

## HINDLIMB OSTEOLOGY AND DISTRIBUTION OF BASAL DINOSAUROMORPHS FROM THE LATE TRIASSIC OF NORTH AMERICA

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**ABSTRACT**—The recent discovery of early dinosauriforms from North America demonstrates that they were contemporaries with dinosaurs and other basal archosaurs during a substantial portion of the Late Triassic Period. Hindlimb material (femora, tibiae, a fibula, astragalocalcanea, and phalanges) of *Dromomeron romeri*, a non-dinosauriform dinosauriform from the Petrified Forest Member of the Chinle Formation from north-central New Mexico, is described. A new species of *Dromomeron* from the lower portion of the Chinle Formation (eastern Arizona) and Dockum Group (northern Texas) is also described, based on several disarticulated femora and tibiae. *D. romeri*, *Lagerpeton*, and the new taxon form the sister group to all other dinosauriforms and demonstrate that this clade, Lagerpetidae, persisted well into the Norian. Lagerpetidae is supported by several synapomorphies: femoral head hook-shaped in medial and lateral views; ventral emargination on the anterolateral side of the femoral head; an enlarged posteromedial tuber of the proximal end of the femur; femoral crista tibiofibularis larger than the medial condyle; anteromedial corner of the distal end of the femur forms 90° or acute (>90°) angle; and a posterior ascending process of the astragalus. An ontogenetic series of the femur of *Dromomeron* indicates that some character states previously used in phylogenetic analyses of early dinosaurs may be ontogenetically variable.

### INTRODUCTION

By the beginning of the Middle Triassic, the clade Archosauria had diversified into two lineages, Pseudosuchia and Ornithodira (Gauthier et al., 1988; Sereno, 1991; Gower and Sennikov, 2000; Nesbitt, 2003). Pseudosuchian archosaurs include the phytosaurs, aetosaurs, “rauisuchians,” and crocodylomorphs, whereas the Ornithodira includes the pterosaurs, a variety of basal dinosauriforms and dinosauriforms, and dinosaurs (including birds) (Benton and Clark, 1988; Benton, 2004). Throughout the Triassic Period, the pseudosuchians dominated ornithodirans in terms of size and diversity (Benton, 2004). By the end of the Triassic, all pseudosuchian clades were extinct except for Crocodylomorpha, and ornithodirans became taxonomically diverse and globally distributed. The early history of Pseudosuchia is well documented throughout Gondwana and Laurasia, but the early history of Ornithodira is only well-known from the Middle Triassic of Argentina. This material includes the incomplete skeletons of the earliest known basal dinosauriforms *Lagerpeton* Romer, 1971, *Marasuchus* Sereno and Arcucci, 1994a, and *Pseudolagosuchus* Arcucci, 1987.

*Lagerpeton chanarensis* (estimated at 70 cm in length from the femur) is known from the complete hindlimb, pelvis, and partially articulated series of dorsal and caudal vertebrae from several specimens (Romer, 1971, 1972; Arcucci, 1986; Sereno and Arcucci, 1994b). Because of its phylogenetic placement, *Lagerpeton* is critical for understanding the interrelationships among dinosauriforms and basal ornithodirans, and has been used repeatedly to polarize character states among dinosaurs (Novas, 1989, 1992, 1996; Sereno and Arcucci, 1994a, 1994b; Arcucci, 1997). All of the aforementioned authors agree that *Lagerpeton* is the basal-most member of Dinosauromorpha, and the sister-taxon to Dinosauriformes. Though well-preserved, known material of *Lagerpeton* lacks certain diagnostic dinosauriform character states (e.g., the presence of an anterior trochanter), thus supporting its basal position.

Our understanding of the early evolution of Ornithodira is further hampered by the uncertainty of the phylogenetic position of pterosaurs (Benton, 1985; Wellnhofer, 1991; Bennett, 1996; Unwin, 1999; Peters, 2000; Hone and Benton, 2007). Because pterosaurs appear in the fossil record as derived flying archosaurs, they share few unambiguous synapomorphies with other archosaurs that would elucidate their ancestry. Additionally, the controversial *Scleromochlus* is poorly preserved and many morphological features are open to interpretation, making comparisons difficult (Padian, 1984; Sereno, 1991; Bennett, 1996; Benton, 1999).

Irmis et al. (2007) reported the first occurrence of a Late Triassic non-dinosauriform dinosauriform. This new taxon,

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*Dromomeron romeri*, from the Chinle Formation of New Mexico clearly indicates that non-dinosauriform dinosauromorphs were contemporaneous with dinosaurs and pseudosuchians in North America during the Late Triassic and had a broader geographic distribution than previously believed. Here, we fully describe the hindlimb of *Dromomeron romeri*, name and describe a new second species of *Dromomeron*, and demonstrate that non-dinosauriform dinosauromorphs had an extensive evolutionary history in the Late Triassic of North America. Furthermore, a growth series of femora from the new taxon provides a better understanding of the ontogeny of character states in non-dinosauriform dinosauromorphs.

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York; **BMNH**, The Natural History Museum, London, United Kingdom; **GR**, Ruth Hall Museum of Paleontology, Ghost Ranch, NM; **MB**, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; **MCP**, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **MOTT VPL**, Museum at Texas Tech, Vertebrate Paleontology Locality; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, NM; **PVL**, Instituto Miguel Lillo, Tucumán, Argentina; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin, TX; **TTUP** Texas Tech University Paleontology Collections, Lubbock, TX; **UCMP**, University of California Museum of Paleontology, Berkeley, CA; **UNLR**, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **ZPAL**, Instytut Paleobiologii PAN, Warsaw, Poland.

**Anatomical Abbreviations**—**a**, articulates with; **aap**, anterior ascending process; **ald**, anterolateral depression of the astragalus; **am**, anteromedial process of the distal portion of the tibia; **amp**, anteromedial process; **at**, anterior trochanter; **as**, astragalus; **cal**, calcaneum; **c-a**, calcaneum–astragalus suture; **cc**, cnemial crest; **cr**, crack associated with crushing; **ct**, crista tibiofibularis; **faa**, facies articularis antitrochanterica; **f**, fibula; **fl**, flange; **fo**, foramen; **ft**, fourth trochanter; **“ft”**, location of the fourth trochanter in other archosaurs; **ftd**, fourth trochanter depression; **gr**, groove; **lc**, lateral condyle; **lia**, linea intermuscularis cranialis; **lip**, linea intermuscularis caudalis; **mfe**, distal origin of *M. femorotibiales externus*; **mt**, medial tuber; **pc**, posterior corner; **pl**, posterior lateral process of the distal portion of the tibia; **plc**, posterolateral condyle of the tibia; **pmc**, posteromedial condyle of the tibia; **pmd**, posteromedial depression of the astragalus; **pap**, posterior ascending process; **r**, ridge; **samp**, slot for the anteromedial process of the astragalus; **sp**, slot for the posterior ascending process of the astragalus; **tc**, tibial condyle of the femur; **ts**, trochanteric shelf; **ve**, ventral emargination.

## SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869 *sensu* Gauthier and Padian, 1985  
 DINOSAUROMORPHA Benton, 1985 *sensu* Sereno, 1991  
 LAGERPETIDAE Arcucci, 1986 new converted clade name

**Definition**—All taxa more closely related to *Lagerpeton charnensis* Romer, 1972 than to *Alligator mississippiensis* Daudin, 1801, *Eudimorphodon ranzii* Zambelli, 1973, *Marasuchus lilloensis* Sereno and Arcucci, 1994a, *Silesaurus opolensis* Dzik, 2003, *Triceratops horridus* Marsh, 1889, *Saltasaurus loricatus* Bonaparte and Powell, 1980, and *Passer domesticus* Linnaeus, 1758.

**Diagnosis**—Differentiated from all other archosaurs by the following unambiguous synapomorphies: 1) presence of a hook-shaped femoral head, 2) a lateral emargination ventral to the femoral head, 3) an enlarged posteromedial tuber of the proximal end of the femur, 4) an enlarged crista tibiofibularis of the distal end of the femur, 5) an anteromedial corner of the distal

end of the femur that forms an angle near or less than 90°, and 6) an astragalus with a posteriorly situated ascending process.

### *DROMOMERON* Irmis et al., 2007

**Diagnosis**—Differs from all other dinosauromorphs in possessing the following synapomorphies: 1) a concave posterolateral surface of the crista tibiofibularis of the distal end of the femur; 2) distinct scar on the anterior surface of the distal end of the femur; and 3) posterolateral condyle of the proximal portion of the tibia is ventrally deflected or “hooked.”

**Type Species**—*Dromomeron romeri* Irmis et al., 2007.

### *DROMOMERON ROMERI* Irmis et al., 2007

**Holotype**—Complete left femur, GR 218 (Fig. 1).

**Paratypes**—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 234, a complete right femur; GR 222, a complete left tibia; and GR 223, a complete astragalocalcaneum.

**Referred Material**—GR 238, partial articulated skeleton; GR 239, isolated right tibia (cnemial crest crushed); NMMNH P-35379, a complete astragalocalcaneum; AMNH FR 2721, distal portion of a femur; AMNH FR 30648, distal portion of a right tibia; AMNH FR 30649, distal portion of a right tibia.

**Diagnosis**—Differs from *Dromomeron gregorii* (see below) and all other basal dinosauromorphs in possessing the following autapomorphies: 1) absence of a distinct ridge for the attachment of the *M. caudifemoralis longus* (=4<sup>th</sup> trochanter); 2) presence of a sharp ridge on the anteromedial edge of the distal end of the femur; 3) presence of a lateral tuberosity on the anterolateral edge of the distal end of the femur; and 4) a large crest on the anteromedial edge of the astragalus and associated anteromedial concavity on the distal tibia.

**Locality and Horizon**—Site 3, Hayden Quarry, Ghost Ranch, Rio Arriba County, New Mexico, USA. The Hayden Quarry is in the lower portion of the Petrified Forest Member of the Upper Triassic Chinle Formation (Irmis et al., 2007). The referred NMMNH specimen is from the nearby Snyder Quarry (Zeigler et al., 2003), located stratigraphically higher within the Petrified Forest Member. Material collected by Baldwin for Cope (AMNH FR 30648 & 30649) is from the same general area as the other quarries, near Arroyo Seco, and is most likely from the Petrified Forest Member, although its exact provenance is unclear. The Petrified Forest Member in this area is Norian in age based on palynological age constraints and vertebrate biostratigraphy (Litwin et al., 1991; Lucas, 1998; Heckert et al., 2005; Parker, 2006; Irmis et al., 2007).

### *DROMOMERON GREGORII* sp. nov.

**Etymology**—*gregorii*, for the late Joseph T. Gregory, who studied and described many of the fossil vertebrates from the Otis Chalk quarries.

**Holotype**—TMM 31100-1306, complete right femur (Fig. 2).

**Paratypes**—Additional specimens found within the same quarry (Quarry 3): TMM 31100-464, right femur; TMM 31100-1308, right femur; TMM 31100-1234, right femur; TMM 31100-764, right femur; TMM 31100-278, right tibia; TMM 31100-1314, left tibia.

**Referred Material**—UCMP 25815, distal portion of a left femur from the *Placerias* Quarry.

**Diagnosis**—Differs from *Dromomeron romeri* in possessing a distinct ridge for the attachment of the *M. caudifemoralis longus* (=4<sup>th</sup> trochanter), the presence of an anterior trochanter and trochanteric shelf, robust proximal and distal ends of the femora, the intercondylar groove of the distal femur is reduced to a slit in

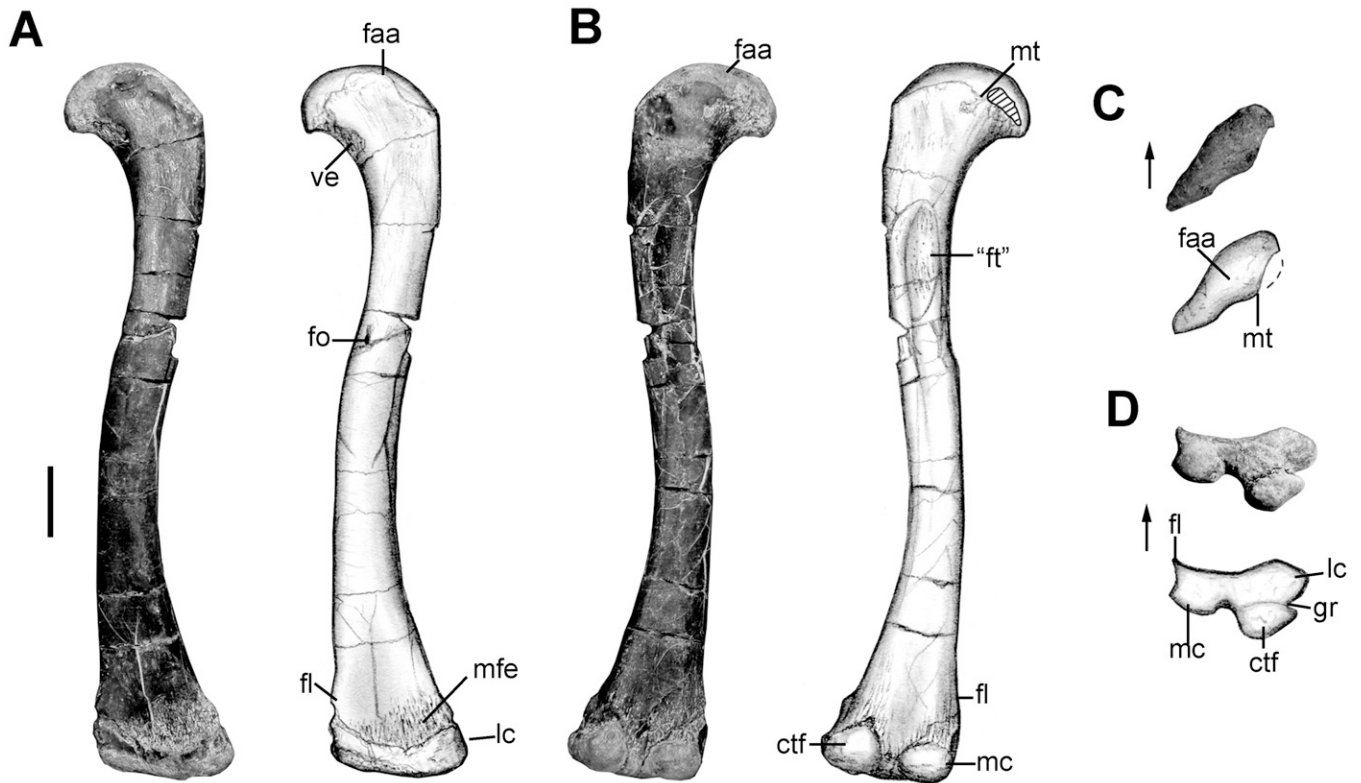


FIGURE 1. The holotype left femur of *Dromomeron romeri* (GR 218) in **A**, anterolateral view; **B**, posteromedial view; **C**, proximal view; **D**, distal view. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

