Journal of Vertebrate Paleontology

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/ujvp20

A new drepanosauromorph (Diapsida) from East–Central New Mexico and diversity of drepanosaur morphology and ecology at the Upper Triassic Homestead Site at Garita Creek (Triassic: mid-Norian)

Isaac Pugh, Sterling J. Nesbitt, Andrew B. Heckert, René Lauer & Bruce Lauer

To cite this article: Isaac Pugh, Sterling J. Nesbitt, Andrew B. Heckert, René Lauer & Bruce Lauer (04 Jul 2024): A new drepanosauromorph (Diapsida) from East–Central New Mexico and diversity of drepanosaur morphology and ecology at the Upper Triassic Homestead Site at Garita Creek (Triassic: mid-Norian), Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2024.2363202

To link to this article: https://doi.org/10.1080/02724634.2024.2363202

Published online: 04 Jul 2024.

Journal of Vertebrate Paleontology e2363202 (17 pages)

DOI: 10.1080/02724634.2024.2363202

ARTICLE

A NEW DREPANOSAUROMORPH (DIAPSIDA) FROM EAST–CENTRAL NEW MEXICO AND DIVERSITY OF DREPANOSAUR MORPHOLOGY AND ECOLOGY AT THE UPPER TRIASSIC HOMESTEAD SITE AT GARITA CREEK (TRIASSIC: MID-NORIAN)

ISAAC PUGH,[1,2*] STERLING J. NESBITT,[1] ANDREW B. HECKERT,[2] RENÉ LAUER,[3] and BRUCE LAUER[3]
[1]Department of Geosciences, Virginia Tech, Blacksburg, VA 24061, U.S.A., isaacp22@vt.edu, sjn2104@vt.edu;
[2]Department of Geological and Environmental Sciences, Appalachian State University, Boone, NC 28608, U.S.A., heckertab@appstate.edu;
[3]Lauer Foundation for Paleontology, Science, and Education, Wheaton, IL 60189, U.S.A., rene@lauerfoundationpse.org, bruce@lauerfoundationpse.org

ABSTRACT—The Late Triassic was home to great tetrapod diversity, with a mixture of endemic Triassic groups and others with extant descendants. These two groups are represented in microvertebrate accumulations, but their fossils are mixed and fragmentary, leading to challenges in confidently identifying them. Among the Triassic endemic groups, drepanosauromorphs are among the most unusual and easily recognized, but many details of their anatomy are obscured by the lack of three-dimensional and matrix-free specimens. Here we describe new material, including a new species, using isolated but three-dimensional drepanosauromorph elements from the Homestead Site at Garita Creek, an Upper Triassic microvertebrate locality near Garita Creek, New Mexico. This site has thus far yielded dozens of isolated drepanosauromorph specimens, including manual/pedal unguals of at least three morphotypes, vertebrae, and caudal unguals (= tail claws). At least two drepanosauromorph species are present based on distinct enlarged ungual morphotypes, with one representing a new *Skybalonyx*-like species, *Unguinychus onyx* gen. et sp. nov., and a second form similar to *Drepanosaurus*. *Unguinychus onyx* may have been fossorial whereas the second morphotype likely represents an arboreal species, possibly indicating that contemporary drepanosauromorphs had different ecologies. For the first time, we report a potential “small” ungual morphotype, and we present a partial caudal ungual exhibiting features distinct from manual and pedal unguals. The identification of isolated and three-dimensional drepanosauromorph fossils expands the diversity of the clade and demonstrates the usefulness of incorporating microvertebrate data into assemblage studies.

http://zoobank.org/urn:lsid:zoobank.org:pub:55D714E4-0FDE-43BE-965D-5D6C3FD3A1E8

Citation for this article: Pugh, I., Nesbitt, S. J., Heckert, A. B., Lauer, R., & Lauer, B. (2024) A new drepanosauromorph (Diapsida) from East–Central New Mexico and diversity of drepanosaur morphology and ecology at the Upper Triassic Homestead Site at Garita Creek (Triassic: mid-Norian). *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2024.2363202

Submitted: November 8, 2023
Revisions received: May 15, 2024
Accepted: May 15, 2024

