

similar studies of metal ions reacting with semiconductor nanocrystals. Mokari *et al.* and Saunders *et al.* have created interesting metal-semiconductor nanocrystal heterostructures by reducing Au³⁺ ions onto InAs quantum dots (29) and CdS/Se nanorods (30, 31). Because Au³⁺ has a much greater electron affinity than Ag⁺, reduction of the ion takes place rather than an exchange reaction. The positive interfacial energy between the two materials drives a phase segregation, similar to our Ag₂S-CdS system, leading to Ostwald ripening. However, epitaxial strain does not play a major role in the Au growth, and these heterostructures continue to ripen into single-metal domains, either at the tip of the rod (CdS/Se), or inside the quantum dot (InAs). In contrast, the epitaxial relationship between the two phases in the Ag₂S-CdS superlattice structures results in strain fields from the lattice mismatch, which cause like segments to repel each other, preventing further ripening.

The resulting striped rods display properties expected of a type I array of Ag₂S quantum dots separated by confining regions of CdS, in agreement with our *ab initio* calculations of the band structure. The visible CdS photoluminescence (PL) is quenched, indicating coupling between materials at the heterojunction (32), and NIR PL from the Ag₂S segments is observed (Fig. 4, D and E). The band gap of the Ag₂S segments depends on their size, matching the bulk value (33) for fully converted nanorods and shifting to higher energy in smaller dots because of quantum confinement (Fig. 4E). In the present configuration, the Ag₂S quantum dots are only very weakly coupled to each other, because the CdS segments are large. Such structures are of interest for colloidal quantum-dot solar cells, where the sparse density of electronic states within a dot may lead to multiple-exciton generation (34). The formation of nanorod superlattices through partial cation exchange can also be applied to other pairs of semiconductors, yielding a broader class of quantum-confined structures. Cation-exchange reactions have already been reported in HgS, Ag₂S, SnS₂, CdS, ZnS, Cu₂S, Bi₂S₃, and Sb₂S₃ (35–37). Two-component combinations of these compounds can produce materials with functional properties ranging from type I (e.g., ZnS-Ag₂S) and type II (e.g., Cu₂S-CdS) band alignments to thermoelectric-power junctions (e.g., CdS-Bi₂S₃).

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- A minority of segments are Ag-rich with little or no S, probably due to the decomposition of Ag-S compounds by the electron beam (38). This beam damage also distorted the phase and prevented accurate images from being acquired with high-resolution TEM.
- For these experiments, TEM images show that the original CdS rods were 5.3 by 50 nm, and the striped rods made from these had 5.3-by-11-nm CdS grains.
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- In both common polymorphs of Ag₂S (cubic and monoclinic), the anion sublattice assumes a body-centered-cubic structure with only slight distortions in the monoclinic phase (39). Several epitaxial relationships were considered, and the epitaxial connection with minimal lattice distortion to the (001) CdS face is the body-centered-cubic (110) face [monoclinic (100) face].
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- When the segments are very close to each other, however, the elastic energy is actually lowered. With only

three atomic layers separating the segments (leftmost point in Fig. 4B), the number of distorted layers in the z direction is small, which results in a smaller repulsive interaction. Additionally, the interaction of the radial distortions from the two segments is cooperative (unlike the z-direction distortions), because they pull the atoms in the same direction. The overall result is a lowering of the elastic energy.

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A Late Triassic Dinosauriform Assemblage from New Mexico and the Rise of Dinosaurs

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It has generally been thought that the first dinosaurs quickly replaced more archaic Late Triassic faunas, either by outcompeting them or when the more archaic faunas suddenly became extinct. Fossils from the Hayden Quarry, in the Upper Triassic Chinle Formation of New Mexico, and an analysis of other regional Upper Triassic assemblages instead imply that the transition was gradual. Some dinosaur relatives preserved in this Chinle assemblage belong to groups previously known only from the Middle and lowermost Upper Triassic outside North America. Thus, the transition may have extended for 15 to 20 million years and was probably diachronous at different paleolatitudes.