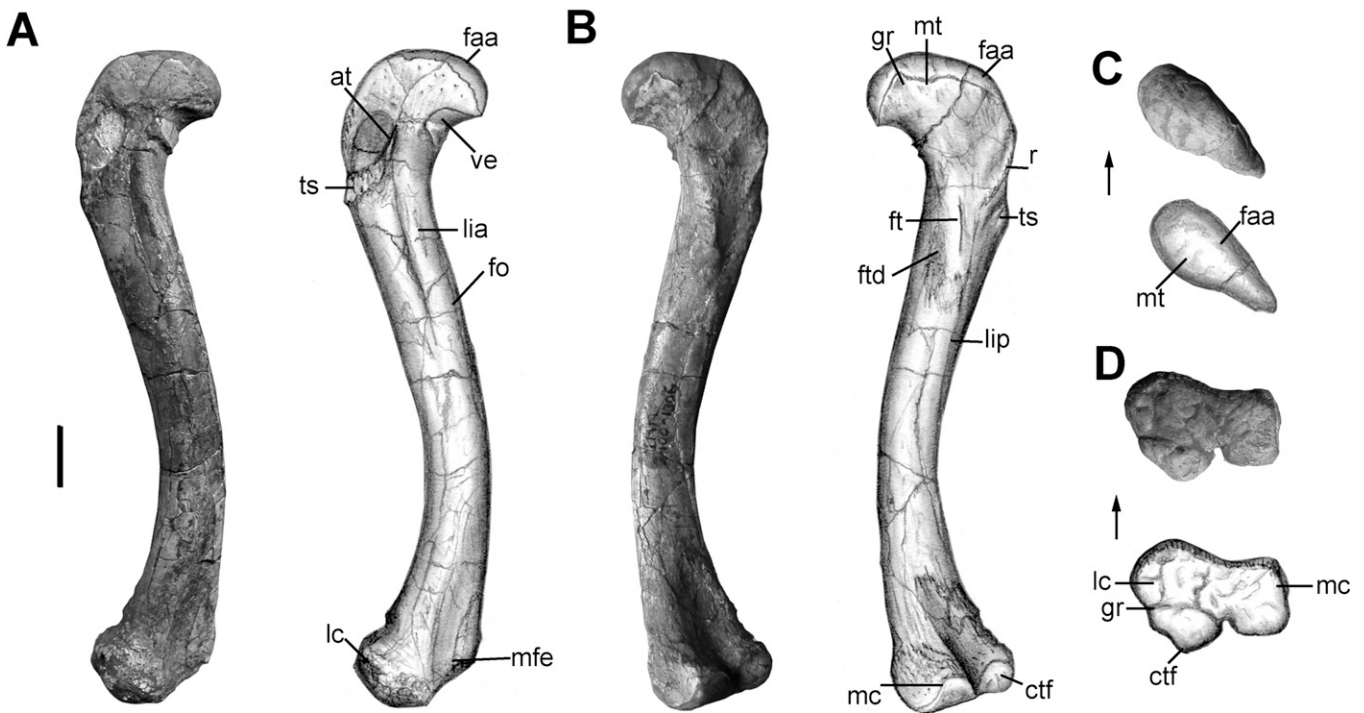


FIGURE 2. The holotype right femur of *Dromomeron gregorii* (TMM-31100-1306) in **A**, anterolateral view; **B**, posteromedial view; **C**, proximal view; **D**, distal view. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

larger specimens (possible autapomorphy), and the lack of an anteromedial concavity on the distal end of the tibia.

**Locality and Horizon**—Otis Chalk Quarry 3 (TMM locality 31100), near Otis Chalk, Texas, USA. Specific locality data is on file at the Texas Memorial Museum of the University of Texas, Austin. Otis Chalk Quarry 3 is in the Colorado City Formation of the Upper Triassic Dockum Group (Lucas et al., 1993; see Lehman and Chatterjee, 2005 and Martz, 2008 for alternate interpretations). The *Placerias* Quarry is near St. Johns, Arizona (UCMP locality A269). Stratigraphically, it is near the base of the Chinle Formation, possibly within the Mesa Redondo Member (Lucas et al., 1997; Parker, 2005).

#### DESCRIPTION

When *Dromomeron* was first described (Irmis et al., 2007), no unambiguously associated specimens were found. Because *Lagerpeton* is only known from the hindlimb, pelvis, and dorsal and caudal vertebrae, only those elements could be identified from isolated remains and assigned to *Dromomeron*. Each element (femur, tibia, astragalocalcaneum) can be independently assigned to a *Lagerpeton*-like taxon using unambiguous synapomorphies (see below). Taxonomic differences between *D. romeri* and *D. gregorii* are noted throughout the description. If only *Dromomeron* is mentioned, the feature is present in both *D. romeri* and *D. gregorii*.

In the summer of 2007, a partially articulated specimen of *Dromomeron romeri* (GR 238) was discovered at the Hayden Quarry (holotype locality). Although the specimen does not preserve the ankle, it confirms that the tibia and femur, as hypothesized by Irmis et al. (2007), belong to the same taxon. The partial fibula and phalanges from GR 238 are described here; other portions of the skeleton will be described elsewhere after preparation is complete.

#### Femur

*D. romeri* is represented by five femora from Site 3 of the Hayden Quarry and an isolated distal portion of a femur (AMNH 2721) from an unknown locality and Arroyo Seco near Ghost Ranch in north-central New Mexico (see Appendix 1). The most complete femur, the holotype (GR 218; Fig. 1), measures 95 mm long and is well preserved, with slight crushing and abrasion in some areas. A paratype right femur of *D. romeri* (GR 238) is one third larger in length (127.6 mm). *D. gregorii* is known from five right femora and one left femur from the Otis Chalk Quarry 3 (TMM loc. 31100), and the distal portion of a left femur from the *Placerias* Quarry (UCMP loc. A269) (see Appendix 1). The most well preserved femur, the holotype (TMM 31100-1306; Fig. 2), measures 96 mm long and is about the same size as the most well preserved femur of *D. romeri* (GR 218). The following description is based primarily on the holotypes of *D. romeri* (GR 218) and *D. gregorii* (TMM 31100-1306), but is supplemented by the paratype specimens.

The femora of *Dromomeron* are S-shaped in lateral view and thus retain the plesiomorphic sigmoidal shape present in basal archosauriforms, pseudosuchians, *Lagerpeton* (Fig. 3), and *Marasuchus* (Hutchinson, 2001). The cross-section throughout the diaphysis is elliptical. *D. gregorii* is more robust than *D. romeri* at the mid-diaphysis. The mid-diaphysis of the holotype of *D. gregorii* measures 9.3 mm anteroposteriorly, whereas the mid-shaft of the comparably sized holotype of *D. romeri* measures 8.0 mm. The cortex of the femoral diaphysis measures ~1 mm or less in thickness and consequently most of the specimens are crushed. At mid-diaphysis, the ratio of the maximum thickness of the cortex to the minimum external diameter is near 0.20 in all specimens examined for both taxa. This ratio compares well with other basal ornithodirans (0.10 – 0.27), whereas the ratio for basal archosauriforms and pseudosuchians is larger (~0.30

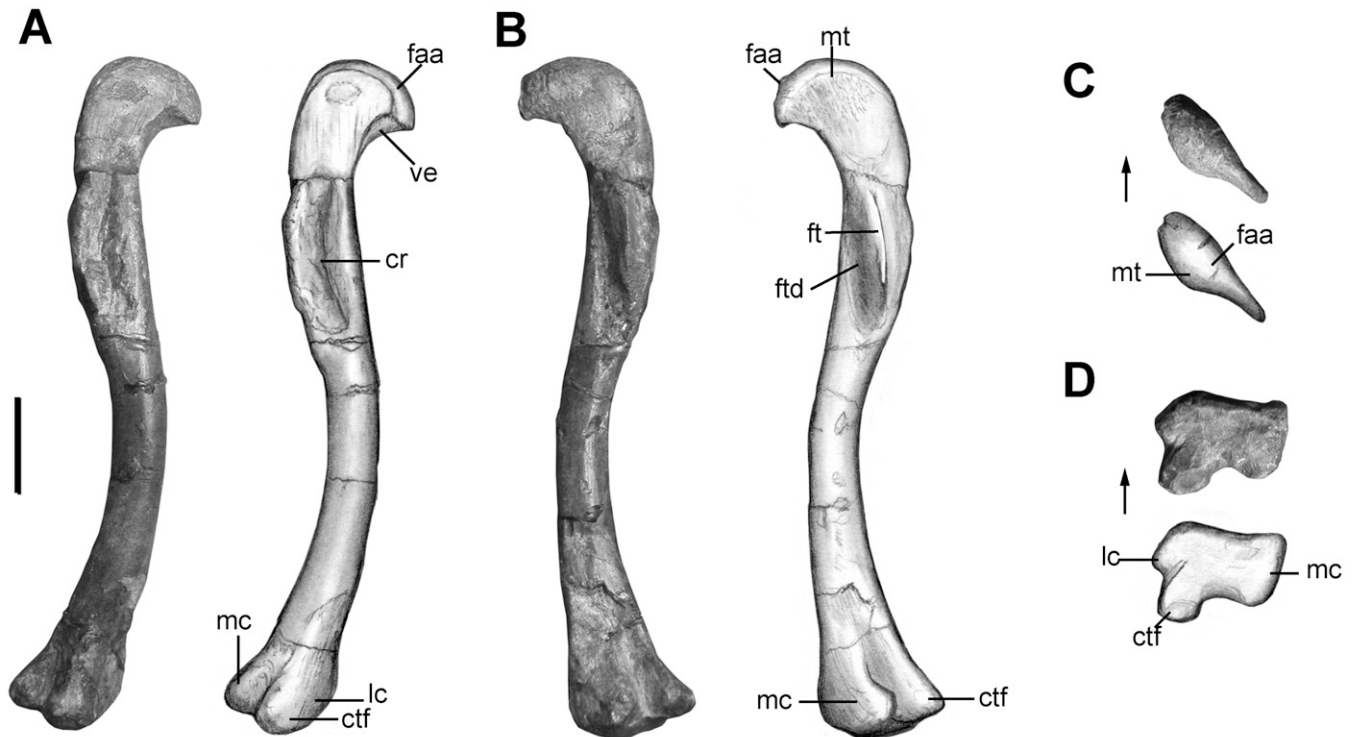


FIGURE 3. The right femur of *Lagerpeton chanarensis* (PVL 4619) in **A**, anterolateral view; **B**, posteromedial view; **C**, proximal view; **D**, distal view. The specimen is badly crushed on the anterolateral side on the proximal half of the shaft. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

with the exception of some rauisuchians) (see Hutchinson, 2001). This ratio is unknown for the femora of *Lagerpeton* and *Marasuchus*.