INTRODUCTION

The great diversity of living tetrapods largely has roots in the Triassic Period, with many extant lineages hypothesized to have originated within the period (Fraser, 2006; Irmis et al., 2011; Irmis et al., 2007, 2011; Padian, 1989, 2012; Padian & Sues, 2015; Sues & Fraser, 2010). Study of Triassic assemblages is crucial to recognizing the earliest members of living groups and the conditions in which they evolved, but unfortunately the fossil record of many small Triassic-aged vertebrates is sparse and fragmentary. Among the more elusive and unique clades of the Triassic are drepanosauromorphs. This group of small-bodied diapsids (all under 1 m in length) has a complex taxonomic history (Berman & Reisz, 1992; Pinna, 1980; Renesto, 1994; Senter, 2004), but has recently been recovered as early diverging non-saurian diapsids possibly related to weigeltisaurids (Pritchard et al., 2021; Pritchard & Nesbitt, 2017), but alternatively within Archosauromorpha (Dilkes, 1998; Renesto & Binelli, 2006; Renesto et al., 2010b; Simões et al., 2022). Drepanosauromorphs are known from low latitudes to northern Pangea but were morphologically diverse with presumably arboreal, fossorial, and possibly aquatic members (Berman & Reisz, 1992; Colbert & Olsen, 2001; Jenkins et al., 2020; Pinna, 1980, 1984, 1986, 1987; Renesto, 1994; Renesto & Binelli, 2006, Renesto et al., 2010b).

Drepanosauromorphs superficially resemble lizards with bird-like skulls and necks, but they collectively encompass a variety of unusual features, with one of the most notable being the terminal caudal element that is modified into a “tail claw” on the likely prehensile caudal series in some species (Berman & Reisz, 1992; Fraser & Renesto, 2005; Pinna, 1980). *Drepanosaurus unguicaudatus* exhibits a highly modified forelimb, with the ulna modified to a compact crescent shape and having two greatly elongated carpals (Pinna, 1980; Pritchard et al., 2016). Another common feature in the group is the greatly enlarged ungual on the second digit of the manus, which has been

*Corresponding author.
Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

Published online 04 Jul 2024

regarded as diagnostic to at least genus and has been used to predict drepanosauromorph life-modes (Gonçalves & Sidor, 2019; Jenkins et al., 2020). Articulated and relatively complete specimens of seven species—*Drepanosaurus unguicaudatus*, *Megalancosaurus endennae*, *M. preonensis*, *Vallesaurus cenensis*, *V. zorzinensis*, and *Hypuronector limnaios*—are known, with multiple specimens of both species of *Megalancosaurus* and of *Hypuronector*. Each of these species are preserved as slab specimens and in largely similar quiet water environments, with all but *Hypuronector* being from the Upper Triassic Zorzino Limestone of Italy (Colbert & Olsen, 2001; Pinna, 1980; Renesto, 1994; Renesto and Binelli, 2006; Renesto et al., 2010b).

Though most drepanosauromorph specimens tend to occur as crushed, two-dimensional skeletons in slabs of limestone (Renesto et al., 2010b), there are a few exceptions of three-dimensional remains from the Upper Triassic of the western U.S.A. (Gonçalves & Sidor, 2019; Harris & Downs, 2002; Jenkins et al., 2020; Pritchard & Nesbitt, 2017; Pritchard et al., 2016) and fissure fill material in the U.K. (Fraser & Renesto, 2005; Renesto & Fraser, 2003). Thus, three-dimensional drepanosauromorph elements, even when isolated, offer unique morphologic insight, as the anatomy, position in the body, and taxonomy can be hypothesized from more complete specimens. Here we describe isolated three-dimensional drepanosauromorph specimens from the Homestead Site at Garita Creek (or "Homestead"), an Upper Triassic microvertebrate locality near Garita Creek, New Mexico, and the implication of coexisting drepanosauromorphs with distinct anatomy and life modes.

Curational Statement

The Lauer Foundation provides the scientific community and other museums with permanent access to their own curated fossil collection for the purposes of exhibition, study, and education. They guarantee public access to type and figured specimens, as well as specimens listed or cited in publications together with other scientifically important specimens.

PROVENANCE

The fossils we describe here were all recovered from a site termed the "Homestead Site at Garita Creek," or "Homestead," near the type section of the Garita Creek Formation in east-central New Mexico (Fig. 1). We document key details of its collection here because it has an unusual history. A more extensive treatment will be provided elsewhere (see Lauer et al., 2023), but this is the first manuscript on Homestead fossils other than a brief review (Heckert et al., 2023). The Homestead Site at Garita Creek is located on private land within a larger, open-range cattle ranch in east-central New Mexico. Sometime in the 1980s a ranch foreman informed Betty (Reid) Martin and her father about fossils he had seen on the site and allowed them to investigate and collect. They identified large bones and a vertebra and contacted the New Mexico Museum of Natural History and Science in Albuquerque (NMMNH). Betty and her father donated fossils to the NMMNH, and museum staff and/or volunteers visited this and other sites and collected fossils as well. It is possible that a few specimens were reported from the site by Hunt et al. (1989), as NMMNH records for localities 425 and 426 match the legal coordinates of the site.

