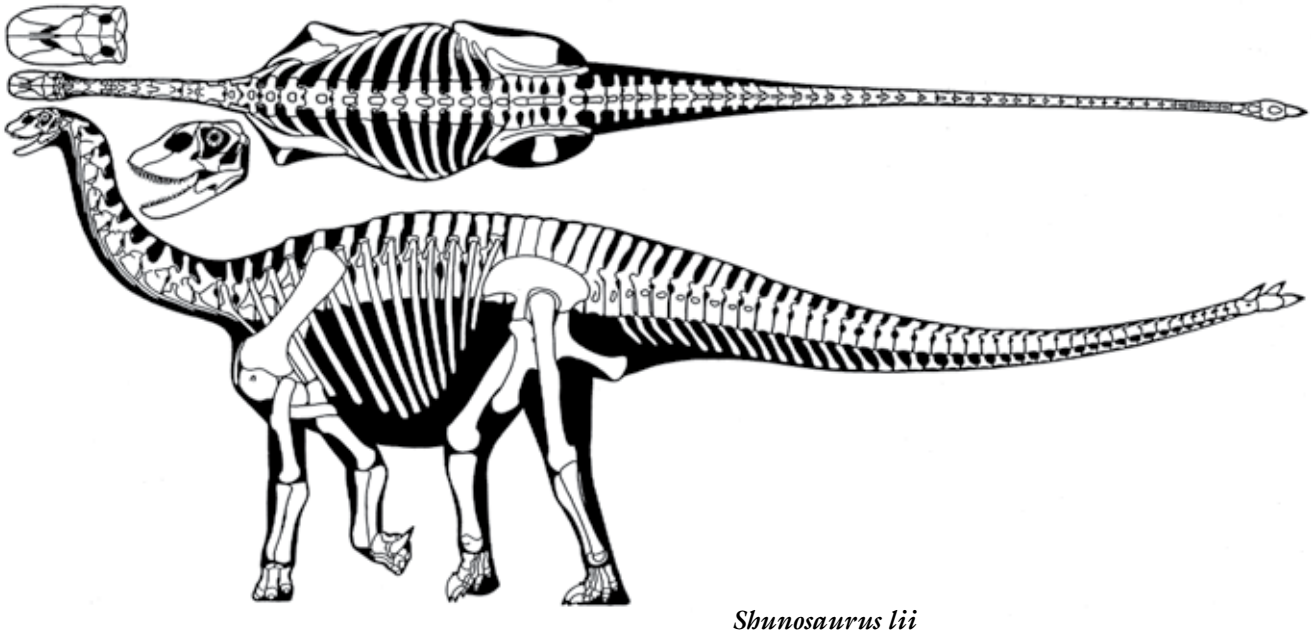
FOSSIL REMAINS Minority of skulls, majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long. Pair of small, paired spikes probably near tip of tail.
AGE Probably Middle Jurassic, Bajocian or Bathonian.
DISTRIBUTION AND FORMATION Niger; Irhazer.
NOTE The only sauropod known to have tail spikes.

Shunosaurus lii
9.5 m (30 ft) TL, 3 tonnes

FOSSIL REMAINS Numerous skulls and skeletons, completely known.
ANATOMICAL CHARACTERISTICS Neck short by sauropod standards. Tail tipped by small, spiked club. Legs long relative to size of body.
AGE Late Jurassic, Bathonian and/or Callovian.
DISTRIBUTION AND FORMATION Central China; Xiashaximiao.
HABITAT Heavily forested.
HABITS Fed at medium heights. Defense included high-velocity impacts from tail club.
NOTES Almost as short necked as *Brachytrachelopan*. The only sauropod known to have had a tail club.



Shunosaurus lii



Shunosaurus lii

PRINCETON FIELD GUIDE TO DINOSAURS

"I have been looking forward to this book for years. Gregory Paul has set the standard for how prehistoric animals are reconstructed in scientific illustrations. As with all his work, the illustrations in this book are made with a near-fanatical quest for accuracy. This will be a popular and much-used reference for a wide audience of dinosaur enthusiasts."

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