The femoral head is directed anteromedially, similar to the plesiomorphic condition found in basal archosauriforms, pseudosuchians, and early dinosaurs (Carrano, 2000). The dorsal surface and ventral margin of the femoral head meet at a sharp acute angle that Sereno and Arcucci (1993) described as “hook-shaped” in *Lagerpeton*. The neck leading to the anterior-most portion of the head is more elongated than that of other ornithodirans and appears to be unique to *Lagerpeton* and *Dromomeron*. An anterolateral tuber on the proximal portion is absent in all specimens. The pseudosuchian *Effigia okeeffeae* (AMNH FR 30587) also lacks an anterolateral tuber (Nesbitt, 2007) though phylogenetic analysis (Irmis et al., 2007; this study) suggests that the absence in this taxon is convergent with that of Lagerpetidae, which represents a unique condition among ornithodirans. The anterolateral surface of the proximal end of the femur is slightly convex in *Dromomeron*, in contrast to the completely flat anterolateral surface of *Lagerpeton* (listed as an autapomorphy by Sereno and Arcucci, 1994b). The proximal articular surface arcs nearly 180 degrees from the ventral “hook” of the head to the posterior edge of the proximal surface. Here, the bone, though well ossified, has a spongy texture typical of the articular ends of reptile limbs. The dorsal articular surface is convex. The posteromedial tuber (termed “medial tuberosity” in Sereno and Arcucci, 1994b) is medially expanded nearly obscuring the anteromedial tuber, similar to *Lagerpeton*. The anteromedial tuber, though worn off in GR 218 and not well preserved in other *D. romeri* specimens, is present in the well-preserved examples of *D. gregorii*. A shallow cleft separates the anteromedial and large posteromedial tubera. Unlike in dinosaurs, the path for the ligamentum capitis femoris is not marked by a distinct cleft. The facies articularis antitrochanterica (Baumel and Witmer, 1993) extends slightly more ventrally on the posteromedial side of the femoral head than on the anterolateral side. This expansion is typical of dinosauromorphs and is useful in identifying ornithodiran versus pseudosuchian femora (Nesbitt et al., 2007).

Unique to *Lagerpeton* and *Dromomeron* is an emargination that lies on the lateral surface ventral to the articular head (see Figs. 1, 2). A sharp rim outlines the dorsal and posterior extent of the ventral emargination. The bone has an unfinished texture within the emargination.

The anterolateral surface of the proximal portion of the femora of *D. romeri* and smaller specimens of *D. gregorii* is smooth, whereas a small anterior trochanter (attachment site of the M. ilirotrochantericus caudalis) is present on the two largest specimens of *D. gregorii* (TMM 31100-1306 and TMM 31100-464). The anterior trochanter is rugose, tapers dorsally, and is not separated from the shaft. The more well-preserved TMM 31100-1306 also bears a small but distinct trochanteric shelf, which like the anterior trochanter is rough in texture. The shelf wraps around the posterolateral edge of the proximal part of the femur and arcs ventrally, eventually merging with the linea intermuscularis caudalis.

A faint linea intermuscularis cranialis originates on the medial edge of the anterior trochanter and continues anteroventrally toward a small foramen in *Dromomeron gregorii*. In the vicinity of this foramen, the linea intermuscularis cranialis divides into two parallel ridges separated by a shallow furrow. The medial of these two ridges extends distally as an even fainter line, gently arcing toward the anteromedial edge of the distal portion of the femur. This feature is also present in the basal sauropodomorph *Saturnalia tupiniquim* (Langer, 2003). An additional small ridge lies proximal to the posterior and lateral expression of the trochanteric shelf. It parallels the trochanteric shelf (Fig. 2). This small ridge is also present, although more distinctly, in some

specimens of *Coelophysis bauri* (e.g., AMNH FR 30617). A small proximally opening foramen is located on the anterolateral edge just dorsal to mid-portion of the shaft in both *D. romeri* and *D. gregorii*. A distinct ridge for the attachment of the M. caudifemoralis longus (fourth trochanter) is absent in the holotype (GR 218) and all other specimens of *D. romeri*. Although *D. romeri* lacks a “fourth trochanter,” a faint, rugose muscle scar marks the insertion point for the M. caudifemoralis longus; this is best preserved in GR 219. The proximal extent of the muscle scar is just below the neck of the femoral head, and forms an elongate, elliptical rugose area on the posteromedial surface of the femur. This scar gradually narrows distally, traversing the shaft posterolaterally. The scar ends where it merges with the linea intermuscularis caudalis at the diaphysis. This well-developed scar indicates that the presence/absence of the fourth trochanter does not necessarily correlate with the development of the femoral retractor muscles (Norell and Makovicky, 1999). A similar situation (large muscle scar merging with the linea intermuscularis caudalis) is also found in ratite birds (e.g., *Struthio camelus*, UCMP 9349; *Rhea americana*, UCMP 129668; and *Dromaius novaehollandiae*, UCMP 119204), which, like all avialans, lack a distinct fourth trochanter.

The attachment site for the M. caudifemoralis longus in *D. gregorii* is different from both *Lagerpeton* and *D. romeri*. Like most basal archosaurs, the fourth trochanter of *D. gregorii* is mound-like and all specimens have a shallow medial pit (see below), though the position of the trochanter in *D. gregorii* is more proximally located than in pseudosuchians. The proximal half of the fourth trochanter thins into a sharp ridge in the larger specimens of *D. gregorii*. In contrast, *Lagerpeton* has an elongated and enlarged sharp (referred to as “aliform”) attachment site for the M. caudifemoralis longus and a long deep medially adjacent pit (Sereno and Arcucci, 1994b). The fourth trochanter stretches from the proximal head along nearly 1/3 of the proximal length of the femur in *Lagerpeton*. Unlike the fourth trochanter of *Lagerpeton*, the fourth trochanter of *D. gregorii* is well separated from the femoral head.

The distal end is well preserved in the holotype of *D. romeri* (GR 218) and in all six specimens of *D. gregorii* from Otis Chalk Quarry 3; it expands gradually and is much larger in size relative to that of *Lagerpeton*. The distal expansion is comparable in the similarly-sized holotypes of *D. romeri* and *D. gregorii*. The anterior surface bears a muscle scar delineated by a mediolaterally oriented ridge in all of the specimens of *D. romeri* and most of the specimens of *D. gregorii* (see ontogeny section). The amount of surface area covered by this muscle scar varies slightly in its mediolaterally extent in specimens of *D. gregorii*. Proximal to the ridge, the bone texture is unfinished. The muscle scar arcs proximally onto the lateral side of the femur. Here, there is a small laterally directed flange that is formed where the unfinished bone meets finished bone. The position of this muscle scar corresponds to the distal origin of the M. femorotibialis internus (= M. femorotibialis medialis and M. femorotibialis intermedius in Aves) in crocodylians (Hutchinson, 2001). However, the relationship of this muscle scar to the linea intermuscularis cranialis, the presence of a small anteromedial ridge on the distal femur (see below), and the presence of an anterior trochanter/trochanteric shelf (suggesting proximal migration of the derivatives of the M. ilirotrochantericus caudalis), indicate that the scar may represent an enlarged area of distal origin for the M. femorotibialis externus (= M. femorotibialis lateralis in Aves), a condition present in Aves and most basal dinosaurs (Hutchinson, 2001; Carrano and Hutchinson, 2002). A distinct scar where the presumed distal portion of M. femorotibialis externus originates is only present in *Dromomeron* among non-theropod ornithodirans (see character 128 in phylogenetic analysis).

The medial side of the distal end is concave in *D. romeri* and flat or convex in *D. gregorii* and *Lagerpeton*. An autapomorphy

of *D. romeri* is an anteromedial edge that is developed into a sharp ridge extending proximally along the shaft. The anteromedial corner of *D. gregorii* is about 90° in all specimens. In distal view, the anterior edge is more sigmoidal in *D. romeri* than in *D. gregorii*.

The enlarged crista tibiofibularis (= “fibular condyle”) of *Lagerpeton* has been used to differentiate it from all other archosaurs (Sereno and Arcucci, 1994b). *Dromomeron* possesses an enlarged crista tibiofibularis (Figs. 1, 2) that is even more robust than that of *Lagerpeton*. The bulbous crista tibiofibularis also expands medially and restricts the posterior intercondylar groove to a slit in the larger specimens of *D. gregorii*. A shallow but distinct groove separates the crista tibiofibularis from the lateral condyle on the distal surface. A similar groove is present in *Silesaurus*, *Saturnalia*, and coelophysoid theropods. The medial condyle of *D. gregorii* is square-shaped whereas it is rounded in *D. romeri* and *Lagerpeton*. The lateral condyle is gently rounded in *Dromomeron*, similar to other dinosauromorphs and *Euparkeria*. The articular surface of the distal end on *Dromomeron* is covered with a series of small grooves and rounded ridges.

### Tibia

Five tibiae (GR 220, length = 113.2 mm; GR 222, length = 136.6 mm; GR 239, length = 137.3 mm) have been recovered from the Hayden Quarry and referred to *D. romeri* (Fig. 4), and three tibiae assigned to *D. gregorii* (Fig. 5) (TMM 31100-1314, length = 104.9 mm; TMM 31100-278, length = 88.5 mm; TMM 31100-1321, length = 105 mm) are known from Otis Quarry 3. Each tibia can be referred independently to *Lagerpetidae* based on the presence of an enlarged slot for the posterior ascending process of the astragalus on the distal tibia, and can further be referred to *Dromomeron* based on the presence of a ventrally deflected posterolateral condyle on the proximal end.

The proximal portion of the tibia is typical for dinosauromorphs; it has two posterior condyles separated by a shallow groove, and a prominent, anteriorly directed, and rounded cnemial crest. The cnemial crest is directed anteriorly as in *Lagerpeton*, but differs from dinosauriforms where the cnemial crest curves anterolaterally. A small, shallow furrow lies between the cnemial crest and the posterolateral condyle. The anterior portion of the cnemial crest is bulbous similar to *Lagerpeton*. Ventral to the proximal surface, the cnemial crest forms the sharp anterior edge of the tibia for the proximal third of the shaft. This crest extends distally and slightly medially as a faint anterior intermuscular line. It becomes a low crest again distally at the anteromedial corner of the tibia. In *Dromomeron romeri*, this low crest intersects the proximal tip of a robust anteromedial buttress on the distal end of the tibia. This anterior intermuscular line probably delineates the anteromedial border of the origin of *M. tibialis anterior* (Carrano and Hutchinson, 2002). The two posterior condyles are equal in size, but not in shape. The posterolateral condyle terminates in a small point on the posterolateral corner. This corner forms a small hook in lateral view. The posteromedial condyle is gently rounded. Unfinished bone surrounds the posterior condyles. There is no distinct facet for the fibula on the posterolateral condyle. There are small grooves and rounded ridges scattered on the proximal surface of the tibia.

The tibial shaft is nearly round in cross-section at mid-shaft and throughout much of its length. A small, proximally opening foramen is present on the lateral side, one-third of the way down the shaft like in other archosaurs. Poor preservation prevents the identification of the foramen in *Lagerpeton*. There is a flat area for the contact of the fibula on the lateral side on the bottom third of the shaft in both species of *Dromomeron*.

The distal end of the tibiae of *Lagerpeton*, *D. romeri*, and *D. gregorii* differ in several aspects. The anterior margin of the tibiae of *Lagerpeton* and *D. gregorii* are rounded in distal view whereas it is nearly straight in *D. romeri*. All three taxa share a nearly straight posterior edge. A small posterior projection divides the posterior portion of the distal end and stretches proximally; this feature is bordered medially and laterally by grooves in *Lagerpeton* (Sereno and Arcucci, 1994b), but this condition is absent in *Dromomeron*. The posterolateral corner terminates sharply in *Dromomeron*; it is rounded in *Lagerpeton*. All three taxa bear the unique feature of a slot on the posterolateral portion of the distal end for reception of the posterior ascending process of the astragalus. All three taxa have a small anteromedially trending groove on the body of the distal surface of the tibia which originates from the slot that accepts the posterior ascending process of the astragalus. This groove fits the ridge that separates the anterolateral and posteromedial basins of the astragalus (see below). This groove is more distinct and deeper in *D. romeri* (Fig. 4) than in *D. gregorii* (Fig. 5) and *Lagerpeton*. The anteromedial–posterolateral trending groove divides the distal end of the tibia into two distinct anterolateral and posteromedial processes. This groove transects the distal end of the tibia and terminates in a slot that fits an enlarged flange on the anteromedial corner of the astragalus of *D. romeri* (an autapomorphy). A robust anteromedial buttress of bone is present just proximal to this slot in *D. romeri*. The anterolateral process of the distal tibia is rounded and fits into the anterolateral basin of the astragalus. The posteromedial process is larger and fits into the posteromedial basin of the astragalus. *D. gregorii* has a similar set of processes, but they are poorly expressed in comparison. The distal surface of the tibia is poorly preserved in *Lagerpeton*; however, the presence of shallow anterolateral and posteromedial basins of the astragalus suggest that the tibiae had corresponding anterolateral and posteromedial processes as in *Dromomeron* tibiae.

