Title

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Journal

PaleoBios, 35(0)

ISSN

0031-0298

Author

Marsh, Adam D.

Publication Date

2018-12-22

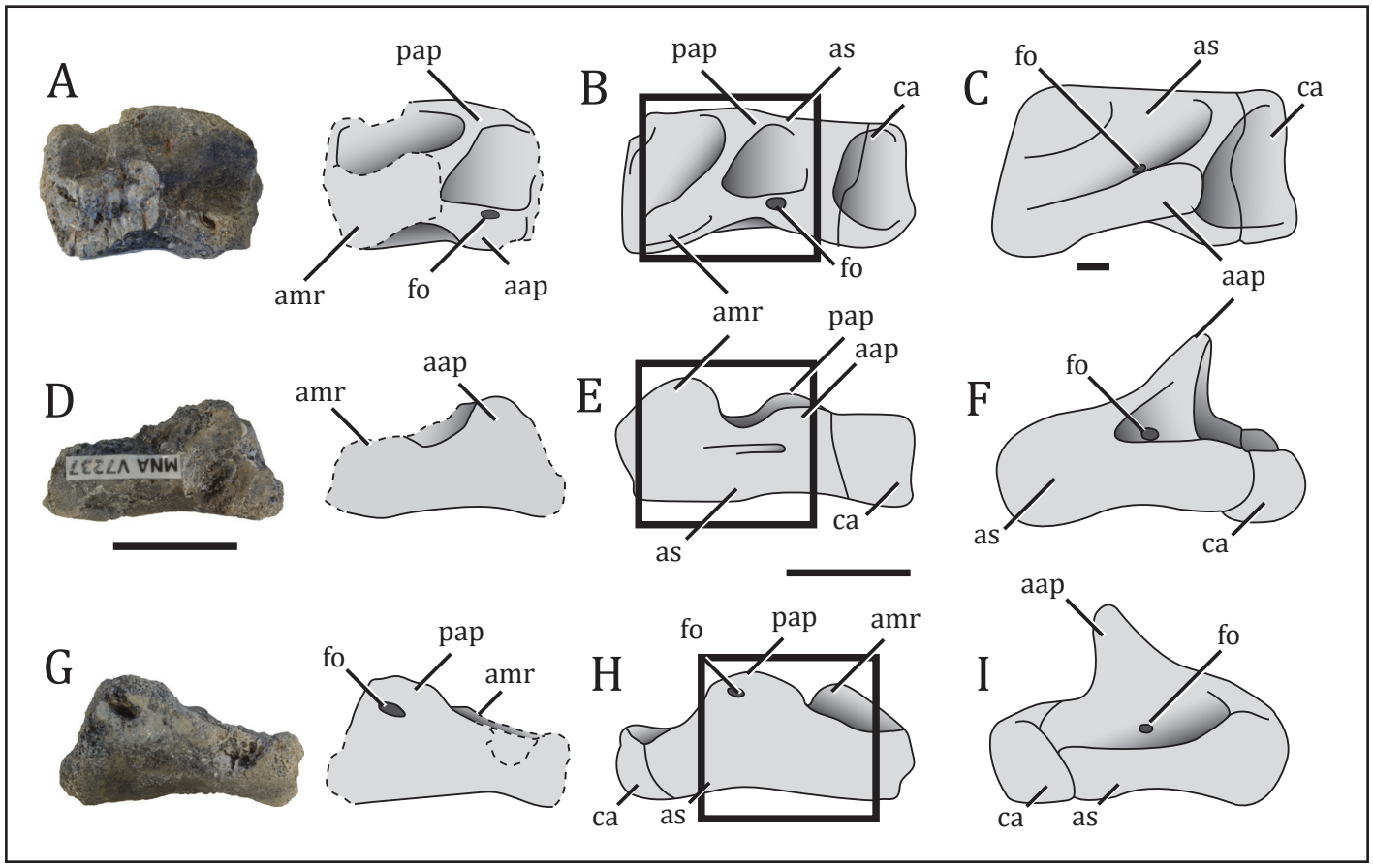
DOI

10.5070/P9351042075

PaleoBios 35: 1–8, December 22, 2018

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



ADAM D. MARSH (2018). A new record of *Dromomeron romeri* Irmis et al., 2007 (Lagerpetidae) from the Chinle Formation of Arizona, U.S.A.