Dinosaurs originated in the Late Triassic Period (1, 2) (Carnian-Norian stages, about 230 to 200 million years ago), when they replaced faunas dominated by a variety of basal archosaurs and other amniotes

(3, 4). Archosaurs are divided into two primary lineages: the Pseudosuchia, which include phytosaurs, aetosaurs, “rauisuchians,” and crocodylomorphs, and the Ornithodira, which include pterosaurs, basal dinosauriforms such as

Lagerpeton and *Marasuchus*, and dinosaurs (5, 6). By the beginning of the Jurassic, all of these clades except the dinosaurs, pterosaurs, and crocodylomorphs became extinct (7). The pace of this faunal turnover is poorly understood, even though Late Triassic skeletal and footprint assemblages are distributed worldwide (8). Most evidence has supported the hypothesis that dinosaurs diversified in the Late Triassic after the more archaic faunas were eliminated, either by rapidly outcompeting the archaic forms or replacing them quickly and opportunistically after they died out for other reasons (1, 2, 6, 9, 10), rather than by more gradual processes of ecological replacement.

Until recently, the only evidence of dinosaur precursors was from the Middle Triassic (Ladinian) terrestrial Chañares Formation of Argentina (11–13). Without evidence from other continents, the South American fossil record suggested that the Middle Triassic basal dinosauriforms gave way to the earliest dinosaurs relatively abruptly at the beginning of the Late Triassic. This understanding of early dinosaur evolution began to change with several new discoveries: *Silesaurus opolensis* (14) demonstrated that basal dinosauriforms survived into the Late Triassic; a reappraisal of the North American dinosaur record suggested that Triassic dinosaurs were less diverse and rarer than previously thought (15); and a reevaluation of putative Triassic ornithischian dinosaurs showed that most were misidentified (16). Here we describe fossils from the upper Chinle Formation (Upper Triassic) Hayden Quarry (HQ) in New Mexico demonstrating that early dinosaur faunal replacement was neither abrupt nor as simple as previously thought and also that much of it occurred in North America.

The HQ was opened to large-scale excavation in 2006, and since then our field crew has collected and cataloged nearly 1300 vertebrate specimens. Stratigraphically, the HQ lies approximately 65 m below the famous Ghost Ranch *Coelophysis* Quarry, 15 m below the Snyder Quarry, and 12 m below the Canjilon Quarry (Fig. 1) (17). These four quarries lie within several kilometers of each other and preserve different but partially overlapping assemblages (Table 1). The HQ assemblage includes pseudopalatine phytosaurs and the aetosaurs *Typochothorax coccinarum*

and *Rioarribasuchus chamaensis*, indicative of a Norian age (17–19).

The HQ has a diverse tetrapod assemblage; in addition to various representatives of phytosaurs, aetosaurs, “rauisuchians,” and other archosauriforms, the HQ preserves several dinosaur taxa, including the basal saurischian *Chindesaurus bryansmalli* and coelophysoid theropods. The sauropodomorph and ornithischian dinosaurs known from high-paleolatitude sites of Europe and Gondwana are absent, as they are from all other North American Triassic assemblages (15, 16). The HQ also contains the remains of non-dinosaurian relatives of dinosaurs: a basal dinosauriform similar to *Silesaurus* and a new non-dinosauriform dinosauriform similar to *Lagerpeton* (a taxon known only from the Middle Triassic of Argentina) (11), which we describe here.

Archosauria Cope 1869 *sensu* Gauthier and Padian 1985; Dinosauriforma Benton 1985 *sensu* Sereno 1991; *Dromomeron romeri*, gen. et sp. nov.

Etymology. *Dromomeron*, from *dromas* (Greek word for running) and *meros* (Greek word for femur); *romeri*, for Alfred Sherwood Romer, who first described the dinosaur precursors from Argentina, including *Lagerpeton*.

Holotype. Complete left femur, specimen number GR 218 (Fig. 2, A to D), deposited in the collections of the Ghost Ranch Ruth Hall Museum of Paleontology (GR).

Paratypes. Additional specimens were found within several feet of the holotype. A right femur, GR 219, and a left tibia, GR 220, may belong to the same individual as the holotype. Additional material includes GR 221, a partial left femur; GR 222, a complete left tibia (Fig. 2, E to H); GR 223, a complete astragalocalcaneum (Fig. 2, I to K); and GR 234, a nearly complete right femur.

Referred material. New Mexico Museum of Natural History (NMMNH) P-35379, a complete astragalocalcaneum.