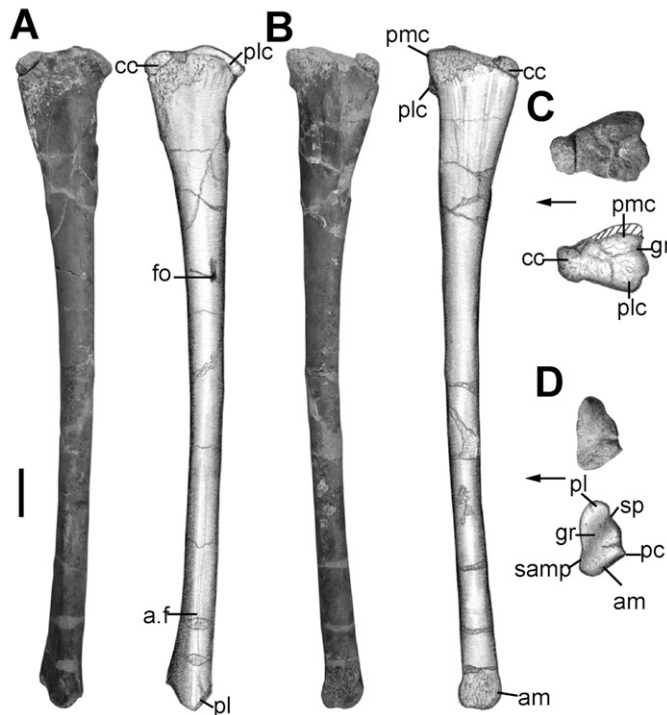


FIGURE 4. The left tibia of *Dromomeron romeri* (GR 220) in **A**, lateral view; **B**, medial view; **C**, proximal view; **D**, distal view. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

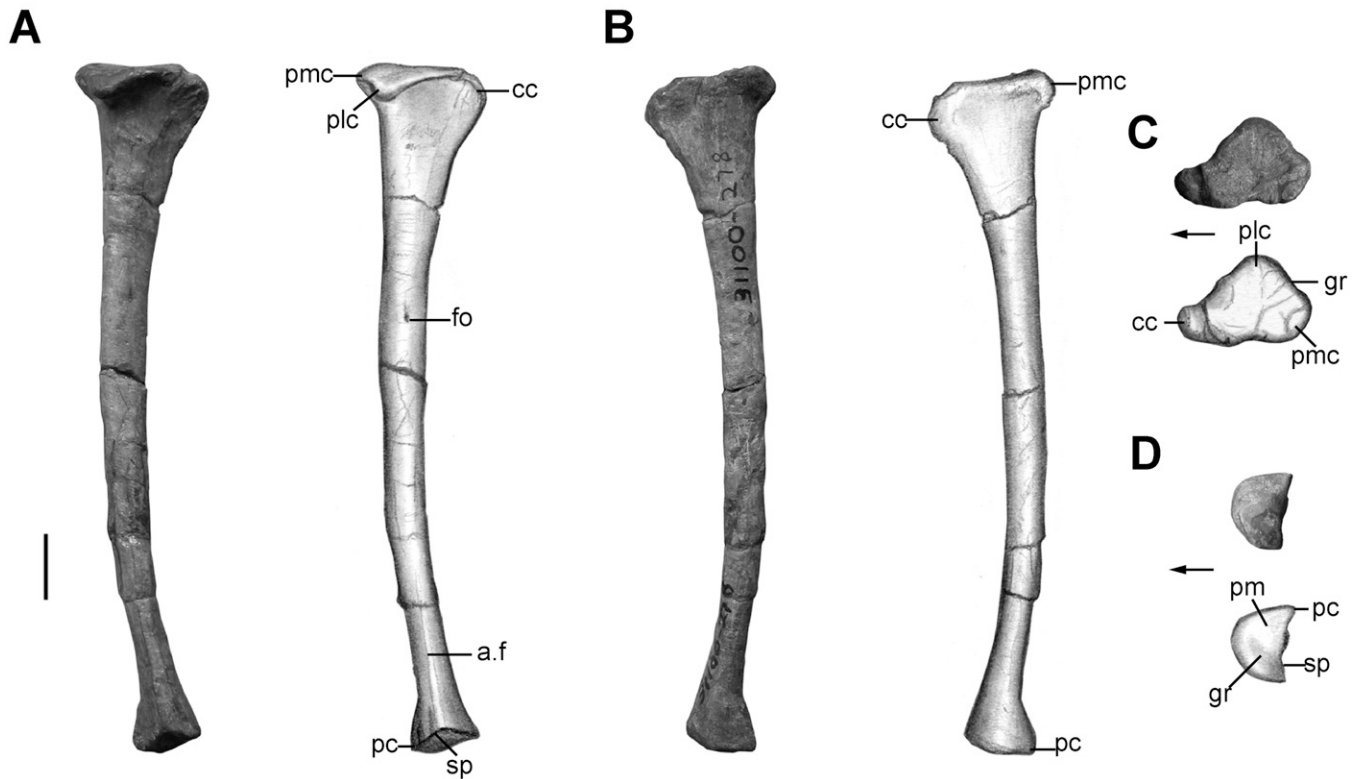


FIGURE 5. The right tibia of *Dromomeron gregorii* (TMM 31100-278) in **A**, lateral view; **B**, medial view; **C**, proximal view; **D**, distal view. Much of the details of the surface TMM 31100-278 were lost during preparation in the 1940's, but the distal surface was reprepared for this project. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

### Fibula

The proximal three quarters of the fibula is preserved in GR 238. This portion of the fibula is 99 mm in length and well preserved despite some mediolateral crushing (Fig. 6). It is smaller in diameter than its corresponding tibia. Though the distal end of the fibula is missing, the relative size of the fibular facet of the astragalocalcaneum of similar-sized specimens of *D. romeri* suggests that the proximal end of the fibula is broader anteroposteriorly than the distal end, similar to the condition in *Marasuchus* (Bonaparte, 1975) and most ornithomirans.

In lateral aspect, the proximal end is asymmetrical, with the posterior end overhanging the shaft farther than the anterior end like in *Lagerpeton* (PVL 4619). This asymmetry gives the posterior edge of the proximal end of the fibula a gently postero-proximally arcing outline in lateral aspect, whereas the anterior border is straighter. The lateral side of the fibula is weakly convex and the medial side is concave. Though accentuated by medio-lateral crushing, a broad medial fossa is present near the proximal end of the bone. The posterior edge of the proximal end is thicker mediolaterally than the anterior edge, and there is some unfinished bone on the posterior side, near the proximal articulation. The posterior side of the medial fossa also exhibits some longitudinal scarring/striations at this thickened area. Similar scarring is present in *Saturnalia* and other basal dinosaurs (Langer, 2003). The proximal surface is rugose and slightly concave, though crushing has shifted the medial side of the proximal surface slightly distally relative to the lateral edge.

A proximodistally elongate tuberosity is present on the anterolateral surface of the fibula, approximately one third of the way down the diaphysis. This tuberosity is approximately 25 mm long, and is likely the insertion site of *M. iliofibularis*. This tubercle begins on the anterior edge of the fibula, and curves

slightly laterally, extending distally down the fibular diaphysis, as in *Lagerpeton* (PVL 4619) and *Marasuchus* (PVL 3871). The *M. iliofibularis* tubercle of GR 238 is slightly less robust and rugose than that of *Lagerpeton* (PVL 4619). Distal to the *M. iliofibularis* insertion, on the anterolateral edge of the shaft near the broken end of the fibula, there is faint longitudinal scarring. This scarring could represent the origin of *M. fibularis longus* and *M. fibularis brevis*, which attach in this area in extant archosaurs (Carrano and Hutchinson, 2002).

### Astragalocalcaneum

An isolated, well-preserved right astragalocalcaneum (GR 223; Fig. 7) was found close to the other remains of *D. romeri* in the Hayden Quarry. An identical left astragalocalcaneum from the Snyder Quarry is referable to *Dromomeron* (NMMNH P-35379) (Irmis et al., 2007), though it was previously referred to a coelophysoid theropod (Heckert et al., 2003). Even though both specimens were found isolated, the astragalocalcaneum share the following two derived character states with *Lagerpeton*: a large posterior ascending process of the astragalus; and the co-ossification of the astragalus and calcaneum (convergent with coelophysoid theropods) (Irmis et al., 2007). Furthermore, they possess a large anteromedial crest that fits perfectly into a corresponding autapomorphic slot in the distal end of the tibia of *Dromomeron romeri*.

The astragalus and calcaneum are co-ossified and a small groove is visible at the articulation between the elements. Among archosaurs, co-ossification of the proximal tarsals only occurs in pterosaurs, *Dromomeron*, *Lagerpeton* (Serenio and Arcucci, 1994b), the ornithischian *Heterodontosaurus* (Santa Luca, 1980), and some theropods (including coelophysoids and avialans; Clarke et al., 2006; Irmis et al., 2007). An anteromedial-

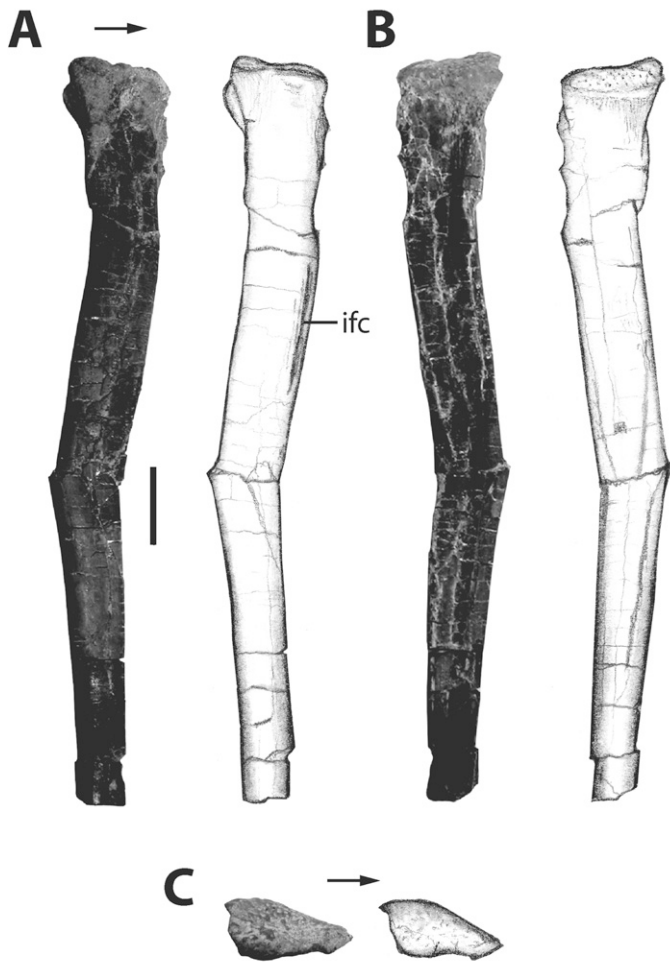


FIGURE 6. The right fibula of *Dromomeron romeri* (GR 238) in **A**, lateral view; **B**, medial view; **C**, proximal view. The specimen is mediolaterally crushed. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

posterolaterally oriented groove divides the fibular facet into portions on the astragalus and calcaneum. A similar condition is present in *Marasuchus* (PVL 3870), *Silesaurus* (Dzik, 2003); in contrast, this articulation is sinuous in *Saturnalia* (Langer, 2003) and directed anteroposteriorly in ornithischians (*Scutellosaurus*, UCMP 130580; *Scelidosaurus*, BMNH R1111), most sauropodomorphs (e.g., *Plateosaurus*, SMNS 13200), and theropods (e.g., *Liliensternus*, MBR. 2175; *Coelophysis*, AMNH FR 30576). The orientation of the articular surface between the astragalus and calcaneum in *Lagerpeton* is not visible in known specimens.

The astragalus of *Dromomeron romeri* is more than twice the mediolateral width of the calcaneum, a synapomorphy of Dinosauromorpha (Sereno and Arcucci, 1994b). The anteroposterior length of the astragalus is constant across the entire width of the element, resulting in a rectangular bone. In contrast, the anteroposterior length of the astragalus of *Lagerpeton* decreases laterally as it approaches the articulation with the calcaneum (Sereno and Arcucci, 1994b). In proximal view, the anterior edge of the astragalus of *Dromomeron* is concave and the posterior edge is nearly straight.

The proximal surface of the posterior edge of the astragalus of *Dromomeron romeri* possesses a posterior ascending process. This process fits into a complementary slot on the posterior side

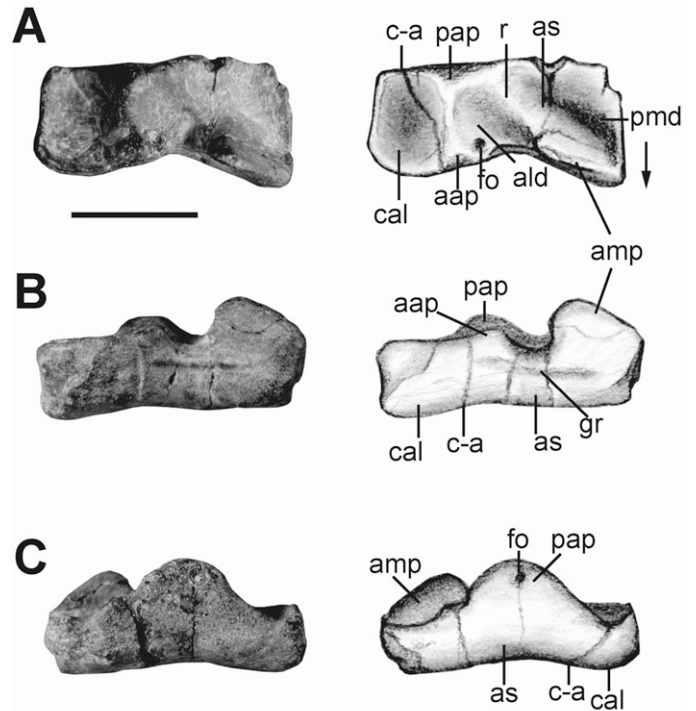


FIGURE 7. The right astragalocalcaneum of *Dromomeron romeri* (GR 223) in **A**, proximal view; **B**, anterior view; **C**, posterior view. Scale equals 1 cm. Arrow indicates anterior direction. See text for anatomical abbreviations.

of the tibia. The posterior ascending process of *Lagerpeton* and *Dromomeron* is unique among ornithodirans, but not among other archosaurs. The astragalus of suchians, including *Effigia okeeffeae* (AMNH FR 30587) and *Typothorax coccinarum* (MCZ 1488), has a similarly positioned posterior process that is slightly lower in height.