Cover: Figure 2 illustrating distal tarsals of dinosauromorphs from the Triassic of Arizona, U.S.A.
Citation: Marsh, A.D. 2018. A new record of *Dromomeron romeri* Irmis et al., 2007 (Lagerpetidae) from the Chinle Formation of Arizona, U.S.A. *PaleoBios*, 35. ucmp_paleobios_42075.

A new record of *Dromomeron romeri* Irmis et al., 2007 (Lagerpetidae) from the Chinle Formation of Arizona, U.S.A.

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The relatively recent discovery and contextualization of silesaurid and lagerpetid dinosauromorphs has led to a revolution in understanding the early evolutionary history of the dinosaurian lineage. Lagerpetids are known from North America and South America in Middle and Upper Triassic rocks, especially the Chinle Formation of New Mexico and the Dockum Group of Texas. Until now, only a single specimen of *Dromomeron gregorii* was known from the Upper Triassic Chinle Formation of Arizona. However, a new lagerpetid astragalus specimen (MNA V7237) from the Owl Rock Member of the Chinle Formation found on Ward Terrace in the Navajo Nation of Arizona is referred to *Dromomeron romeri.* MNA V7237 represents the youngest radioisotopically-dated record of Lagerpetidae, indicating that *D*. *romeri* persisted throughout the entire Norian (Otischalkian into the Apachean) in North America.

Keywords: Upper Triassic, Chinle Formation, Dinosauromorpha, Lagerpetidae, *Dromomeron*

INTRODUCTION

Historically, interpretations of the vertebrate assemblages within the Upper Triassic Chinle Formation of Arizona emphasized a diverse group of 'thecodontians,' now a paraphyletic group comprising pseudosuchian archosaurs (aetosaurs) and non-archosaur archosauromorphs (phytosaurs), with only two coeval representative dinosaur groups (herrerasaurids and coelophysoids) (e.g., Camp 1930, Colbert 1947, 1989, Long and Murry 1995). However, more recent discoveries of dinosaurs and non-dinosaur dinosauromorphs (e.g., Irmis et al. 2007a, Nesbitt et al., 2009a, 2009b, Nesbitt and Ezcurra, 2015, Lessner et al., 2018) from the southwestern United States have cast more light on the diversity of Dinosauromorpha Benton, 1985 and its early evolutionary history up to the end-Triassic extinction.

The alpha taxonomy of coelophysoids within the Chinle Formation and other Upper Triassic sedimentary rocks in western North America is still not well understood, and the presence of herrerasaurids in the Upper Triassic of North America is now doubted based on the reinterpretation of holotype specimens and a more comprehensive understanding of the suite of character states that diagnose avemetatarsalian clades (Nesbitt et al. 2009a, 2010, Nesbitt 2011, Nesbitt and Ezcurra 2015, Marsh et al. 2016, Baron and Williams 2018). More profoundly, discoveries at exceptionally well-sampled Norian sites such as the Hayden Quarry at Ghost Ranch, New Mexico show that non-dinosaur dinosauromorphs not only co-occurred with their dinosaurian relatives, but also may have been more diverse (Ezcurra 2006, Irmis et al. 2007, Nesbitt et al. 2009b) (Fig. 1) . This includes the Lagerpetidae Arcucci, 1986, a clade of non-dinosauriform dinosauromorphs that comprises *Lagerpeton chanarensis* Romer, 1971 from the Chañares Formation of Argentina (Sereno and Arcucci 1994a), an unnamed taxon from the Ischigualasto Formation (Martinez et al. 2012), *Ixalerpeton polesinensis* Cabreira et al., 2016 from the Santa Maria Formation of Brazil, and three species within the genus *Dromomeron* Irmis et al., 2007: *D. romeri* Irmis et al., 2007 and *D. gregorii* Nesbitt et al., 2009a from the Chinle Formation and Dockum Group of Arizona, New Mexico, and Texas, and *D. gigas* Martinez et al., 2016 from the Quebrada del Barro Formation of Brazil. A lagerpetid referred to *D. romeri* is present in the Chinle Formation of the Eagle Basin in Colorado (Small 2009, Small and Martz 2013). Hypothetical relationships within Lagerpetidae generally reflect *L. chanarensis* and