Larry Martin began sieving matrix from Homestead in approximately 2004 and recognized that the site contained abundant and rare, Late Triassic microvertebrate fossils. He and Betty purchased a parcel of land encompassing the site and intensively surface collected and sieved matrix for many years, resulting in the recovery of thousands of microvertebrate fossils. The Martins' collection and the site were acquired by the Lauer Foundation for Paleontology, Science, and Education (LF) in 2020 to be used for educational and scientific purposes. Today the Homestead Site at Garita Creek and the previously collected materials are under study by students and staff of the Lauer Foundation's partner institutions: Appalachian State University, Virginia Tech, and the Natural History Museum London, U.K. A memorandum of understanding agreement signed by representatives of each partner institution provides the ability for them to utilize the site for educational field training, collection, and use of these materials for scientific research and publications. Numerous projects are underway to verify the integrity of the collection, but surface collections and preliminary screenwashing by the authors and other partners match the material collected by the Martins taxonomically and in terms of preservation. The site itself is in a low, open area with relatively little stratigraphic exposure. However, there are numerous locally persistent sandstone bodies overlying the site that facilitate correlation. Thus, Homestead and the nearby outcrops are readily correlated to the type section of the Garita Creek Formation (Fig. 1C; Heckert et al., 2023). The site is thus low in the Garita Creek Formation, well beneath a regionally persistent sandstone and conglomerate that has been correlated to the Trujillo Formation (Lucas et al., 2001; Mirzaei et al., 2021).

Historically, the Garita Creek Formation has been considered Adamanian in age (e.g., Lucas et al., 2001 and references therein), although all age-diagnostic assemblages, including the Lamy metoposaur bonebed (Lucas et al., 2010) come from a distinct outcrop to the west. We note that the assemblage at Homestead lacks Adamanian index fossils but does include hybodont shark teeth assigned to *Reticulodus* (e.g., LF 5535), which is common in strata of younger, Revueltian age (Heckert & Lucas, 2006; Voris & Heckert, 2017). This and other lines of evidence (ongoing work) lead us to consider the possibility that, at least locally, the Garita Creek Formation is younger than Adamanian.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York City, New York, U.S.A.; **GR**, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, New Mexico, U.S.A.; **LF**, Lauer Foundation for Paleontology, Science, and Education, Wheaton, Illinois, U.S.A.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **MCSNB**, Museo "Caffi" di Scienze Naturali Bergamo, Bergamo, Italy; **MFSN**, Museo Friulano di Scienze Naturali, Udine, Italy; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **PEFO**, Petrified Forest National Park, Arizona, U.S.A.; **UWBM**, University of Washington Burke Museum, Seattle, Washington, U.S.A.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
DREPANOSAUROMORPHA Renesto, Spielmann, Lucas, and Spagnoli, 2010b
DREPANOSAURIDAE Carroll, 1988 sensu Dilkes, 1998
UNGUINYCHUS ONYX, gen. et sp. nov.
(Figs. 2 and 3)

Type [and only] Species— *Unguinychus onyx*.

Holotype—LF 5575, ungual with a broken distalmost portion. We identify this as a manual ungual, likely from digit II, side unknown, based on comparison with *Skybalonyx skapter* (See Jenkins et al., 2020, and Figs. 2, 3).

Etymology—'Unguis' claw (Latin); 'nychus' claw (Greek); 'onyx' claw (Greek); the species name acknowledges the sole element representing it.

Paratypes—LF 5351, LF 5358; LF 5361; LF 5374; LF 5375; LF 5376; LF 5389; LF 5390; LF 5584, side unknown for all. All are