Locality and horizon. Site 3, HQ, Ghost Ranch, Rio Arriba County, New Mexico, USA. The HQ is in the lower portion of the Petrified Forest Member of the Upper Triassic Chinle Formation. The referred NMMNH specimen is from the nearby Snyder Quarry (20), also within the Petrified Forest Member. The Petrified Forest Member in this area is of Norian age, according to fossil pollen and vertebrate biostratigraphy (17–19, 21, 22).

Diagnosis. Differs from all other dinosauriforms except *Lagerpeton chanarensis* in possessing a hook-shaped femoral head (Fig. 2A), a lateral emargination ventral to the femoral head (Fig. 2A), an enlarged postero-medial tuber on the proximal portion of the femur (Fig. 2, B and C), an enlarged crista tibiofibularis on the distal end of the femur (Fig. 2D), a posteromedial crest on the distal end of the tibia (Fig. 2H), and an astragalus with a posterior ascending process (Fig. 2, I

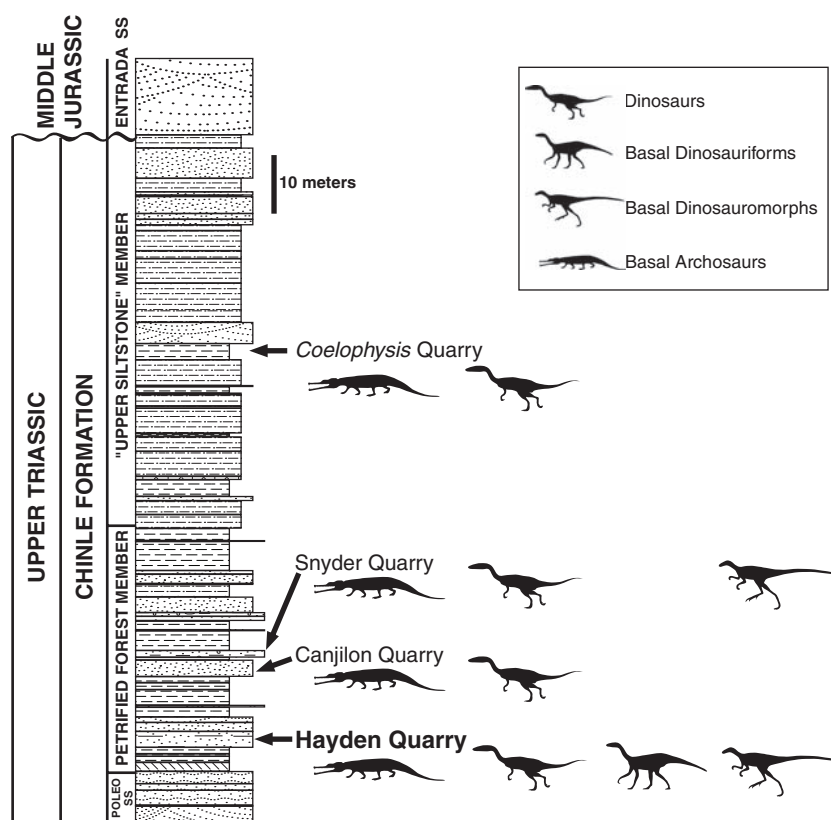


Fig. 1. Stratigraphic position of the HQ and related assemblages. SS, sandstone.

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to K); differs from *Lagerpeton* in possessing a much larger crista tibiofibularis; and differs from all other basal dinosauromorphs in the absence of a fourth trochanter (Fig. 2, A and B), the presence of a sharp ridge on the antero-

medial edge of the distal end of the femur (Fig. 2D), and a large crest on the anteromedial edge of the astragalus (Fig. 2I) (autapomorphies).

Phylogenetic analyses consistently place *Lagerpeton chanarensis* closer to dinosaurs than

to pterosaurs and pseudosuchians (6, 11, 23) (Fig. 3). The referred tibiae of *Dromomeron* share two synapomorphies with *Lagerpeton*: a distal end with a posteromedial crest (Fig. 2H) and a posterolateral concavity for the reception of the posterior ascending process of the astragalus. The distal end of the tibia of *Dromomeron* also possesses an anteromedial concavity for the reception of the enlarged anteromedial crest of the astragalus, creating an anteromedial-posterolateral groove in the distal end of the tibia (Fig. 2, E and H). The astragalus overlaps the calcaneum dorsally (Fig. 2K). The calcaneum is triangular in dorsal view, widening anteriorly and narrowing posteriorly (Fig. 2I). Our phylogenetic analysis places *Dromomeron* as the sister taxon to *Lagerpeton* and recovers this clade as the sister taxon to all other dinosauromorphs (Fig. 3) (17).