A small anteroposteriorly oriented ridge originates on the lateral side of the posterior ascending process of the astragalus, dividing the tibial and fibular facets. As the ridge reaches the anterior margin, it expands proximally to form a small process. This small pyramid-shaped process may be homologous to the anterior ascending process of dinosauriforms. The anterior processes of *Dromomeron romeri* and dinosauriforms occupy the same position on the astragalus and both serve to separate the tibia from the fibula. However, there is no distinct facet on the tibia of *D. romeri* (GR 222) that would articulate with this small anterior process, unlike the condition in dinosauriforms. Furthermore, the anterior process of *Dromomeron* lacks the proximomedially facing concavity that articulates with the distal portion of the tibia in dinosaurs. A small foramen is located on the medial portion of the small anterior process in *Dromomeron*. No foramen is present on the anterior side of the process (unlike most dinosauriforms).

A low, rounded ridge originates on the medial side of the posterior ascending process of the astragalus and extends anteromedially to a large, proximally projecting crest on the anteromedial edge of the distal portion of the tibia. This ridge divides the anterolateral and posteromedial basins. The posteromedial basin is ~30% larger than the anterolateral basin. The anterolateral basin opens anteriorly and is bordered posteriorly by the posterior ascending process, anterolaterally by the small anterior process, and anteromedially by the large proximally projecting crest. The posteromedial basin opens medially and is bordered



anteriorly by the large proximally projecting process and posteriorly by a small rim. A similar set of basins is present in *Lagerpeton*, but they are much more distinct in *Dromomeron romeri* (the distal portion of the tibia of *D. gregorii* suggests that the astragalus would also have two basins separated by a ridge). Furthermore, the basins correspond to convex surfaces of the distal articular end of the tibia of *Dromomeron*. No such convex surfaces of the distal articular end of the tibia exist in *Lagerpeton*. The absence of these features of the distal end of the tibia suggest that either the articulation between the tibia and astragalus was not as closely appressed as that of *Dromomeron*, or that the distal end of the tibia of *Lagerpeton* is incompletely preserved. The configuration of basins divided by a low ridge is unique to *Lagerpeton* and *Dromomeron* among dinosauriforms, but occurs in many suchians (e.g., *Shuvosaurus*, crocodylomorphs). The basins and ridges on the astragalus have a precise complementary fit to the distal surface of the tibia, suggesting that the articulation had little room for extensive soft tissue.

A large proximally projecting crest is located on the anterior edge on the medial half of the astragalus of *Dromomeron romeri*. This crest is unique to *D. romeri* and articulates with a distinct facet on the tibia. Although the astragalus of *D. gregorii* is unknown, a similar anteromedial crest is probably absent because the tibia of *D. gregorii* lacks a facet for the reception of this crest. The crest reaches its maximum height at its lateral end and then decreases in height medially. The proximal edge of the process is blade-like, the posterior surface is flat, and the anterior surface is slightly convex. The posteromedial corner of the astragalus is slightly expanded proximally. The presence of both a well-developed posterior ascending process and proximal anteromedial crest tightly locks the astragalus with the tibia, rendering the astragalocalcaneum completely immobile in the mesotarsal ankle joint.

The posterior side of astragalus is mediolaterally convex. This posterior ascending process is situated in the center of the posterior margin of the astragalus. The medial and lateral proximal margins are symmetrical and a small foramen is located on the posterior side of its posterior ascending process. It is not clear if a foramen is present at the same location in *Lagerpeton*, but it occurs in the corresponding location in the astragalus of the suchian *Effigia okeeffeae* (AMNH FR 30587; Nesbitt, 2007). This feature has not been reported in any other pseudosuchian; however, the foramen is very small and the apparent absence of the feature in other taxa may be related to the quality of preservation. The medial side is crescent-shaped with a small depression is located in its center.

The anterior side of the astragalus is convex mediolaterally, but concave in proximal view. The large, proximally projecting anteromedial process dominates the medial half of the astragalus. A shallow mediolaterally oriented groove is located in the middle of the anterior surface. A similar groove is also present in *Marasuchus* and other dinosauriforms (Sereno and Arcucci, 1994a), including basal theropods (Smith et al., 2007). The distal surface of the astragalus of *D. romeri* is mediolaterally convex.

The calcaneum is similar to that of most other dinosauriforms except *Marasuchus*. There is no calcaneal tuber unlike pseudosuchians and basal archosauriforms. The proximal surface is simply concave and surrounded by a thin, distinct rim. The angles of the anterolateral and posterolateral corners are about 90°. A small groove defines the calcaneum-astragalus contact and indicates that the ventral portion of the calcaneum is positioned underneath the astragalus where the two meet. This configuration is typical for basal dinosauriforms (Sereno and Arcucci, 1994a). In lateral view, the calcaneum is crescent-shaped. The ventral side is smoothly convex as in other dinosauriforms and there is no flat surface for the articulation with distal tarsal IV. In contrast, the ventral surface of the calcaneum is flat in *Eupar-*

*keria* and pseudosuchians. Sereno and Arcucci (1994) argued that the flat ventral surface represents the plesiomorphic state for Archosauria.

## Pes

Several partially articulated pedal digits from the left pes are present in GR 238 (Fig. 8). The identification of the elements as phalanges II-2, II-3 (ungual), III-2, III-3, IV-1, and IV-2 are based on comparisons to *Lagerpeton* and *Marasuchus*. The shafts of all non-terminal phalanges are slightly deeper dorsoventrally than broad mediolaterally, with the exception of IV-2, where the opposite is true. The distal ends of all non-terminal phalanges have extensor pits on their dorsal surfaces, and well-developed lateral and medial condylar ridges. The condylar ridges form an arc of approximately 270°. In dorsal or ventral aspect, the long axes of the lateral condylar ridges are parallel to the long axes of the phalanges, whereas the medial condylar ridges have long axes that extend proximolateral–distomedial relative to the long axes of the phalanges. Phalanges III-2, III-3, IV-1, and to a slightly lesser degree IV-2, are unique in that the lateral ligament pits are well-excavated, but medial pits are completely absent, though some extremely faint scarring is present in the area where they would be. Some small theropod dinosaurs (e.g., *Masiakasaurus*) possess medial ligament pits that are shallower relative to the lateral ones; however, both collateral ligament pits are still well developed (Carrano et al., 2002). The medial surfaces of the phalanges of *Lagerpeton* (PVL 4619) are poorly preserved, but it is clear that medial ligament pits are present at least in II-2, III-2, IV-2, IV-3, and IV-4, suggesting that the absence of these pits may be an autapomorphy of *D. romeri* or *Dromomeron* (Fig. 8C, 8H).

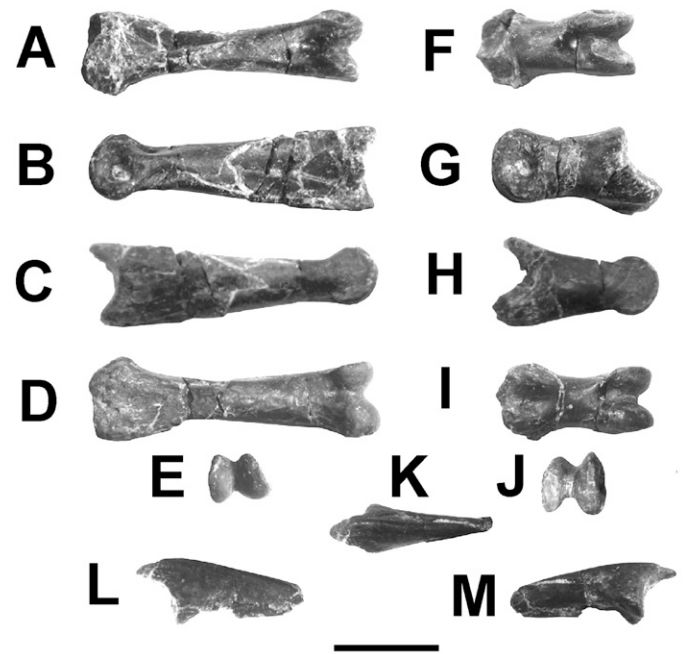


FIGURE 8. The phalanges of *Dromomeron romeri* (GR 238). Phalanx IV-1 in **A**, dorsal view; **B**, lateral view; **C**, medial view; **D**, ventral view; **E**, anterior view. Phalanx III-3 in **F**, dorsal view; **G**, lateral view; **H**, medial view; **I**, ventral view; **J**, distal view. Phalanx II-3 (ungual) in **K**, medial view; **L**, dorsal view; **M**, lateral view. Scale equals 1 cm.

Phalanx II-2 is missing both its dorsal and ventral intercondylar process at the proximal end. Despite the breakage, it is clear that the dorsal intercondylar process is asymmetrical, and slightly medially placed relative to the long axis of the phalanx. Two well-developed articular facets are still clearly present, separated by a sharp keel on the midline of the proximal surface. The dorsal surface bears almost no depression at its distal end where the hyperextensor pit would be. The ventral surface is marked by two low tubercles on the lateral and medial edges that are heavily scarred. Both muscle scars extend distally for half the length of the phalanx and have rounded, triangular apices. The medial scar extends slightly further distally than the lateral one. These tubercles are likely insertion points for tendons of flexor muscles (e.g., *M. flexor digitorum longus*). Distal to the flexor tubercles, a shallow fossa is present on the ventral surface, between the proximal tips of the condylar ridges. The medial ligament pit is not as deeply excavated as the lateral pit, and is situated slightly higher dorsally on its condylar ridge. The condylar ridges are subequal in size.

Phalanx II-3 (ungual) (Fig. 8I–K) is extremely mediolaterally asymmetrical, and only weakly recurved. The proximal surface has two deep, kidney-shaped articular facets for the distal condyles of II-2; these facets are separated on the midline by a low keel. A short dorsal intercondylar process extends proximally. This triangular eminence is also asymmetrical, with its midline located medially relative to the midline of the body of the unguis. The dorsal surface of the dorsal intercondylar process is not parallel to the ventral edges of the proximal articular facets, but is canted slightly medially. Several longitudinal scars are present on the dorsal surface of the dorsal intercondylar process, and may indicate the terminal insertion of *M. extensor digitorum longus*. The dorsal edge of the unguis is sharp, but smoothly rounded. This edge is weakly concave medially, and its proximal end intersects the proximal articular surface just dorsal to the dorsal apex of the medial articular facet. Here, the dorsal edge of the unguis merges with the mediolateral edge of the dorsal intercondylar process. The ventral surface of the unguis has a shallow depression near the proximal end with two small, scarred tubercles on either side, likely marking the insertion for tendons of flexor muscles (e.g., *M. flexor digitorum longus*). The lateral edge of the ventral surface of the unguis is sharper and more flange-like than the low, rounded medial edge. The medial blood groove is situated higher dorsally than the lateral groove, and neither groove extends to the proximal articular facet. The medial blood groove is very deep dorsoventrally, as can be seen in cross section at the broken distal tip.

Phalanx III-2 has a well-developed dorsal intercondylar process that is similar in its asymmetric development to that of II-3; however, the midline keel of the proximal articular surface of III-2 extends onto the lateral side of the ventral surface of the dorsal intercondylar process. A small, triangular ventral intercondylar process is also present, but does not extend further proximally than the dorsal intercondylar process. On the ventral surface, a shallow fossa near the proximal end is bordered by two triangular flexor tubercles. These tubercles are more robust and heavily scarred than those of II-2, and the medial tubercle extends further distally than the lateral one, though neither extends past half the ventral length of the phalanx, unlike II-2. In contrast to the medial side, the scarring on the lateral flexor tubercle extends dorsally up along the lateral edge of the proximal articular surface, nearly reaching the dorsal face of the phalanx. The shaft of III-2 is rotated about its long axis slightly laterally at its distal end. This twisting is most apparent in ventral aspect, because the distal apex of the medial flexor tubercle points toward the proximal end of the lateral condylar ridge. A deep extensor pit is developed on the dorsal surface, just proximal to the ginglymus. Ventrally, a shallow fossa is also present proximal to the ginglymus. The lateral condylar ridge is

more robust than the medial ridge, particularly ventrally, and its ligament pit is the deepest of all preserved phalanges. When articulated, the asymmetric development of the distal condyles and the medial orientation of the long axis of the medial condyle combine to divert phalanx III-3 medially relative to the long axis of III-2.

Phalanx III-3 (Fig. 8F–J) has a much more symmetrical dorsal intercondylar process compared to other phalanges. Its ventral intercondylar process is also well-developed and extends further proximally than the dorsal process, contrasting with the condition in III-2. This gives the lateral and medial edges of the proximal articular facets an extremely concave appearance in lateral or medial aspect. The extensor pit of III-3 is the deepest of any of the phalanges, and it is bordered by a faint rounded rim (more prominent on its medial side) that occupies almost the entire distal half of the dorsal surface of the phalanx. A small, elliptical foramen is present on the medial face of III-3, near the proximal end. Ventrally, two robust, triangular flexor tubercles are present. They do not extend as far distally relative to those of III-2, and the scarring on them extends dorsally on both the medial and lateral face of the phalanx (though it is more pronounced laterally). As in III-2, the lateral condylar ridge is more well-developed than the medial ridge, especially ventrally. The ventral fossa between the proximal ends of the condylar ridges is deeper and more well-rimmed in III-2 than in any of the other phalanges.