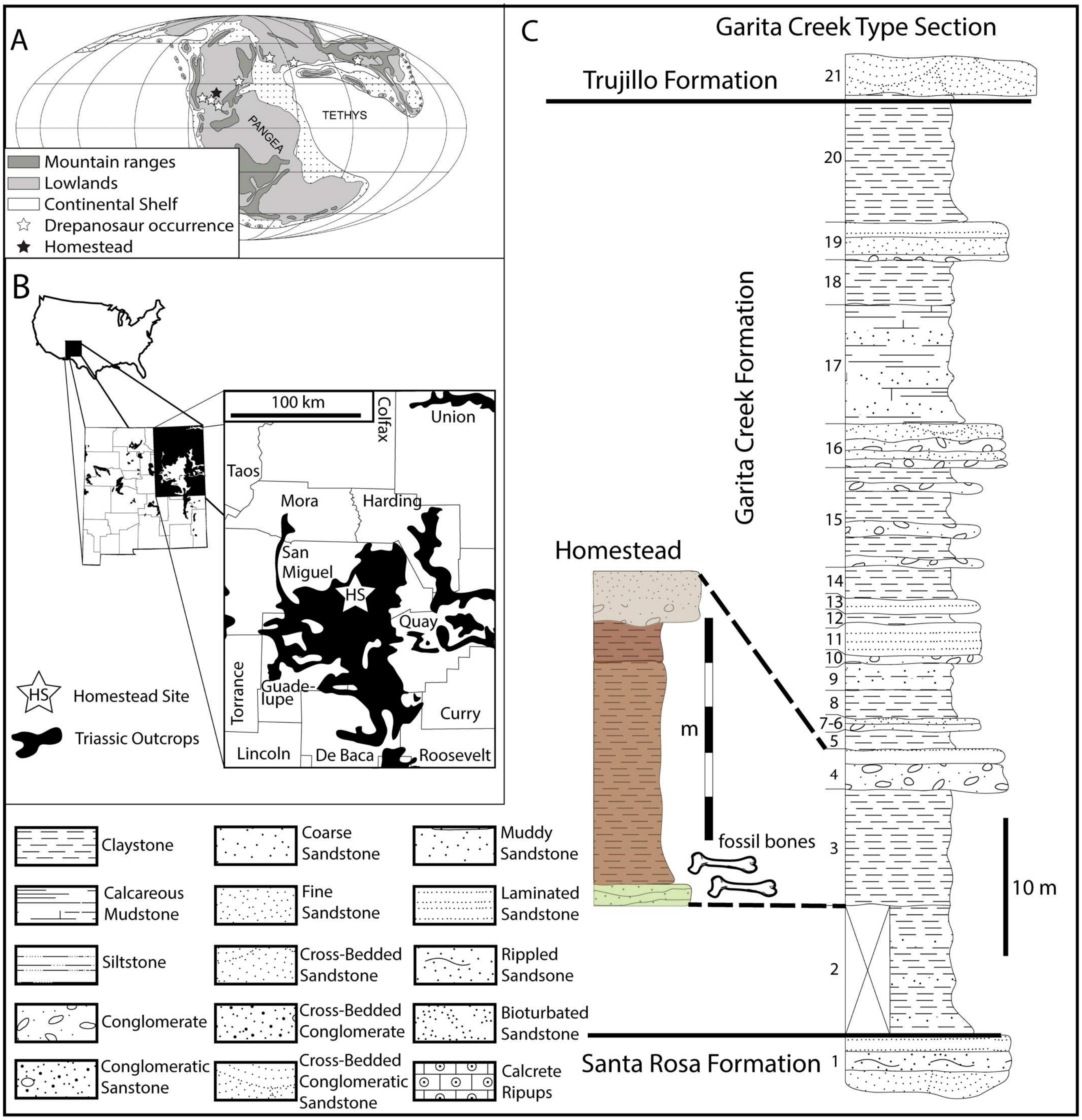

FIGURE 1. Index map and stratigraphic sections showing the location of the Homestead at Garita Creek. **A**, map of Pangea showing approximate position of known drepanosaur records (modified from Renesto et al., 2010b:fig. 46). **B**, index maps showing Triassic strata in eastern New Mexico and the approximate location of Homestead. **C**, stratigraphic section measured at the Homestead correlated to the type section of the Garita Creek Formation of Lucas and Hunt (1989).

unguals with broken distal portions likely from digit II of the manus (Fig. 3). Unguals are the only confidently identified material of *Unguinychus onyx* given that there is more than one drepanosauromorph at the same locality (see below).

Diagnosis—*Unguinychus onyx* differs from all drepanosauromorphs in the possession of the following combination of character states on the manual ungual (illustrated in Fig. 2), with autapomorphies marked with *: two distinct and nearly separated articular cotyles (1); cotyles oriented proximoventral to the rest of the ungual (2); each cotyle nearly as long in the proximo-ventral dimension as the ungual is dorsoventrally deep (3); two foramina on the midline of the symmetrical axis on the articular surface, one dorsal and one ventral (4); a proximal surface dorsal to the cotyles and nearly perpendicular to the dorsal surface of the main body in lateral view (5); a low, bi-lobed flexor region, raised less

