PROTHERO

were recovered 11 meters above the base of the Morrison Formation within a fine-grained sandstone with depositional features indicating an ephemeral fluvial system. Taphonomic indicators, including a high degree of articulation and skin impressions, argue for little to no fluvial transport and the presence of soft tissues at the time of burial.

Disarticulated cranial material includes both dentaries, surangulars, prearticulars, splenials, hyoids, jugals, quadratojugals, quadrates, squamosals and pterygoids, right articular, maxilla, palatine and vomer, left postorbital and prefrontal, and a partial braincase. Most of the vertebral column, ribs and gastralia are represented, except the atlas, axis and some mid-caudals. Limb materials include shoulder girdles, forelimbs and the right hindlimb. The left side of the body preserves a 30 cm2 skin impression consisting of small scales 2-3 mm in diameter. This suggests that juvenile allosaurs possessed scaly integument. This represents the most derived tetanuran to retain this character, otherwise present in more basal theropods such as *Carnotaurus*.

Overall length of the specimen is estimated at 4 m with a hip height of 1 m and skull length of 36 cm, suggesting that this animal is a juvenile. Furthermore, size-independent morphological characteristics—including open cranial and postcranial sutures, forelimb and hindlimb proportions, and juvenile bone surface texture—are also indicative of a juvenile specimen.

Comparisons with juvenile and adult allosaur material from the Cleveland-Lloyd Quarry, and material of a new allosaur (DINO 11541), suggest that this new specimen is not *Allosaurus fragilis*, based primarily on a relatively flat ventral jugal margin, and the shape of the caudal neural spines. These characters together with a wide obturator notch on the pubis of the adult specimen are consistent with characters present on DINO 11541, suggesting that these two animals belong to a distinct species of *Allosaurus*.

A NEW SAUROPOD TRACKSITE FROM THE UPPER JURASSIC MORRISON FORMATION WITH PRESERVED SKIN AND FOOT-PAD IMPRESSIONS

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A newly discovered sauropod tracksite from the Upper Jurassic Morrison Formation in Shell, Wyoming, provides new information about sauropod foot morphology, locomotion dynamics, and resultant substrate deformation. Several track-bearing horizons are preserved in crevasse-splay deposits associated with channel sandstones and paleosols dated at 155 to 144 Ma. Individual trackways appear to be wide-gauge and, as such, are likely attributable to titanosaurs.

Tracks occur as convex hyporelief and concave epirelief casts on the undersides of sandstone beds and range from 20 to greater than 100 cm in diameter and 10 to 60 cm deep. Exposed cross-sections reveal lobate- to asymmetrical lobate-shaped impressions with clear deformation of immediately underlying beds. Variations exist among prints of the same size and shape, reflecting changes in substrate consistency and differentially preserving 0 to 5 digits (pes) and rare skin and foot-pad impressions.

Skin impressions appear as symmetrical to elongate hexagonal surfaces ranging from 0.75 to 1.2 cm along the principal axis, separated by depressions with V-shaped profiles. This pattern of repeated polygonal units in relief is consistent with that of an infilled track with scale impressions, rather than a mudcracked surface.

A NEW GOBIOSUCHID CROCODYLIFORM TAXON FROM THE CRETACEOUS OF MONGOLIA

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We report a new fossil crocodyliform taxon found in the Cretaceous Red Beds of the Zos Canyon (Mongolia). This new form shares numerous derived characters with *Gobiosuchus kielanae*, also known from the Late Cretaceous of Mongolia (Bayn Dzak locality). However, it is distinguished from *Gobiosuchus kielanae* by the presence of six autapomorphic characters. Some of these are unusual morphologies for a crocodylomorph and concern the presence of a well developed spiked armor (e.g., retroarticular process with a well developed ornamented posterolateral spike-like process and presence of extremely well developed keels on dorsal and lateral cervical osteoderms, the height of which is approximately as long as the lateromedial extension of the dorsal osteoderms).

The phylogenetic relationships of *Gobiosuchus* and the new taxon are evaluated through a parsimony analysis of 193 characters scored across 50 taxa. In all the most parsimonious hypotheses, the new taxon is depicted as the sister group of *G. kielanae*, forming a strongly supported clade diagnosed by 14 unambiguous synapomorphies (e.g., palpebrals fused to each other and the frontal, excluding it from the orbital margin, external surface of ascending process of jugal exposed posterolaterally, dorsal surface of posterolateral process of squamosal ornamented with three longitudinal ridges, dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges, cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements, presence of appendicular osteoderms, and closed supratemporal fenestra). This clade is positioned basally among crocodyliforms, although it is apparently more closely related to mesoeucrocodylians than to protosuchids (i.e., rejecting the monophyly of a large clade traditionally referred as "Protosuchia").

The phylogenetic context of this new form, together with previously known taxa, provides another insight into the diversity achieved by late appearing basal crocodyliforms of Central Asia, as recorded in Upper Cretaceous beds of Mongolia.