Phalanx IV-1 (Fig. 8A–E) is the longest of all preserved phalanges, and its medial face is crushed along its proximal half (though distortion to the proximal articular surface is less pronounced than along the shaft). The short dorsal intercondylar process is more rounded and less triangular than those of the other phalanges. The proximal articular facet is cup-shaped with no midline keel or separation into distinct lateral and medial facets. The ventral flexor tubercles are only faint bumps of scarred bone, in contrast to the robust tubercles present in the other phalanges. A small, elliptical foramen is present on the ventral surface of IV-1 at the middle of the shaft. Distally the lateral condylar ridge is more robust than the medial ridge, and is particularly bulbous ventrally, where it is nearly twice as wide mediolaterally than the medial condylar ridge. In distal aspect, this also results in the ventral portion of the lateral condylar ridge being laterally directed relative to the dorsal portion. The extensor pit on the dorsal surface of the distal end is only developed as a shallow fossa.

Phalanx IV-2 has a well-developed proximal articular surface similar to that of III-3 in most details. A small piece of the medial edge of the proximal articular facet is missing. The flexor tubercles are only slightly less robust than those of III-3. As in III-3, scarring associated with the tubercles extends further dorsally on the lateral side. A broad, shallow extensor pit occupies most of the distal half of the dorsal surface. Slightly more scarring is present on the medial face of the intercondylar ridge than in III-2, III-3, and IV-1, but no fossa is present. A small elliptical foramen is present on the medial face of IV-2, in a similar position to the foramen on III-3. As mentioned above, the shaft is wider mediolaterally than tall dorsoventrally. As in the other non-terminal phalanges, with the exception of II-2, the lateral intercondylar ridge is more bulbous and well-developed than the medial ridge.

#### Specimens From Other Localities

**AMNH FR 2721**—In a series of publications in the 1880s, E. D. Cope named three species of *Coelophysis*: *C. longicollis*; *C. bauri*; and *C. willistoni* (Cope, 1887a; 1887b; 1889). Cope (1887b) identified a small proximal portion of a tibia (AMNH FR 2721) and assigned it to *C. bauri*. This identification and assignment was later confirmed by von Huene (1906), who also

illustrated it for the first time (Huene, 1915; fig. 41a, b, c). Oliver Rauhut (unpublished note in collections) recently re-identified the specimen as a distal portion of a femur. We agree with this identification and assign the specimen to *Dromomeron* based on the presence of a large, inflated crista tibiofibularis. Furthermore, AMNH FR 2721 shares with *Dromomeron romeri* a distinct sharp anteromedial edge of the distal end of the femur.

The provenance of this specimen is speculative. Most authors (Padian, 1986; Hunt and Lucas, 1991; Sullivan et al., 1996) agree that the holotype locality of Baldwin's *Coelophys* is near "Arroyo Seco" in the Petrified Forest Member and not from the overlying "siltstone member" of the Chinle Formation. Thus, this specimen and all other known specimens of *D. romeri* are probably restricted to the Petrified Forest Member of the Chinle Formation in the Chama Basin.

**AMNH FR 30648 and AMNH FR 30649**—Two distal portions of tibiae assignable to *D. romeri* were found among uncurated specimens associated with Baldwin's *Coelophys* material. The preservation and matrix are identical to other specimens collected by Baldwin near "Arroyo Seco". The distal portions of the tibiae are identical to those of the referred tibiae of *D. romeri*, preserving the following diagnostic characters: a slot on the posterior side that receives the posterior ascending process of the astragalus; and another slot for the reception of the large anteromedial dorsal process of the astragalus.

**UCMP 25815**—The distal portion of a left femur was found in the *Placerias* Quarry (UCMP loc. A269) near St. Johns, Arizona. It bears the diagnostic inflated crista tibiofibularis and is thus referable to *Dromomeron*. It lacks the flared anteromedial corner that is autapomorphic for *D. romeri*, and is therefore referable to *D. gregorii*.

**TTU-P Specimens**—Proximal portions of femora from a dinosauromorph are known from MOTT VPL 3869 and MOTT VPL 3898 from the Upper Triassic Dockum Group of northern Texas. MOTT VPL 3869 (Neyland Quarry) is situated low in the Cooper Canyon Formation (Lehman and Chatterjee, 2005; Martz, 2008), a unit that is probably at least partially temporally equivalent to the Petrified Forest Member (sensu Woody, 2006) of the Chinle Formation (Hunt and Lucas, 1989; Martz, 2008). MOTT VPL 3898 (Headquarters South) is in the middle portion of the Cooper Canyon Formation (Martz, 2008). These specimens (TTU-P 11282; TTU-P 11877) possess the following character states that are shared among *Lagerpeton*, *D. romeri*, and *D. gregorii*: a hook-shaped femoral head, a ventral emargination on the anterolateral side on the femoral head, and an enlarged medial tuber of the proximal femur. Additionally, two distal portions of femora (TTU-P 10866; TTU-P 11186) are known from these same localities. The crista tibiofibularis is large relative to the medial condyle, but it is more similar in size to that of *Lagerpeton* than to the inflated crista tibiofibularis of *Dromomeron*. Because none of these specimens preserve autapomorphies of *Lagerpeton* or *Dromomeron*, these specimens can only be assigned to Lagerpetontidae.

#### ONTOGENY OF *DROMOMERON GREGORII*

The ontogeny of most extinct archosaurs remains poorly understood. Basic studies of crocodylian (Brochu, 1992), avian (Starck, 1993), and extinct basal archosaur (Irmis, 2007) ontogeny have illuminated variability in archosaur ontogenetic pathways, the limits of osteological data, and the interplay of ontogeny and phylogeny. Nonetheless, very little is known about basal ornithodiran ontogeny, particularly how it might affect the interpretation of characters used to reconstruct the phylogeny of basal dinosauromorphs and dinosaurs.

Six *Dromomeron gregorii* right femora of different sizes (Fig. 9) allow a discussion of the differentiation (for definition, see Brochu, 1992) of character states in a growth series of basal-

most ornithodirans. The preservation of each femur varies considerably from pristine to severely crushed. Nonetheless, careful comparisons of several character states illuminate ontogenetic trends in *D. gregorii*. We make no decisions regarding relative maturity, because maturity and size may not be directly correlated with ontogenetic stage (Brinkman, 1988; Brochu, 1992, 1996; Irmis, 2007; Colbert and Rowe, 2008); however, we use relative size to estimate relative ontogenetic stage because age information from histology is not available. We compare specimens of *Lagerpeton* with specimens of *D. gregorii* and suggest the relative ontogenetic stage to which they might pertain. Also, it is important to note that our discussion of the ontogeny of *D. gregorii* is only based on six specimens and that it is possible that some of the differences below represent variation independent of ontogeny (individual, population, taxonomic/phylogenetic variation, and/or sexual dimorphism) within the taxa. Furthermore, taphonomic distortion complicates our understanding of morphological changes through ontogeny. Our goal is to identify possible ontogenetic variation that should be considered during descriptions and construction of phylogenetic characters relevant to ornithodiran systematics.

#### Anterior Trochanter and Trochanteric Shelf

TMM 31100-764, 1234, and 1308 do not possess an anterior trochanter or a trochanteric shelf. In the two largest stages, TMM 31100-464 and 31100-1306, an anterior trochanter and trochanteric shelf are present. The presence of these features in the same ontogenetic stage suggests a coupling of the appearance of both the anterior trochanter and trochanteric shelf in *Dromomeron gregorii*. A small rugose area is present in TMM

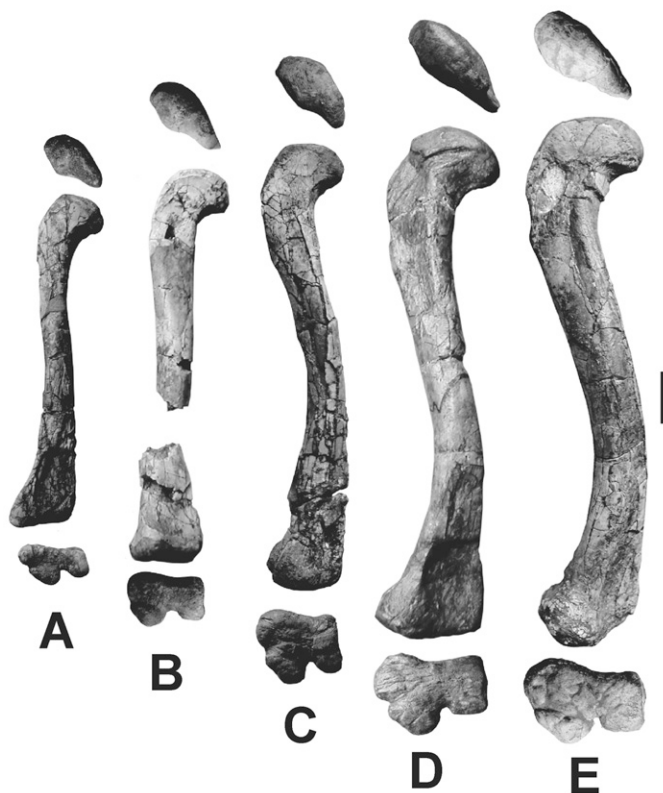


FIGURE 9. Ontogenetic sequence of the femur of *Dromomeron gregorii*. All left elements in proximal (top), anterolateral (middle), and distal (bottom) views. TMM-31100-764 **A**, TMM-31100-1234 **B**, TMM-31100-1308 **C**, TMM-31100-464 **D**, and TMM-31100-1306 **E**. Scale equals 1 cm.

31100-1234 where the anterior trochanter would develop in larger specimens (TMM 31100-464 and 31100-1306). A muscle scar in this position is similar to a muscle scar in *Alligator* and other pseudosuchians (e.g., *Effigia okeeffeae*, *Hesperosuchus agilis*, *Typhothorax coccinarum*). This scar is the lateral insertion of the M. puboischiofemoralis internus pars dorsalis and is already present on the femur of hatchling *Alligator mississippiensis* (Brochu, 1992). However, an anterior trochanter and trochanteric shelf are typically considered osteological correlates of the insertions of M. iliotrochantericus caudalis and M. iliofemoralis externus, respectively; both of which are derivatives of the ancestral reptilian M. iliofemoralis, which inserts on a proximodistally broad area only the lateral femoral shaft, just distal to M. puboischiofemoralis internus in extant crocodylians (Hutchinson, 2001; Carrano and Hutchinson, 2002).

The presence or absence of an anterior trochanter (= 'lesser trochanter' and attachment site for the M. iliofemoralis caudalis) has been a crucial character in basal archosaur systematics. Bakker and Galton (1974) used the presence of an anterior trochanter to separate dinosaurs from other basal archosaurs and this has been variously followed by other basal archosaur systematists (Gauthier, 1986; Novas, 1992, 1996; Juul, 1994; Sereno and Arcucci, 1994a; Benton, 1999; Langer and Benton, 2006). Additionally, the presence or absence of the trochanteric shelf is used to support various ornithodiran clades, most recently Dinosauriformes (Novas, 1996). Recent basal archosaur phylogenies (e.g., Novas, 1996) also recover the presence of anterior trochanter as a synapomorphy of the Dinosauriformes, because the non-dinosauriform dinosauromorph *Lagerpeton* and pterosaurs do not have one. The presence of an anterior trochanter associated with a trochanteric shelf in dinosauriforms suggests that these two features appear at the same time in the phylogenetic history of Dinosauriformes. This is supported by the presence of both a trochanteric shelf and anterior trochanter in the femora of *Marasuchus*, *Pseudolagosuchus*, *Silesaurus*, *Herrerasaurus*, and *Saturnalia*. However, some basal dinosaur specimens lack a trochanteric shelf but retain the presence of an anterior trochanter. This is most clearly seen in *Coelophys* (Colbert, 1990; Raath, 1990). Smaller specimens of *Saturnalia tupiniquim* (e.g., MCP 3846-PV) possess a well-developed anterior trochanter but only display a rugose low ridge instead of a well-defined shelf. This evidence seems to suggest that the presence/absence of a trochanteric shelf is *in part* an ontogenetic character. Rowe (1986) established that the avian M. iliofemoralis externus and M. iliotrochantericus caudalis were derivatives of the ancestral reptilian M. iliofemoralis, in part as evidenced by the fact that the division is recapitulated during avian ontogeny (Romer, 1927; Rowe, 1986). Hutchinson (2001) further hypothesized that the presence of both an anterior trochanter and trochanteric shelf can be used as osteological correlates to infer the presence of M. iliofemoralis externus and M. iliotrochantericus caudalis.