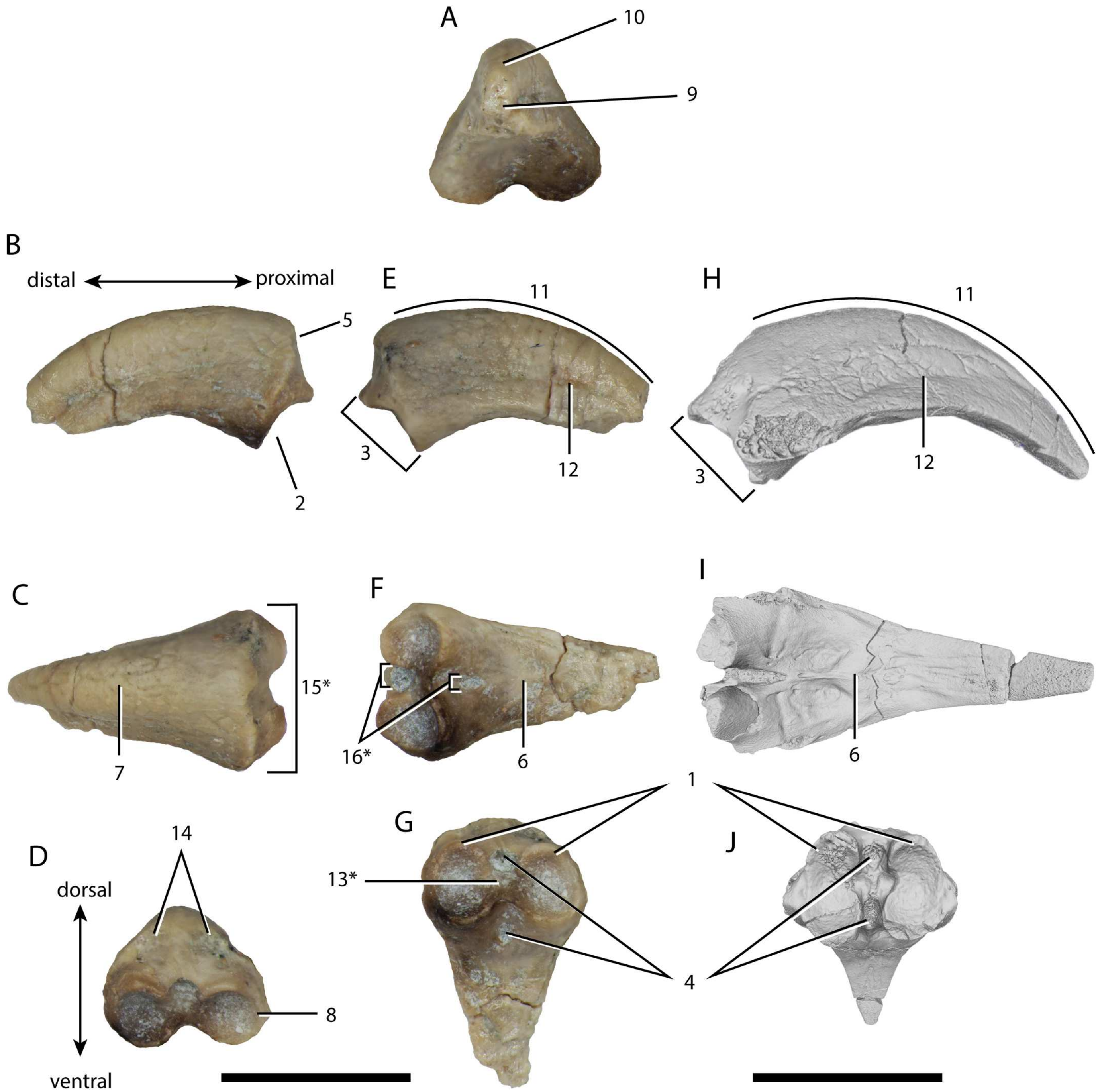

FIGURE 2. *Unguinychus onyx* holotype LF 5575 in distal, **A**, left lateral, **B**, dorsal, **C**, proximal, **D**, right lateral, **E**, ventral, **F**, and articular, **G**, view in comparison with *Skybalonyx skapter* holotype PEFO 43703 in right lateral, **H**, ventral, **I**, and articular, **J**, views. Diagnostic character states marked with numbers and autapomorphies starred referring to character states in the diagnosis, with select characters also observed in *Skybalonyx* also marked. *Skybalonyx* is shown from a digital model compiled from CT data. Left scale bar equals 5 mm and applies to **A**–**G**. Right scale bar equals 10 mm and applies to **H**–**I**.

than 10% of the dorsoventral depth of the ungual body where it is located, on the ventral surface distal to the foramina and cotyles (6); lack of sculpturing on the dorsal surface of the body (7); cotyles lacking lateral flanges (8); an approximately triangular transverse cross section along the body (9); smooth, bowed dorsal margin of the main body in transverse cross section (10); minor curvature (85–90°) along the entire preserved length from the proximal to the distal portion (11); pronounced grooves on the lateral surfaces (12); *a proximal articular facet with each half connected by a constricted portion less than half the proximo-ventral length of either cotyle (13); *two unconnected grooves on the proximo-dorsal portion of the ungual (14); *proximal articular region wider than the main body (15); *a dorsal foramen of greater diameter than the ventral foramen (16).