PALEOPHYLOGEOGRAPHY AND PHYLOGENETIC RECONSTRUCTION

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Paleophylogeography is the study of phylogenetic and geographic history within species using fossil data. Whereas phylogeography of extant taxa is studied using molecular markers, paleophylogeography is limited to quantitative morphological data. As with genes, morphological traits have a variety of evolutionary rates that differ trait to trait and group to group. And as with genes, a particular trait will only be useful if it evolves quickly enough for divergence to have accumulated, but slowly enough not to have been unduly 'saturated' by evolutionary reversals. Multivariate traits are often superior for paleophylogeographic work because, *ceteris paribus*, the probability of exact evolutionary convergence decreases with dimensionality; however, univariate traits, *ceteris paribus*, diverge more quickly and may provide better resolution for some problems. New research on mammals indicates that linear measurements of teeth and skulls evolve at a rate that is amenable for studying taxa separated by 1,000s to 10,000s of years, multivariate measurement of molar shape is appropriate for taxa separated by 10,000s to 1,000,000s of years, and discrete presence-absence traits are appropriate for divergences of 1,000,000s to 10,000,000s of years.

With conspecific samples, the probability that an older and younger sample may belong to the same ancestor-descendant lineage is high enough to warrant explicit testing. Traditional discrete-character cladistic analysis is not adequate in this case because its nested data can only resolve relative recency of common ancestry; for discrete traits, stratocladistics is the only method currently available. For quantitative traits, either multivariate or univariate, a number of techniques are available, including maximum-likelihood and Bayesian analysis. Multivariate shape data are particularly amenable to these techniques through analysis of the scores of population means after superposition and rotation to orthogonal axes. Tree support can be assessed by bootstrap techniques in which the members of each population are resampled, population means recalculated, and reordination and tree construction iteratively performed.

TAXONOMY AND SYSTEMATICS OF THE HOLOTYPE OF *HADROSAURUS FOULKII* (DINOSAURIA, ORNITHOPODA) FROM THE LATE CRETACEOUS OF EASTERN NORTH AMERICA

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Hadrosaurus foulkii, the first dinosaur in the Americas known from relatively complete remains, is the type of the family Hadrosauridae. The holotype of this historically significant taxon has been reexamined to ascertain its systematic position and phylogenetic importance. *H. foulkii* is diagnosed on the basis of two autapomorphies: the presence of a hook-like preacetabular process on the ilium that thins dorsoventrally and has a dorsal edge that arches 180 degrees anteroventrally, and the possession of an ischial shaft that arches dorsodistally, forming a dorsally concave profile. A phylogenetic analysis of 105 characters that includes *H. foulkii* and 19 hadrosaurids (8 hadrosaurines, 6 lambeosaurines, and 5 non-hadrosaurid iguanodontians) was performed on PAUP 4.0b10, using a branch-and-bound search under both ACCTRAN and DELTRAN parsimony options. The strict consensus cladogram of 3111 most-parsimonious trees (length = 191, consistency index = 0.64, retention index = 0.74) is very poorly resolved, indicating *Hadrosaurus foulkii* as part of a large polytomy composed of euhadrosaurian taxa, with some internal differentiation into higher clades (i.e., *Maiasaura*, *Brachylophosaurus*, *Lophorhothon*, *Gryposaurus*). However, the majority rule consensus tree indicates that *Hadrosaurus foulkii*, *Kritosaurus australis*, and Euhadrosauria have an unresolved relationship with each other, but are otherwise the sister-group to *Telmatosaurus* within the context of the Hadrosauridae.

BIOGEOGRAPHY AND DIVERSITY PATTERNS OF NORTH AMERICAN RHINOCEROSES

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In the process of a systematic revision of the North American Rhinocerotidae, a number of striking biogeographic patterns emerged. During the late Eocene, only one species (*Trigonias osborni*) is common, but there are rare specimens of *Subhyracodon mitis*. In the Oligocene, North American rhino faunas were very low in diversity and homogeneous, with only one species each in three genera (the common *Subhyracodon*, plus the rare *Amphicaenopus* and *Penetrigonias*) in the Orellan and Whitneyan. Although these faunas are largely known from the Great Plains, rare occurrences in the Gulf Coast and California confirm this pattern. By the Arikareean, the diversity was reduced to one lineage (*Diceratherium*), but there were two sympatric species of *Diceratherium* in many locations in North America. They include the large *D. armatum*, and the smaller *D. annectens*, each of which shows sexual dimorphism in large quarries such as the Frick 77 Hill Quarry in Niobrara County, Wyoming. With the invasion of *Menoceras* in the latest Arikareean, diversity increased briefly as several species of both genera coexisted (along with the rare immigrant *Floridaceras*), then decreased following the extinction of *Floridaceras* and *Diceratherium*. In the middle-late Miocene, most North American faunas produce at least two rhino genera, typically a browser (an aceratherine, such as *Aphelops* or *Peraceras*) and presumed grazer (a teleoceratine, such as *Teleoceras*). However, rhinos were very rare in Miocene faunas of the Rockies and Great Basin (compared to horses and camels in those faunas), while they were extremely abundant in contemporaneous deposits from the Great Plains. Unique endemic dwarfed species were found in the Gulf Coastal Plain, and the Santa Fe Group of New Mexico also produces a unique short-nosed species of *Teleoceras*, which may have had a tapir-like proboscis (like that of the cadurcodont amynodont rhinos).

DOES LAMNOID TOOTH TERMINOLOGY NEED REVISION?

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For nearly a century the lamnoid tooth terminology developed by Leriche with minor modifications by Applegate (1965) and Compagno (1988) has been used successfully by paleontol-

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