An anterior trochanter and trochanteric shelf are absent in all specimens of *Lagerpeton chanarensis*, *D. romeri*, and small specimens of *D. gregorii*, but are present in larger specimens of *D. gregorii*. The anterior trochanter is always present in large specimens. As pointed out above, its absence in smaller specimens may be ontogenetically controlled (Gauthier, 1986; Novas, 1996). An anterior trochanter is also present in two pseudosuchian archosaur taxa (*Ornithosuchus longidens* and *Riojasuchus tenuisiceps*), but their phylogenetic position within Pseudosuchia suggests that the anterior trochanter arose in these taxa independent of Dinosauromorpha (Hutchinson, 2001). The presence of an anterior trochanter and trochanteric shelf in larger specimens of a non-dinosauriform dinosauromorph indicate several possibilities that are not mutually exclusive: 1) all known *Lagerpeton chanarensis* and *D. romeri* material pertains to juveniles and the anterior trochanter and trochanteric shelf is not yet expressed, though it was present in these taxa; 2) *D. gregorii* evolved the

trochanteric shelf and anterior trochanter independently of dinosauriforms; 3) the M. iliofemoralis splits into M. iliofemoralis externus and M. iliotrochantericus caudalis in all dinosauromorphs, but these do not appear as separate muscle scars until adulthood; 4) *D. gregorii* is more closely related to dinosauriforms than it is to *Lagerpeton* and *D. romeri*; and/or 5) *Lagerpeton* and *D. romeri* independently lost the anterior trochanter and trochanteric shelf.

There are five different specimens of *Lagerpeton* with femora (UNLR 06; PVL 4619, PVL 4625, PVL 5000, MCZ 4121). The sizes of the specimens do not differ significantly, suggesting that all of the specimens are about the same ontogenetic stage (femur length ~80 mm). The status of ossification of the neurocentral sutures in the vertebrae of PVL 4625 is unknown. There is nothing about the *Lagerpeton chanarensis* specimens that is inconsistent with the hypothesis that they represent juveniles, and that the anterior trochanter and trochanteric shelf have not yet developed. However, at present there is no available positive evidence in favor of this hypothesis. Alternatively, it is possible that the anterior trochanter and trochanteric shelf evolved independently in *D. gregorii* and Dinosauriformes. This hypothesis cannot be ruled out because independent evolution of these characters is just as parsimonious as the loss of the characters in *Lagerpeton chanarensis* and *D. romeri* (both require two steps).

We prefer to envisage the evolution of the anterior trochanter and trochanteric shelf as a single unit because of the proximate phylogenetic position of Lagerpetidae to Dinosauriformes, and because these features are morphologically and positionally homologous across these taxa. Note that this preference between ambiguous distributions also maximizes the support for conjectures of primary homology (de Pinna, 1991).

The synchronous development of both the anterior trochanter and the trochanteric shelf supports Hutchinson's (2001) hypothesis that the M. iliofemoralis splits into M. iliofemoralis externus and M. iliotrochantericus caudalis early in ornithodiran history. The phylogenetic pattern of co-appearance of the anterior trochanter and the trochanteric shelf is significant, because it suggests that proximal migration of the ancestral M. iliofemoralis was concomitant with its division into M. iliofemoralis externus and M. iliotrochantericus. In contrast, if the trochanteric shelf appeared earlier in ornithodiran phylogeny than the anterior trochanter, this would suggest that the M. iliofemoralis migrated proximally but still existed as a single muscle, and subsequently divided in more derived ornithodirans. It appears that the osteological correlate of this event does not manifest itself until adulthood. This is corroborated by the general fact that as archosaurs age and become larger, muscle scars become more prominent (Brochu, 1992).

The largest specimen of *D. romeri* (GR 234) lacks an anterior trochanter (and trochanteric shelf), even though it is approximately one third larger than the largest specimen of *D. gregorii* (TMM 31100-1306). The significance of this difference is unclear at present. It could indicate that *Dromomeron romeri* (and *Lagerpeton*) never developed an anterior trochanter. Conversely, at least this individual of *Dromomeron romeri* might have reached maturity at larger size compared to *D. gregorii*.

#### Fourth Trochanter and Surrounding Area

The area for attachment for the M. caudifemoralis (often called the "fourth trochanter") exhibits little change throughout the ontogenetic series. The presence of a fourth trochanter on the smallest femora (TMM 31100-764 and 1234) is consistent with the development of the fourth trochanter in hatchling *Alligator* (Brochu, 1992); however, a few slight differences are worth noting. The well-preserved fourth trochanter in TMM 31100-1234 indicates that smaller specimens of *D. gregorii* had a mound-like fourth trochanter with a rounded ridge at its center.

The larger specimens (TMM 31100-464 and TMM 31100-1306) show a differentiation of the fourth trochanter. The proximal half is identical to the smaller specimens, whereas the distal half becomes bulbous with no central ridge. At its distal end, the fourth trochanter expands anteroposteriorly in these specimens. The depression medial to the trochanteric ridge remains small in TMM 31100-764, 1234, 1308, and 464, but disappears in TMM 31100-1306. This depression is the insertion point for the *M. caudifemoralis longus* (Brochu, 1992; Hutchinson, 2001). Brochu (1992) did not describe any ontogenetic changes for this muscle scar in *Alligator mississippiensis*.

#### **Linea Intermuscularis Cranialis and Linea Intermuscularis Caudalis**

The linea intermuscularis cranialis is only present in the largest specimen, TMM 31100-1306. The equivalent ridge in *Alligator* serves as the insertion site for *M. iliofemoralis*, and is present in hatchlings (Brochu, 1992). The linea intermuscularis cranialis also separates the origins of *M. femorotibialis internus* and *M. femorotibialis externus* in extant crocodylians, and their respective homologues, *M. femorotibialis medialis*, *M. femorotibialis intermedius* and *M. femorotibialis lateralis*, in Aves (Hutchinson, 2001; Carrano and Hutchinson, 2002). In extant Aves, the ancestral *M. iliofemoralis* has migrated dorsally and split into *M. iliofemoralis externus* and *M. iliotrochantericus caudalis*, and no longer inserts on the linea intermuscularis cranialis (Hutchinson, 2001), which is also likely the case for *Dromomeron* and other basal dinosauromorphs. The “primary adductor scar” of Brochu (1992), equivalent to the linea intermuscularis caudalis in birds (Baumel and Witmer, 1993), is also present in hatchling *Alligator* (Brochu, 1992). The linea intermuscularis caudalis in *D. gregorii* also appears early in ontogeny; it is present in TMM 31100-1234, 1308, 464, and 1306. The condition in the smallest specimen, TMM 31100-764, is unclear. In *Dromomeron*, the linea intermuscularis caudalis likely separated the *M. femorotibialis externus* (= ‘*M. femorotibiales lateralis*’ in Aves) origin from the insertions of *M. caudifemoralis brevis* (which inserts more proximally in extant crocodylians, but on the lateral side of the fourth trochanter in ornithodirans) and *M. adductor femoris* (Hutchinson, 2001; Carrano and Hutchinson, 2002). The presence of both the linea intermuscularis cranialis and linea intermuscularis caudalis in basal ornithodirans such as *Dromomeron gregorii* lends further support to Hutchinson’s (2001) hypothesis that the presence of these intermuscular lines (and the associated inference of division of the ancestrally single *M. femorotibialis* into two components) constitute synapomorphies of Archosauria.

#### **Deep Scar on the Anterior Side of the Distal Portion of the Femur**

The anterior surface of the distal femur of *D. romeri* and *D. gregorii* is marked by a deep, rugose, and well-developed scar that corresponds to the distal edge of the origin of the *M. femorotibialis externus* (Figs. 1, 2, 9); this is a synapomorphy of *Dromomeron*. The deep scar is clearly present in TMM 31100-764, 1234, and 1308, its presence is unclear in TMM 31100-464, and the feature is poorly developed in TMM 31100-1306. A rounded muscle scar is present in TMM 31100-1306; there is a distinct ridge in this position on TMM 31100-764, 1234, and 1308. Unfinished bone dorsal to the ridge is present in TMM 31100-764, 1234, 1306, and 1308. On the anterior face of the distal portion of the femur, this scar is bounded medially by a rounded to sharp flange (= ‘anteromedial ridge’ of Irms et al., 2007), and laterally by a knob of rugose bone. If the anteromedial ridge is homologous to the medial epicondylar crest of non-avian theropods (Rauhut, 2003; Smith et al. 2007), then it likely separated the distal origins of *M. femorotibialis externus* (anteriorly) and *M. femorotibialis internus* (posteromedially). Similar scars in this

position are not present in extant crocodylians (Brochu, 1992) and birds (Baumel and Witmer, 1993). However, similar scars are present in many non-avian dinosaurs, particularly in neoceratosaurs and carcharodontosaurids, where the medial epicondylar crest is hypertrophied and associated with a broad, shallow fossa.

A large fossa of rugose bone is present on the medial side of the distal end of the femur on the medial condyle. It is bordered medially by a ridge that separates this fossa from more finished bone on the anteromedial side of the distal femur. The ridge starts on the medial condyle and arcs anteroproximally. This feature may be homologous with the medial epicondylar crest of non-avian theropods, and probably represents the distal portion of the origin for the *M. femorotibialis externus*, a feature that is present in many dinosaurs (e.g., *Coelophysis bauri*). A well pronounced anteromedial ridge is present in the two small specimens (TMM 31100-764 and 1234). Though less well-preserved, femora TMM 31100-1308 and 464 show a similar but less pronounced ridge. The largest example, TMM 31100-1306, lacks this anteromedial ridge. Instead, a rugose muscle scar covers the anteromedial corner of the distal femur. The finished surface distal to the ridge is nearly flat in specimens TMM 31100-764, 1234, and 1308, whereas a small concave muscle scar is present in TMM 31100-464.

#### **Closure of the Intercondylar Groove**

As femur length increases, the posterior intercondylar groove becomes narrower and more slit-like (Fig. 7). This results from the inflation of the crista tibiofibularis and the square-shaped mediolateral expansion of the medial condyle. The intercondylar groove is just a thin slit in the largest specimen, TMM 31100-1306. This feature may only be present in *D. gregorii* because equivalently sized specimens of *D. romeri* have a much smaller medial condyle that does not constrict the width of the intercondylar groove. Alternatively, the ontogenetic stage represented by TMM 31100-1306 may not be present in the known sample of *D. romeri*.

#### **Features Conserved Throughout Ontogeny**

Conserved features are equally informative as ontogenetic transformations. The curvature of the shaft is very similar in all of the specimens, specifically comparing TMM 31100-764 and TMM 31100-1306. In lateral view, the shaft is anteriorly bent and is sigmoidal. The head is inturned nearly 45° in all specimens. Ventral emargination of the femoral head, an important character that unites *Lagerpeton chanarensis*, *D. romeri*, and *D. gregorii*, is clearly developed in all specimens. The distinctness of the anteromedial ridge/medial epicondylar crest that separates the finished bone from the unfinished bone is variable among specimens without any pattern. The expression of this feature is also size independent in *D. romeri*, and is probably affected by individual variation and quality of preservation.

The morphology of the femoral head is also similar in different-sized specimens. All have a convex proximal surface and both a small anteromedial tuber and a large posteromedial tuber separated by a slight groove. The area of the articular surface does not change relative to overall femur size. Furthermore, the relative sizes of the proximal head versus the distal articular surfaces do not change.

#### **Ontogeny Conclusions**

The specimens of *Dromomeron gregorii* demonstrate several ontogenetic trends as femur size increases: (1) the anterior trochanter begins as a low rugosity, and develops into a distinct ridge with a trochanteric shelf; (2) the distal part of the fourth trochanter becomes more bulbous and less ridge-like, and the

depression medial to it disappears; (3) the linea intermuscularis cranialis appears only in the largest specimens; (4) the distal scar for the *M. femorotibialis externus* becomes less well developed; (5) a fossa on the medial side of the distal end of the femur shallows; and (6) the posterior intercondylar groove narrows. The overall shape of the femoral shaft and the morphology of the femoral head do not change through ontogeny. This is similar to the ontogeny of the *Alligator* femur, though several small changes occur to the femoral head in early post-natal ontogeny of this taxon, and the linea intermuscularis cranialis is present early in the ontogeny of the *Alligator* femur (Brochu, 1992).

Although this sample only includes an ontogenetic series of femora, it is one of the few ontogenetic series of basal ornithodirans. The ontogenetic changes in *D. gregorii* are important, particularly because they affect the polarity of characters used to diagnose Dinosauromorpha and its inclusive clades. For example, the sequence demonstrates that the presence of an anterior trochanter and trochanteric shelf result in part from ontogenetic changes, so the absence of these features on any one specimen is not necessarily phylogenetically informative. This insight complements similar conclusions for basal theropods (Tykoski, 2004). This does not mean that the presence/absence of an anterior trochanter is not a useful character, just that care should be taken to ensure that such characters are scored across taxa from specimens of equivalent ontogenetic stage. Thankfully, most femoral characters used in phylogenetic analyses (e.g., Sereno and Arcucci, 1994b; Benton, 2004; Langer and Benton, 2006; Irmis et al., 2007) are ontogenetically conserved in *D. gregorii*, validating their use.

At present, the ontogenetic series of *Dromomeron gregorii* can only be calibrated using relative size. Therefore, we have little idea of the completeness of the ontogenetic series (i.e., does it capture most of the ontogenetic variation of *Dromomeron*). Furthermore, we cannot assign absolute ages to the specimens. Future histological sampling can help answer these questions, and can also determine whether the largest of the specimens is fully grown.