Unguinychus onyx differs from *Skybalonyx skapter* (Jenkins et al., 2020) by the midline connection of the articular cotyles in all specimens, proximo-ventrally oriented cotyles, a dorsal

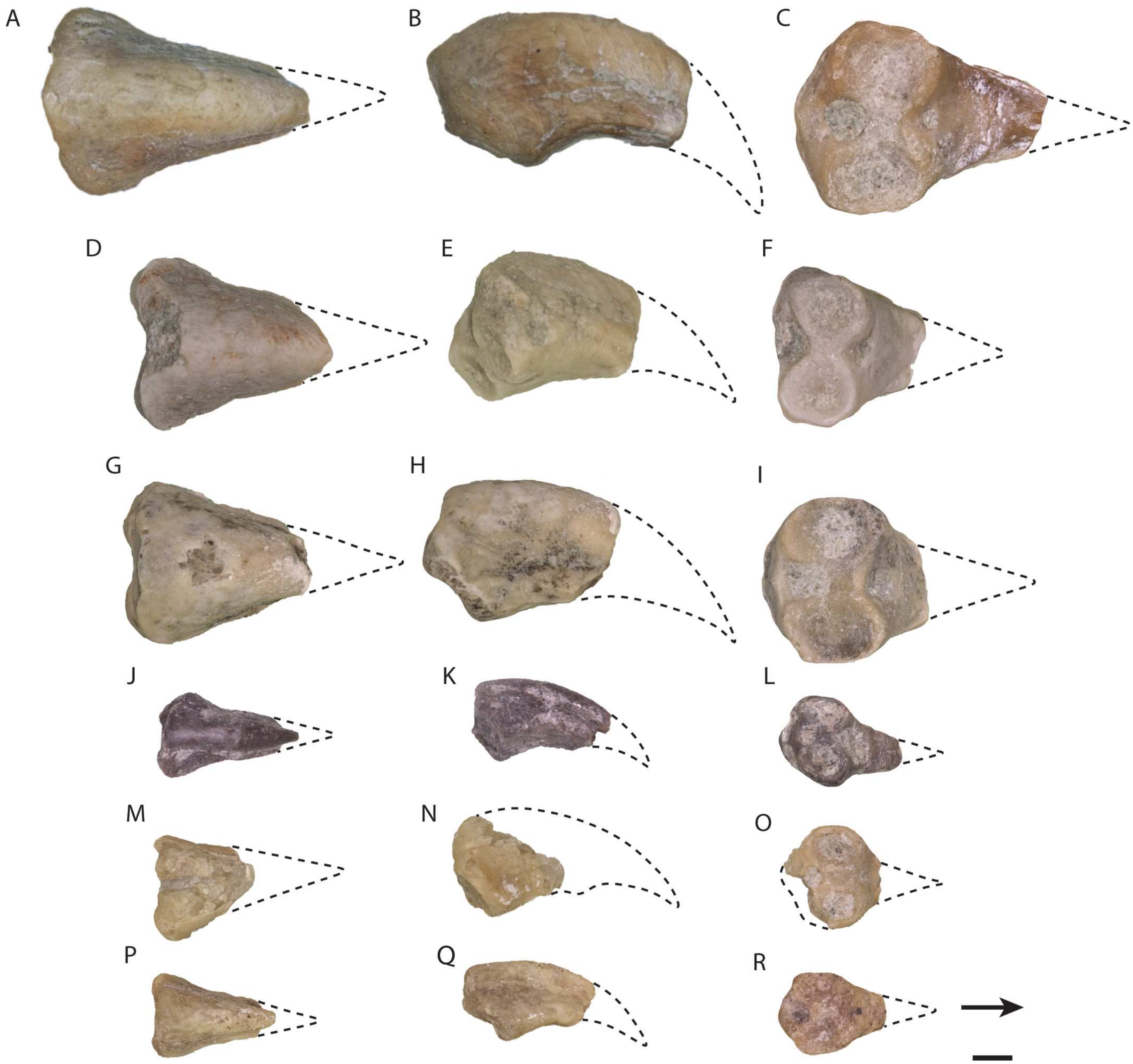

FIGURE 3. Select *Unguinychus* paratype unguals known from Homestead. Paratypes LF 5351, **A**–**C**, LF 5358, **D**–**F**, LF 5374, **G**–**I,** LF 5361, **J**–**L**, LF 5375, **M**–**O**, and LF 5376, **P**–**R** are each shown, from left to right, in dorsal, right lateral, and articular view. Dashed lines show predicted form for especially damaged portions. Arrow points anteriorly. Scale bar equals 1 mm.