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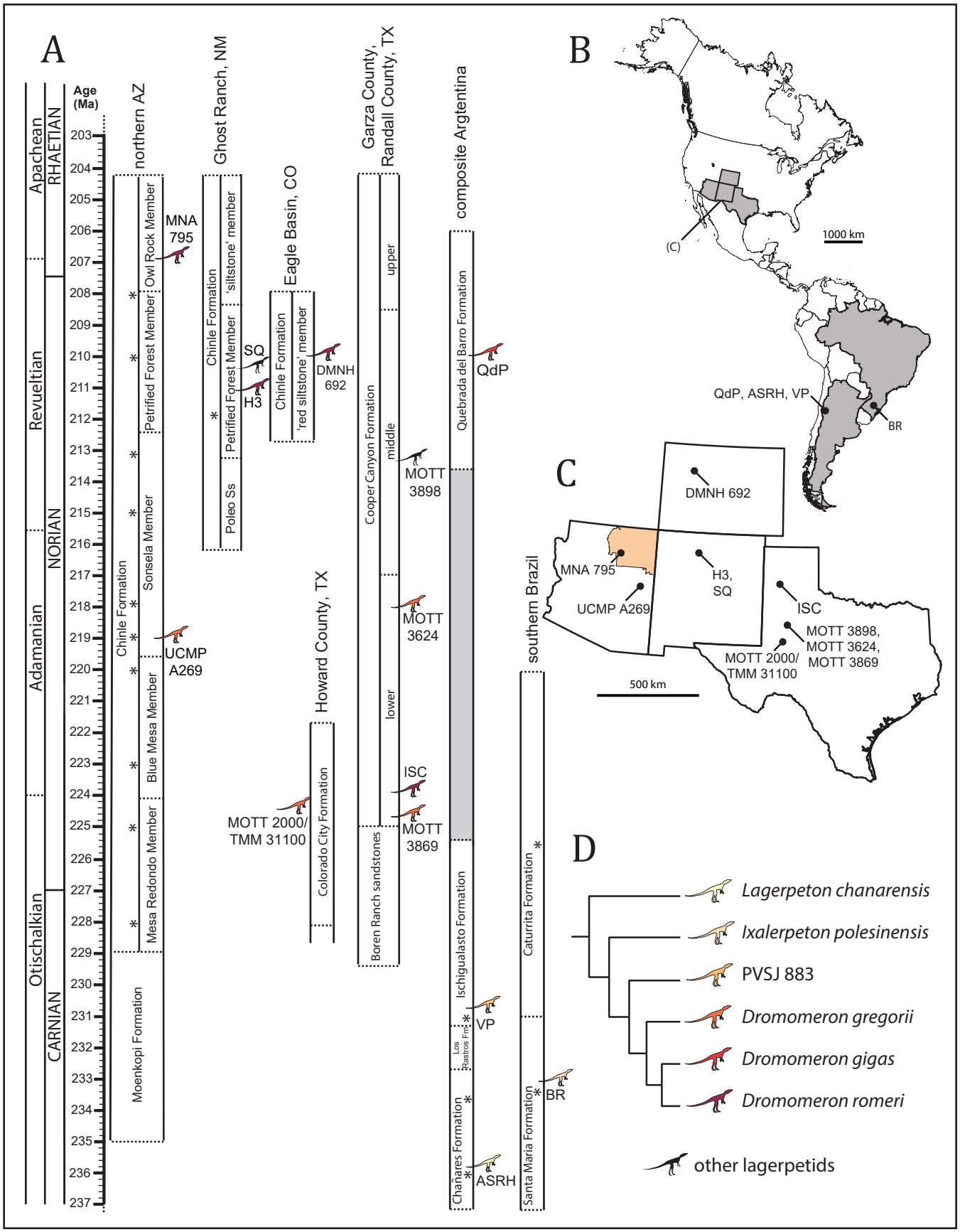

Figure 1. See caption on top of page 3.