Although most of the HQ material is disarticulated, several diagnostic elements of each taxon have been recovered. Material of the *Silesaurus*-like dinosauriform includes a partial tooth-bearing dentary (GR 224) (Fig. 2L), an ilium (GR 225) (Fig. 2M), and a proximal femur (GR 195) (Fig. 2, N to O). This material may be

Table 1. Tetrapods from Chinle Formation quarries in the Chama Basin, New Mexico. Hayden Quarry, HQ; Canjilon Quarry, CN; Snyder Quarry, SQ; *Coelophysis* Quarry, CO; Petrified Forest Member at Petrified Forest National Park, Arizona, PF. See supporting online material (17) for voucher specimen numbers.

Taxon	HQ	CN	SQ	CO	PF
Metoposauridae	X	X	X		X
Drepanosauridae	X			X	
<i>Vancleavea</i>	X	X		X	X
<i>Pseudopalatus</i> spp.	X	X	X		X
<i>Typothorax coccinarum</i>	X	X	X		X
<i>Rioarribasuchus chamaensis</i>	X		X		X
" <i>Rauisuchia</i> "	X	X	X	X	X
<i>Shuvosaurus</i> -like taxon	X			X	X
Crocodylomorpha	X			X	X
<i>Dromomeron romeri</i>	X		X		
<i>Silesaurus</i> -like taxon	X				
<i>Chindesaurus bryansmalli</i>	X				X
Coelophysoidea	X	X	X	X	X



Fig. 2. Dinosauriforms from the HQ. (A to D) Femur of *D. romeri* (GR 218) gen. et sp. nov. in anterior (A), posterior (B), proximal (C), and distal (D) view. (E to H) Tibia of *D. romeri* (GR 222) in anterior (E), lateral (F), proximal (G), and distal (H) view. (I to K) Astragalocalcaneum of *D. romeri* (GR 223) in proximal (I), anterior (J), and posterior (K) view. (L to O) *Silesaurus*-like dentary (GR 224) in medial view (L), ilium (GR 225) in lateral view (M), and proximal femur (GR 195) in proximal (N) and posterior (O) view. (P) *Chindesaurus bryansmalli*

femur (GR 226) in posterior view; and (Q) coelophysoid theropod fused tibia, fibula, and astragalocalcaneum (GR 227) in anterior view. Abbreviations are as follows: antero-medial crest (amc), antero-medial process (amp), antero-medial ridge (amr), brevis fossa (bf), calcaneum (ca), cnemial crest (cn), crista tibiofibularis (ct), groove (gr), lateral emargination (le), meckelian groove (mg), notch (n), posterior ascending process (pap), posteromedial crest (pmc), posteromedial tuber (pmt). Scale bars, 1 cm.

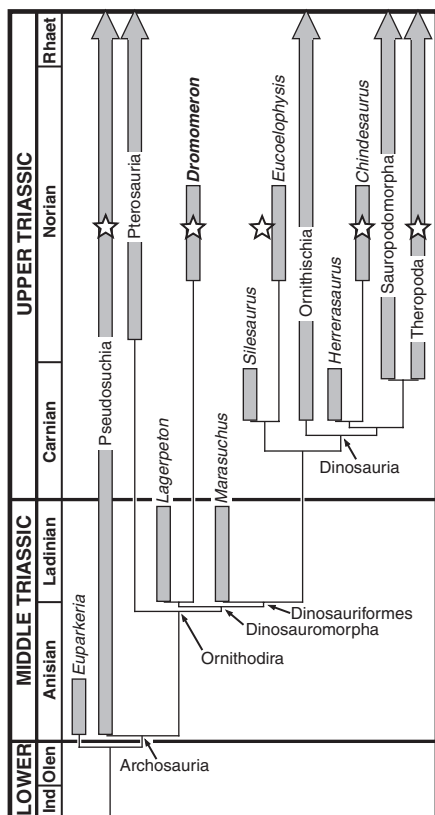


Fig. 3. Phylogenetic position of *D. romeri* gen. et sp. nov. among archosaurs. A single most-parsimonious tree was recovered from a parsimony analysis of 26 taxa and 127 characters (17). Pseudosuchia, Ornithischia, Sauroptomorpha, and Theropoda have been collapsed for brevity. Stars indicate taxa present in the HQ. For lineages that do not extend into the Jurassic, the length of the gray bar indicates stratigraphic imprecision. Ind, Induan; Olen, Olenekian; Rhaet, Rhaetian.