foramen of greater diameter than the ventral one, proximodorsal grooves, and a lack of palmar depressions.

Unguinychus onyx differs from *Ancistronychus paradoxus* (Gonçalves & Sidor, 2019) by having a relatively smooth dorsal surface, an approximately triangular transverse cross section, lateral grooves visible in transverse cross section, non-parallel lateral surfaces, midline foramina, articular surface wider than the rest of the ungual, a presumably non-bifurcating tip, and a bi-lobed flexor region.

Unguinychus onyx differs from *Drepanosaurus unguicaudatus* (MCSNB 5728) and GR 697 in having a bi-lobed flexor region as opposed to a hemispherical tubercle, being about as laterally wide as dorsoventrally tall, having dorsal and ventral midline foramina, and in the articular cotyles being the laterally widest part of the ungual.

Unguinychus onyx differs from LF 5359 (new drepanosauromorph morphotype, see below) by having a relatively smooth dorsal surface, an approximately triangular transverse cross section, lateral grooves visible in cross section, non-parallel lateral surfaces, midline foramina, and a bi-lobed flexor region.

Unguinychus onyx cannot be differentiated from *Avicranium renestoi* (Pritchard & Nesbitt, 2017) and other drepanosauromorph material from the *Coelophysis* Quarry (Renesto et al., 2010b; Nesbitt pers. obs.) or *Dolabrosaurus aquatilis* (Berman & Reisz, 1992) because of the lack of comparative elements. Nevertheless, *Avicranium renestoi* and possibly *Dolabrosaurus* *aquatilis* are likely younger in age based on stratigraphic and biostratigraphic correlations (Berman & Reisz, 1992; Lucas et al., 2001; Schwartz & Gillette, 1994). Though *Dolabrosaurus aquatilis* lacks a complete manus, if the original interpretation of the manus preserving digits two through five is correct then an enlarged ungual would not be expected as in *Unguinychus* (Berman & Reisz, 1992).

Locality, Horizon, and Age—The specimens are from an overbank mudstone at the Homestead Site at Garita Creek in the lower portion of the Garita Creek Formation. Clade level identifications of the following are also present at Homestead: the Hybodont shark *Reticulodus synergus* (LF 5535), actinopterygians (LF 5533), the lungfish *Arganodus* sp. (LF 5534), a coelacanth (LF 6320), metoposaurid temnospondyls (LF 6321), lepidosauromorphs (LF 5398), tanystropheids (LF 6322), trilophosaurids (LF 5397), phytosaurs (LF 5537), aetosaurs, including cf. *Typothorax* (LF 5536), rauisuchids (LF 5538), crocodylomorphs (LF 5540), and dinosauromorphs (LF 5539) (Heckert et al., 2023); these will be described and illustrated more fully in subsequent work. Coprolites are also abundant. Based on biostratigraphy by Lucas and Hunt (1989) and Hunt et al. (2005), the Garita Creek Formation is Carnian in age, though in process zircon dating and biostratigraphy, especially the presence of *Reticulodus* and cf. *Typothorax* at the site suggest that the site is younger, likely within the Revueltian faunal stage of the mid Norian (Heckert et al., 2023). Since initial study of Chinle Formation correlations, magnetostratigraphy and isotope stratigraphy have extended the temporal range of the Norian (Muttoni et al., 2004), further illustrating that it is necessary to reevaluate stratigraphic correlations in east–central New Mexico.

Taxonomic Comments—In addition to the differences from the enlarged unguals described above, *Unguinychus onyx* is distinctive from non-enlarged drepanosauromorph manual and pedal unguals in possessing a bi-lobed and greatly reduced flexor region. *Unguinychus onyx* differs from caudal "unguals" in the following character states: the ventral foramen is located near the articular surface as opposed to midway along the length of the element; proximo-dorsal grooves; a ventral bi-lobed flexor region; a proximal articular region wider than and nearly as deep as the main body; and a lack of shelf-like flanges. No other taxon identified from the Garita Creek Formation has similar or predicted ungual morphology.