Figure 1. Relative stratigraphic locations of fossil localities. **A.** Adapted from Riggs et al. 2003, Martz 2008, Irmis et al. 2011, Ramezani et al. 2011, 2014, Martinez et al. 2012, Mariscano et al. 2015, Sarigül 2016, Ezcurra et al. 2017, Martz and Parker 2017, Langer et al. 2018, Lessner et al. 2018). **B, C**. Geographic distribution of lagerpetids. **D.** Hypothetical relationships within Lagerpetidae from Müller et al. (2018). Asterisks indicate radiometric dates, and silhouettes indicate approximate stratigraphic position of lagerpetid specimens. Tan color represents the Navajo Nation. Silhouette of *Dromomeron* by Nobu Tamura, used under the Creative Commons Attribution-ShareAlike 3.0 Unported license ([http://creativecommons.org/licenses/by-sa/3.0/]). Vector maps of North America, Central America, and South America were used from [FreeVectorMaps.com]; Materials and Methods for full links. **Abbreviations**: **ASRH**, A.S.R. Hill; **BR**, Buriol ravine; **H3**, Hayden quarry #3; **lSC**, lower Sunday Canyon; **QdP**, Quebrada del Puma; **SQ**, Snyder Quarry; **VP**, Valle Pintado.

I. polesonensis as early members of the Lagerpetidae, the *Dromomeron* clade being more derived with respect to the unnamed taxon from the Ischigualasto Formation (Langer et al. 2017, Nesbitt et al. 2017, Müller et al. 2018) (Fig. 1D). Stratigraphic and geographic locations of these lagerpetids are shown in Fig. 1.

With the exception of a referred specimen from the *Placerias* Quarry near St. Johns, Arizona, the fossil record of lagerpetids from the Chinle Formation of Arizona is depauperate compared to the Chinle Formation in New Mexico, where the Hayden Quarry at Ghost Ranch preserves associated skeletal remains of *D. romeri*, and the nearby Snyder Quarry also preserves a *Dromomeron* astragalocalcaneum (Irmis et al. 2007, Nesbitt et al. 2009b, Smith et al. 2018) (Fig. 1). Described here is a new specimen of Lagerpetidae referable to *D. romeri* from the Chinle Formation of Arizona at Ward Terrace on the Navajo Nation. The specimen from the Owl Rock Member on Ward Terrace may represent the youngest known lagerpetid in North America, if not worldwide, and provides further evidence for the long and geographically spread stratigraphic range of the lagerpetid fossil record.

Institutional abbreviations—DMNH, Denver Museum of Natural History, Denver, Colorado; **GR,** Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **MOTT**, Museum of Texas Tech locality; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **PEFO**, Petrified Forest National Park, Arizona; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **TMM**, Vertebrate Paleontology Laboratory, University of Texas, Austin, Texas; **TTU-P**, Museum of Texas Tech University Paleontology, Lubbock, Texas; **UCMP**, Museum of Paleontology, University of California, Berkeley, California.

MATERIALS AND METHODS

The specimen described here from MNA 795 was collected as a part of a project by crews from the MNA in the 1980s on the Navajo Nation and was included in Randy Kirby's thesis on the Upper Triassic assemblages in the Owl Rock Member of the Chinle Formation (Kirby 1991) (Fig. 1A, C). Preparation of this material was accomplished with "airscribe and carbon needle" in addition to unknown adhesives and consolidants (Kirby 1991, p. 32). The lagerpetid specimen from MNA 795 (see below) was found with unionid bivalves (*Antediplodon* cf. *cristonensis* [Meek 1875], MNA N9282), partial paramedian osteoderms of the aetosaur, *Typothorax coccinarum* Cope, 1875 (e.g., MNA V5583), and pseudopalatine phytosaur squamosals (e.g., MNA V7143). Much of the collection from this locality includes field and collection tags identifying Ornithischia Seeley, 1887, Rauisuchidae Huene, 1942, *Postosuchus* Chatterjee, 1985, or Sphenosuchidae Huene, 1942, but an apomorphy-based approach to identification (Bell et al. 2004, Nesbitt et al., 2007, Nesbitt and Stocker 2008, Bell et al. 2010) can only constrain most of these specimens to the level of Archosauria Cope, 1869, except for partial shuvosaurid limb bones (e.g., MNA V5615). More precise locality information is reposited at MNA and is available to qualified researchers upon request.