referable to *Eucoelophysis baldwini*, a *Silesaurus*-like dinosauriform known from the same stratigraphic unit (15, 17). The dentary shares two synapomorphies with *Silesaurus*: striated tooth bases that partially fuse to the jaw (unlike ornithischian dinosaurs) and a Meckelian groove near the ventral border of the dentary that extends to the anterior tip (Fig. 2L). The teeth are subtriangular with enlarged denticles, a labial basal swelling of the crown, and a distinct narrowing at the base of the crown similar to the herbivorouslike teeth of other archosaurs (16, 24). They lack the distinct striations found toward the tip of *Silesaurus* teeth (14). The ilium shares with *Silesaurus* an enlarged brevis fossa and shelf, which is open laterally (Fig. 2M). The femoral head is triangular in proximal view (Fig. 2N) and bears a small notch ventrally (Fig. 2O); both of these characters are found in *Silesaurus*, *Eucoelophysis*, and *Pseudolagosuchus* (15).

A complete femur (GR 226) displays an autapomorphy of *Chindesaurus bryansmalli*: an

elongate, subrectangular femoral head with a flat proximal surface (15) (Fig. 2P). One example of recovered coelophysoid material is a fused tibia, fibula, and astragalocalcaneum (GR 227) (Fig. 2Q); the fusion of these elements is present in coelophysoid and neoceratosaur theropods (25), and a specimen from the nearby Snyder Quarry also displays this character (16, 26). An unambiguous coelophysoid synapomorphy present in GR 227 is a small anteromedial process on the distal fibula that overlaps the ascending process of the astragalus (Fig. 2Q) (25).

The HQ assemblage changes our picture of the early evolution of dinosaurian faunas in several ways. First, it documents that a mixed assemblage of true dinosaurs and their basal dinosauriform relatives lived together along with other typical Triassic tetrapods in the Norian. Our investigations have found the same co-occurrences in several other Chinle Formation and Dockum Group localities in Arizona, New Mexico, and Texas (15, 17). Therefore, the HQ assemblage cannot be explained by time-averaging of sedimentation or redeposition of earlier fossils [which is confirmed by our sedimentological and stratigraphic analysis of HQ (17)]. The HQ assemblage also reinforces the pattern that low-paleolatitude faunas of southern North America differ from the high-paleolatitude faunas of Europe, Greenland, South America, and South Africa in lacking basal sauroptomorph and rare ornithischian dinosaurs. This biogeographic disparity may reflect a real large-scale climatic or latitudinal effect (27), smaller-scale community or ecological differences, or merely facies-dependent sampling biases.

The HQ assemblage and others of western North America and Europe document the persistence of basal dinosauriforms well into the Late Triassic. In Argentina, *Lagerpeton*, *Marasuchus*, and *Pseudolagosuchus* are confined to the Middle Triassic (Ladinian) Chañares Formation and never occur with dinosaurs (1, 3). However, the Late Triassic (Carnian and Norian) forms differ from their Middle Triassic relatives, indicating a continued diversification of these groups. The age range of the HQ fossils and our assessment of other assemblages and their ages in North American museum collections imply that these dinosaurs and non-dinosaurian dinosauriforms coexisted for at least 15 to 20 million years. There are too few radiometric dates of Late Triassic localities to permit a more precise time calibration, but it is nonetheless clear that the Late Triassic faunal replacement was not abrupt. Rather, it was protracted and possibly diachronous, as evidenced by paleolatitudinal faunal differences across Late Triassic Pangaea. The appearance of the first dinosaurs in the Ischigualasto assemblage (1), along with the late occurrences of basal dinosauriforms from the HQ assemblage, extends the transition time from assemblages of dinosaur precursors to assemblages exclusively of dinosaurs and indicates that

models of rapid competitive or fortuitous replacement are not correct.

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