## PHYLOGENY

The early members of Ornithodira are represented by a handful of partial skeletons from the Triassic. Even though *Dromomeron* is only known by hindlimb material, the well-preserved elements provide a new look at the early members of Ornithodira. Therefore, a phylogenetic analysis of 27 taxa was modified from Irmis et al. (2007) to determine the relationships of *D. romeri* and *D. gregorii* among basal archosaurs. 26 ingroup taxa were considered in the present analysis: seven pseudosuchians and 19 basal ornithodirans, and one taxon, *Euparkeria*, was chosen as an outgroup based on its recovered position outside Archosauria in previous basal archosaur phylogenies (Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999). Specimens from nearly all taxa were examined in person by at least one of the authors, and none are suprageneric taxa.

The data matrix consists of 130 characters (1-127 from Irmis et al. 2007; see Appendix 2 for three new characters and Appendix 3 for revised scorings) gathered from various basal archosaur and ornithodiran phylogenetic datasets (Gauthier, 1986; Sereno, 1986; Benton & Clark, 1988; Sereno, 1991; Parrish, 1993; Sereno and Novas, 1994; Juul, 1994; Sereno et al., 1994; Bennett, 1996; Novas, 1996; Benton, 1999; Sereno, 1999; Rauhut, 2003; Yates, 2003; Butler, 2005; Langer and Benton, 2006), and is a modified version of the matrix used in Irmis et al. (2007). All characters were weighted equally and treated as unordered. The parsimony analysis was performed using PAUP\* v4.0b10 (Swofford, 2002), and consisted of heuristic searches with 10,000 random addition replicates utilizing tree bisection and reconnection (TBR) branch swapping. Nodal support was assessed using nonparamet-

ric bootstrapping, with 1,000 bootstrap replicates, TBR branch swapping, and 10 random addition sequences for each pseudoreplicate. Decay indices were calculated using TreeRot v.2c (Sorenson, 1999).

A strict consensus tree (Fig. 10; 301 steps, consistency index [CI] = 0.471, retention index [RI] = 0.735) was obtained from two most parsimonious trees in which the relative positions of *Lesothosaurus*, *Heterodontosaurus*, *Scutellosaurus* could not be resolved. This analysis recovered a phylogenetic hypothesis consistent with most previous basal archosaur phylogenies (e.g., Benton and Clark, 1988; Sereno, 1991). *Lagerpeton*, *D. romeri* and *D. gregorii* form a monophyletic clade supported by the following seven unambiguous synapomorphies: femoral head hook-shaped in medial and lateral views (character 80 [1]); ventral emargination on the anterolateral side of the femoral head (character 82 [1]); posteromedial tuber of femoral head absent (character 84[1]); femoral crista tibiofibularis larger than the tibial condyle (character 91 [1]); posteromedial crest on distal tibia (character 95 [1]); posterior ascending process of the astragalus (character 103 [1]); anteromedial corner of the distal end of the femur forms an angle near 90° or acute (>90°) (character 129 [1]). The sister-taxon relationship between *D. romeri* and *D. gregorii* is supported by the following three unambiguous synapomorphies: anteromedial margin of the distal end of the tibia acute (character 97 [1]); deep scar on the anterior surface of the distal portion of the femur (character 128 [1]); posterolateral condyle of the proximal portion of the tibia hooked (character 130 [1]). The monophyly of *Dromomeron* as the sister-taxon to *Lagerpeton* is strongly supported (Fig. 10). However, we further tested the position of *Dromomeron* in different portions of the tree because it is possible that the amount of missing data could obscure its relationships. Constraining *Dromomeron* to be closer to all other dinosauromorphs than to *Lagerpeton* requires the addition of six steps, and constraining *Dromomeron* as the sister taxon to all dinosauromorphs (including *Lagerpeton*) requires five additional steps. Most of the characters supporting Lagerpetontidae are not found in any other taxa and were previously considered autapomorphies of *Lagerpeton chanarensis* (Sereno and Arcucci, 1994b).

## DISCUSSION

The discovery of *Dromomeron romeri* demonstrated that basal dinosauromorphs survived well into the Late Triassic and coexisted with early dinosaurs (Irmis et al., 2007). It also demonstrated that basal dinosauromorphs had a wider geographic range than previously thought. However, with *D. romeri* only known from one locality, it was unclear how widespread temporally and geographically this taxon was. The discovery of *D. gregorii* and other remains assignable to *Dromomeron* provide important new data for addressing these questions. Furthermore, they record the existence of a clade of *Lagerpeton*-like animals, here named Lagerpetidae, and the discovery of *D. gregorii* reinforces the conclusions of Irmis et al. (2007) regarding the tempo of the rise of dinosaurs in North America.

### Distribution of *Dromomeron* in the Late Triassic of North America

Specimens assigned to *Dromomeron* all derive from the southwestern United States. They are distributed stratigraphically throughout the Upper Triassic, and geographically throughout the American southwest. This demonstrates that *Dromomeron* was a persistent component of Late Triassic faunas in the southwestern United States.

*Dromomeron romeri* is currently restricted to the Petrified Forest Member of central New Mexico in the Chama Basin. We have identified specimens from the Hayden Quarry (the type locality), the Snyder Quarry, and several other localities in the

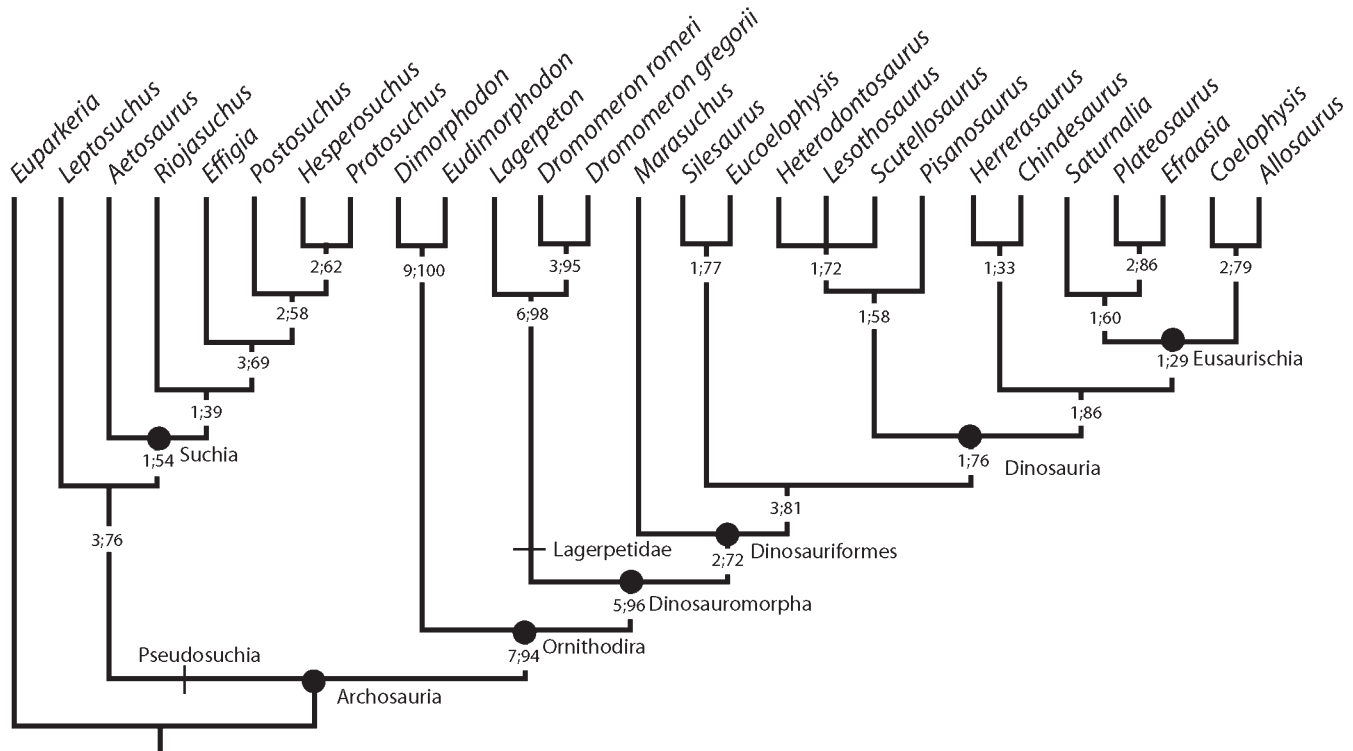


FIGURE 10. Phylogeny of the Archosauria and the relationships of *Dromomeron*. (27 taxa, 130 characters, characters weighted equally and unordered, strict consensus of two most parsimonious trees shown; tree length equals 301, consistency index [CI] 0.471, retention index [RI] 0.735). Support values (left, decay; right, bootstrap) are listed at each node.

area (see Appendix 1). The Petrified Forest Member in this area is Norian in age based on fossil pollen and vertebrate biostratigraphy (see discussion in the supplemental information of Irmis et al., 2007). These strata are generally considered to be younger than those that contain *Dromomeron gregorii* in Texas (e.g., Lucas, 1998). Specimens from the Chama Basin localities represent the youngest occurrence of non-dinosauriform dinosauro-morphs anywhere in the world. Roughly contemporaneous strata at Petrified Forest National Park in northern Arizona appear to lack *Dromomeron romeri* (Irmis et al., 2007), though this may simply be a sampling bias.

*Dromomeron gregorii* is known from both the Dockum Group of Texas and the Chinle Formation in northern Arizona. The specimens from the Otis Chalk Quarries in Texas are generally interpreted to be stratigraphically low within the Dockum Group (Lucas et al., 1993; see Lehman and Chatterjee, 2005 for alternate view). Similarly, the *Placerias* Quarry in Arizona is possibly within the Mesa Redondo Member, near the base of the Chinle Formation (Lucas et al., 1997). These stratigraphic records are important because they demonstrate that basal dinosauro-morphs were already present during deposition of the earliest Upper Triassic strata in the southwestern United States.

Indeterminate basal dinosauro-morph material assignable to the Lagerpetidae is also recorded from the upper portion of the Cooper Canyon Formation of the Dockum Group of Texas. These strata are considered roughly equivalent with the Petrified Forest Member of the Chinle Formation (e.g., Lucas, 1998). Although this material cannot be assigned to a specific taxon, it indicates the presence of non-dinosauriform dinosauro-morphs in younger Upper Triassic strata of Texas.

*Dromomeron romeri* and *D. gregorii* do not appear to overlap stratigraphically, though sample size is very limited. This may indicate some biostratigraphic potential, but the relative rarity of specimens and small number of localities makes *Dromomeron* a poor biostratigraphic indicator at present. More importantly, the presence of two different species separated in time demonstrates that basal dinosauro-morphs continued to evolve and diversify throughout the Late Triassic; they were not simply Middle Triassic relics.

The stratigraphic and geographic distribution of *Dromomeron* is also important because it reinforces the co-occurrence of basal dinosauro-morphs with dinosaurs. The *Placerias* Quarry assemblage includes both *D. gregorii* and some of the oldest North American dinosaurs (Lucas et al., 1992; Nesbitt et al., 2007), indicating that this co-occurrence was maintained for millions of years. The type locality of *D. gregorii* also preserves at least one dinosaur specimen, a proximal femur referred to *Chindesaurus bryansmalli* (Long and Murry, 1995; Nesbitt et al., 2007). Combined with the original co-occurrences in the Hayden and Snyder quarries (Irmis et al., 2007), this indicates that the co-existence of basal dinosauro-morphs and dinosaurs was widespread both temporally and geographically during the Late Triassic of the southwestern U.S.

#### Lagerpetidae

The robust relationships at the base of Dinosauromorpha indicate the utility of naming the clade containing *Lagerpeton*, *D. romeri* and *D. gregorii*. Here we resurrect the family Lagerpetidae (Arcucci, 1986), convert it to a clade name, and define it phylogenetically for the first time (see Systematic Paleontology

section). Our phylogenetic analysis supports the inclusion of *Lagerpeton chanarensis*, *D. gregorii*, and *D. romeri* within the Lagerpetidae. This clade is robustly supported by seven unambiguous synapomorphies (see Phylogeny section above).

The existence of a clade of basal dinosauromorphs outside Dinosauria significantly changes our view of early dinosauromorph evolution. Previously, phylogenies suggested that the dinosaur precursors from the Middle Triassic Chañares Formation in Argentina were successive isolated outgroups to Dinosauria (e.g., Sereno and Arcucci, 1994b). Each branch was occupied by a single taxon, and there were no clades including multiple taxa between pterosaurs and dinosaurs. The recognition of Lagerpetidae as a clade and the sister-group relationship of *Silesaurus opolensis* and *Eucoelophysis* (Nesbitt et al., 2007; Irmis et al., 2007) demonstrates that basal dinosauromorphs were more diverse than previously thought, and evolved into several clades that existed during the Middle and Late Triassic, partially overlapping in time and space with early dinosaurs. We expect that further fieldwork and examination of museum collections will increase the known diversity of the Lagerpetidae and other basal dinosauromorphs.

Most of the autapomorphies listed by Sereno and Arcucci (1993) for *Lagerpeton* now represent synapomorphies of Lagerpetidae or are present in elements not preserved in *D. romeri* and *D. gregorii*. Currently, the presence of a blade-like fourth trochanter is the only unambiguous character that separates *Lagerpeton* from *Dromomeron*.

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