Vector maps of North America, Central America, and South America were used from [https://freevectormaps.com/world-maps/north-america/WRLD-NA-01-0002], [https://freevectormaps.com/world-maps/central-america/WRLD-CAM-01-0002], and [https://freevectormaps.com/world-maps/south-america/WRLD-SA-01-0002].

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869 *sensu* Nesbitt, 2011
AVEMETATARSALIA Benton, 1999 *sensu* Nesbitt, 2011
ORNITHODIRA Gauthier, 1986 *sensu* Nesbitt et al., 2017
DINOSAUROMORPHA Benton, 1985 *sensu* Sereno, 1991
LAGERPETIDAE Arcucci, 1986 *sensu* Nesbitt et al., 2009a
DROMOMERON ROMERI Irmis et al., 2007

Fig. 2A–I

Referred Specimen and Locality—MNA V7237, partial left astragalus (Ceratosauria in Kirby 1991) (Fig. 2A, D, G); locality MNA 795 (Fig. 1C), Billingsley Southeast; Owl Rock Member of Chinle Formation along Ward Terrace; Badger Spring, AZ USGS 7.5 minute quadrangle; Norian (<208 Ma, Ramezani et al. 2011). This locality is most likely Apachean in age (Martz and Parker, 2017).

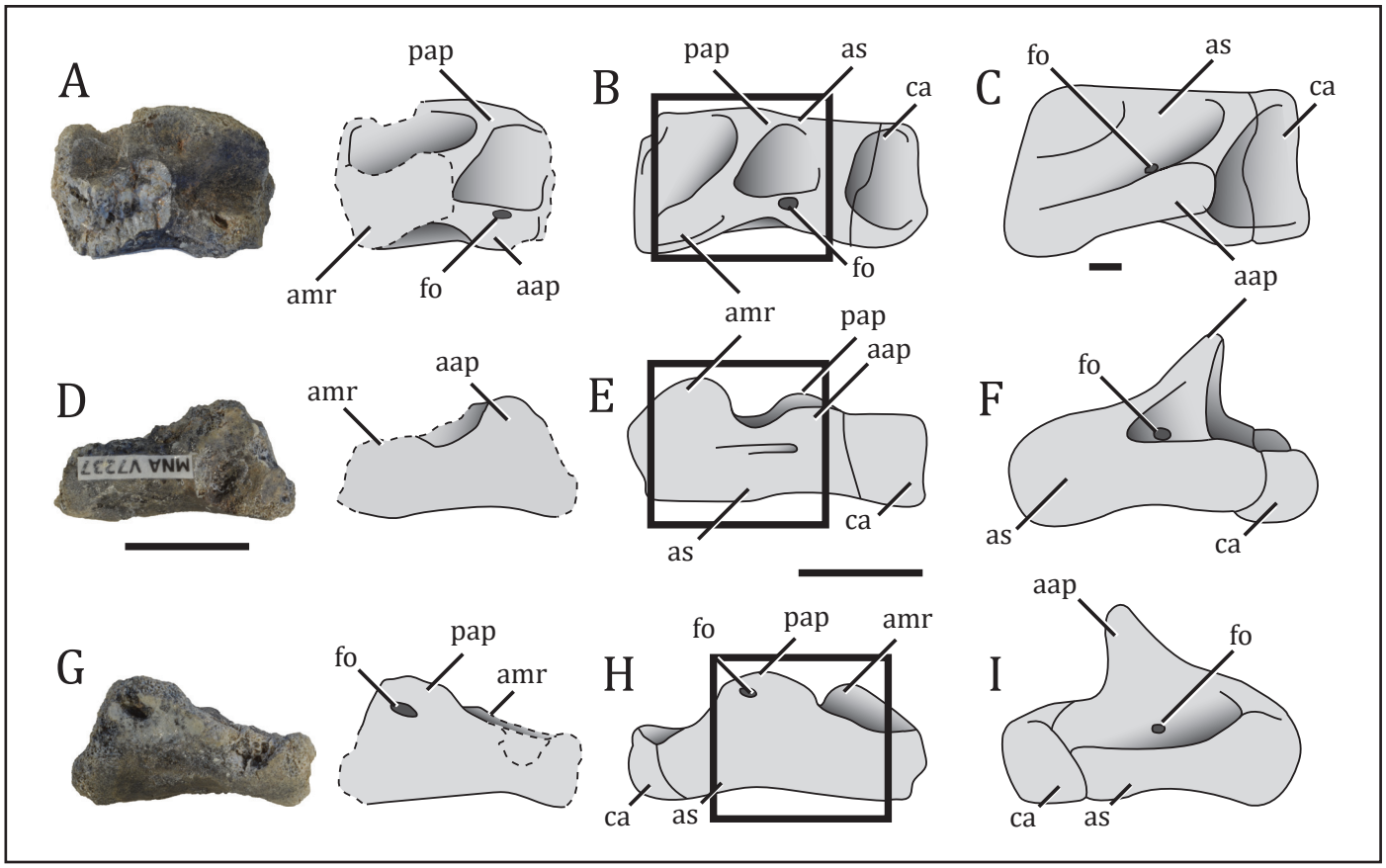

Figure 2. A, **D**, **G.** Images and drawings of the left astragalus of *Dromomeron romeri* from Ward Terrace, MNA V7237. **B**, **E**, **H** (reversed)**.** Drawing of the right astragalocalcaneum of *D. romeri,* GR 223 (paratype). **C**, **F**, **I.** Drawing of the left astragalus and calcaneum of *Dilophosaurus wetherilli*, UCMP 37302 (holotype). Specimens in proximal (A–C), anterior (D–F), and posterior view (G–I). Dashed lines indicate broken margins and black rectangles indicate which region of the astragalus is preserved in common between MNA V7237 and GR 223. **Abbreviations**: **aap**, anterior ascending process; **amr**, anteromedial ridge; **as**, astragalus; **ca**, calcaneum; **ctf**, crista tibiofibularis; **fo**, foramen; **pap**, posterior ascending process. Scale bars=1 cm.

Description and Rationale for Assignment—MNA V7237 belongs to the Lagerpetidae because it preserves a posterior ascending process on the astragalus (Sereno and Arcucci 1994b, Nesbitt et al. 2009b, character 355 in Nesbitt 2011). This specimen can be referred to *Dromomeron romeri* based on the presence of the broken base of a large crest or ridge on the anteromedial edge of the astragalus (Irmis et al. 2007, Nesbitt et al. 2009b).

MNA V7237 is broken laterally and medially so it is impossible to determine if the calcaneum was co-ossified to the astragalus as it is in other lagerpetids, pterosaurs, and coelophysoid theropods (Irmis et al. 2007, Nesbitt et al. 2009a) (Fig. 2). MNA V7237 is mediolaterally elongate and roller-shaped ventrally like that of other ornithodiran archosaurs (Langer et al. 2013, Nesbitt et al. 2017) (Fig. 2D, F), and it is easy to understand why it was originally identified as a theropod (Kirby 1991) owing to the superficial similarity of many dinosauromorph astragali. MNA V7237 preserves both the anterior and posterior ascending processes found in lagerpetids. Early dinosaurs such as *Chindesaurus bryansmalli* Long and Murry, 1995, *Coelophysis bauri* Cope, 1887 (Colbert 1989), and *Dilophosaurus wetherelli* Welles, 1970 (Welles 1954, 1984) lack the posterior ascending process, and the anterior ascending process is especially tall and pyramidal in neotheropods (Fig. 2F). A foramen passes through the top of the posterior process of MNA V7237 in the same place as that of the paratype specimen of *D. romeri,* GR 223 (Nesbitt et al. 2009a), illustrated in Figure 2B, E, and H for comparison. Another foramen penetrates the posterior surface of the anterior ascending process in MNA V7237, which is also shared in other dinosauromorphs (Nesbitt 2011, Langer et al. 2013) (Fig. 2A–C). The prominent anteromedial ridge unique to *D. romeri* is sheared near its base in this specimen, but it was obviously a large structure that was connected to the medial side of the posterior ascending process by an additional low ridge (Irmis et al. 2007, Nesbitt et al.

2009a) (Fig. 2A). This ridge divides the tibial facet into anterolateral and posteromedial basins, much like what is present in GR 223 (Fig. 2A, B). The anteromedial corner of the astragalus in early dinosaurs lacks a crest, and the tibial facet is a single large basin (Nesbitt et al. 2009a, Nesbitt 2011) (Fig. 2C).

DISCUSSION

Prior to 2003, our understanding of the early evolution of the dinosaurian lineage was restricted largely to early-branching taxa such as *Lagerpeton chanarensis*, *Lewisuchus admixtus*, and *Marasuchus lilloensis* from the Middle Triassic Chañares Formation of Argentina (Fig. 1A, B), and early theropod dinosaurs such as *Herrerasaurus ischigualastensis* Reig, 1963 and *Eoraptor lunensis* Sereno et al. 1993 from the Middle to Upper Triassic Ischigualasto Formation of Argentina and coelophysoids from Upper Triassic rocks in North America and southern Africa (i.e., Raath 1977, Colbert 1989, Sereno and Novas 1992, Sereno and Arcucci 1994a, 1994b). A revolution in dinosauromorph anatomy and systematics began with the publication of *Silesaurus opolensis* Dzik, 2003 (Piechowski and Dzik 2010), and subsequent discoveries and reinterpreted taxa all around the world have redistributed character states along the avemetatarsalian evolutionary tree (e.g., Ezcurra 2006, Ferigolo and Langer 2006, Irmis et al. 2007, Nesbitt et al. 2009a, 2009b, Nesbitt et al. 2010, Kammerer et al. 2011, Cabreira et al. 2016, Martinez et al. 2016, Nesbitt et al. 2017). Thus, Lagerpetidae, the earliest group of dinosaur relatives that were once restricted to the Middle Triassic of Argentina, was recognized as a clade that lived alongside silesaurid dinosauriforms, theropods, and sauropodomorphs in the Late Triassic of North American and South America.

Lagerpetids are known from nearly every major terrestrial Upper Triassic rock unit in western North America (Fig 1A). *Dromomeron romeri* was originally named from specimens collected from the Petrified Forest Member of the Chinle Formation in the Hayden Quarry at Ghost Ranch, New Mexico, which is approximately 212 Ma in age (Revueltian, Irmis et al. 2007, 2011, Martz and Parker 2017). An additional astragalocalcaneum is present from the nearby Snyder Quarry (NMMNH P-35379), which is slightly higher stratigraphically relative to the Hayden Quarry but well below the *Coelophysis* Quarry within the 'siltstone member' (Nesbitt et al. 2009a, Whiteside et al. 2015). A lagerpetid referred to *D. romeri* is present in the Chinle Formation of the Eagle Basin in western Colorado (Small and Martz 2013), which has been correlated with the Petrified Forest Member and is Revueltian in age (Small 2009, Langer et al. 2013, Small and Martz 2013) (Fig. 1A, C). However, another specimen referred to *D. romeri* is reported from the lower Sunday Canyon site in the lower part of the Cooper Canyon Formation of Garza County, Texas (Sarigül 2016) (Fig. 1A). *Dromomeron gregorii* and unnamed lagerpetids are known primarily from specimens from the Cooper Canyon Formation and Colorado City Formation of the Dockum Group in Garza County and Howard County, Texas, respectively (Nesbitt et al. 2009a, Martz 2007, 2008, Small and Martz 2013, Lessner et al. 2018) (Fig. 1A, C). The age of these units is not well-constrained outside of vertebrate biostratigraphy, but the horizon containing lagerpetids in the Cooper Canyon Formation (MOTT 3839) may be roughly equivalent to the Petrified Forest Member of the Chinle Formation (~212 Ma, early Revueltian), and that containing *D. gregorii* in the lower part of the Colorado City Formation (MOTT 2000/TMM 31100) may be roughly equivalent to the Mesa Redondo Member of the Chinle Formation (~225 Ma, Otischalkian, Martz 2007, 2008, Ramezani et al. 2011, Sarigül 2016, Martz and Parker 2017, Lessner et al. 2018). A single distal end of a left femur of *D. gregorii* was referred from the *Placerias* Quarry (Fig. 1A, 1C, UCMP 25815, loc. A269) in northeastern Arizona, is now known to be approximately 219 Ma, or Adamanian, in age (Nesbitt et al. 2009a, Ramezani et al. 2014, Martz and Parker 2017). Until now, that specimen was the only lagerpetid known from the Chinle Formation of Arizona.

The oldest dated lagerpetids are found in the Chañares Formation in Argentina (~236 Ma, Mariscano et al. 2015, Ezcurra et al. 2017) or the Santa Maria Formation of Brazil (~233 Ma. Langer et al. 2018), and old forms are found in the Colorado City Formation and Cooper Canyon Formation in Texas, but those units lack reliable radiometric dates (Langer et al. 2013, Lessner et al., 2018, Müller et al. 2018). Lagerpetids were present throughout most of the Late Triassic and persisted well into the Norian (Langer et al. 2013, Müller et al. 2018). Until now, the youngest lagerpetids associated with independent radiometric dates were those from the Hayden Quarry (~212 Ma) and the slightly higher Snyder Quarry within the Chinle Formation in New Mexico (Irmis et al. 2011, Langer et al. 2013). However, the MNA specimen described here from locality MNA 795 is from the Owl Rock Member, which is associated with a U-Pb date from the uppermost Petrified Forest Member at Petrified Forest National Park, which has been dated at approximately 208 Ma (Ramezani et al. 2011) (Fig. 1A). Thus, the specimen here referred to *D. romeri* from the Owl Rock Member at Ward Terrace is no older than 208 million years and is currently the youngest

radioisotopically-dated non-dinosaur dinosauromorph, as other young records (i.e., the Eagle Basin lagerpetid and *Dromomeron gigas*) await more precise age control.

At present, only more derived lagerpetids (*D. romeri* and *D. gregorii*) are identified from the Upper Triassic rocks in Arizona, New Mexico, and Texas (Fig. 1). The Carnian record of Lagerpetidae includes *Lagerpeton chanarensis*, *Ixalerpeton polesinensis*, and PVSJ 883, and is restricted to Gondwana, whereas the Norian record only includes species within the genus *Dromomeron* from Laurasia (except for *D. gigas*, which is from northwestern Argentina). It is unclear whether this temporal and geographic segregation is real or artifactual, as much of the first half of the Norian is missing in Argentina, and lagerpetids are not yet known from the Caturrita Formation in Brazil or the Carnian of North America. Regardless, this specimen of *D. romeri* from the Owl Rock Member of the Chinle Formation on the Navajo Nation extends the stratigraphic range of Lagerpetidae at or above the Norian-Rhaetian boundary, and it may extend from the latest Otischalkian or earliest Adamanian into the Apachean. At least in North America, lagerpetid dinosauromorphs occurred alongside theropod dinosaurs a mere seven million years prior to the end-Triassic extinction.

ACKNOWLEDGEMENTS

This work was funded by the Petrified Forest Museum Association, the Museum of Northern Arizona, and the Doris O. and Samuel P. Welles Fund at the University of California Museum of Paleontology. Thank you to Matt Smith (PEFO), Dave and Janet Gillette (MNA), Pat Holroyd (UCMP), and Kristen MacKenzie (DMNH) for access to specimens in their collections. The MNA specimen from the Navajo Nation was collected under a permit from the Navajo Nation Minerals Department. Any persons wishing to conduct geologic investigations on the Navajo Nation must first apply for and receive a permit from, P.O. Box 1910, Window Rock, AZ 86515 and telephone number (928) 871-6587. This manuscript was greatly improved by suggestions and comments by Bill Parker, Jeffrey Martz and Sterling Nesbitt. This is Petrified Forest National Park Paleontological Contribution No. 60. The views presented herein are those of the author and do not represent the views of the U.S. Federal Government.

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