Taphonomic Comments—Most fossils from the Homestead Site at Garita Creek exhibit some degree of both past and present weathering, drepanosauromorphs included, as evidenced by the missing, and sometimes rounded, distal portions of all *Unguinychus* unguals and perpendicular breaks in numerous specimens (see LF 5359, Fig. 4G–I). This taphonomic process likely eroded some features of the *U. onyx* holotype, such as the low flexor region, which more closely resembles the two ridges observed in the flexor region of *Skybalonyx skapter* (PEFO 43703) in smaller, less weathered specimens. However, even in an unweathered specimen we are confident that most character states, and all autapomorphies, would remain essentially unaltered. We also consider the missing distal portions of each claw to be taphonomic in origin as opposed to an anatomical feature, as the break is inconsistent in both location and degree of rounding from weathering.

DESCRIPTION

Ungual—With all known unguals as isolated finds, it is impossible to say with certainty the position of any ungual on the manus or pes. However, several characters are shared with the enlarged manual unguals of other drepanosauromorphs. The greater size of these unguals relative to the "small" ungual morphotype (see below) implies these unguals would have been the largest present on the animal in life, as observed in *Drepanosaurus unguicaudatus*. Cotyles angled ventrally from the main axis of the ungual are seen in the enlarged unguals of *D. unguicaudatus* (MCSNB 5728), *Ancistronychus paradoxus* (PEFO 42805/UWBM 117331), GR 697, and LF 5359. The proportionally smaller unguals from all described drepanosauromorphs do not have articulations angled ventrally from the main axis. Though the unguals of *Unguinychus onyx* are unique in having an articulation wider than the rest of the ungual, this implies the presence of a large, robust phalanx like that of *D. unguicaudatus*. Proportionally shallow flexor tubercles are also seen in the enlarged unguals of *Drepanosaurus*, *Ancistronychus*, and LF 5359, whereas the smaller unguals have tubercles often as dorsoventrally deep as the main body of the ungual. The anterior positioning of this flexor region is not, to our knowledge, present in any Late Triassic clade other than drepanosauromorphs. Thus, we hypothesize that the unguals presented here represent unguals from the second manual digit of a drepanosauromorph.

Though the distalmost portion is consistently absent because of breakage, all specimens preserve a large portion of the proximal surface. The cotyles of the articulation are highly distinctive, with each cotyle joined by a constricted portion less than half the proximo-ventral length of the cotyles. Nestled in the space dorsal and ventral to this constricted region are the foramina. Jenkins et al. (2020) interpreted these as extensor pits in *Skybalonyx skapter* (PEFO 43703). However, the broken surface of LF 5375 (Fig. 3M–O) reveals that these "pits" extend some distance along the length of the unguals of *Unguinychus onyx*, a condition also seen in CT scans of *S. skapter* (PEFO 43703, see Morphosource at: https://www.morphosource.org/projects/000580888?locale=en). In the ungual of *Skybalonyx* these channels terminate near the middle of the proximo-distal length, and would presumably do the same in *Unguinychus* given that most specimens show no sign of innervating channels in their broken distal cross section. The ventral most of these foramina opens nearly on the ventral surface, whereas the dorsal most is situated approximately 75% along the maximum dorsoventral height of the ungual (Fig. 2). The opening of the dorsal most foramen has a greater diameter than that of the ventral most one, being approximately twice as wide in the holotype (Fig. 2). On the proximo-dorsal surface there are two grooves. They do not join at the median and extend on a trajectory parallel to the proximo-dorsal edges of the ungual. Though weathering may have obscured some surface details, there is little apparent sculpturing on the dorsal or lateral surfaces, though there are prominent lateral grooves. These grooves trend so deeply within the ungual that in transverse cross section the unguals look nearly lobed. The ventral surface is flat, with a sharp angle marking the transition to the lateral surface. The holotype in particular has a very low ventral tubercle (or flexor region), though it is unclear if this is due to weathering, individual variation, or ontogeny. The holotype of *S. skapter*, PEFO 43703, similarly has a low flexor region. Smaller, but less weathered, specimens such as LF 5361 (Fig. 3J–L) indicate this feature is similar in form to smaller specimens of *Skybalonyx* such as referred specimen MNA V12394, with two transverse ridges forming a bi-lobed flexor region. Raised lips on the ventral surface split off from the lateral edges proximally and join with the tubercle, constricting to approximately one-third the width of the ungual at the tubercle.

The overall form of *U. onyx* is similar to that of *Skybalonyx skapter* (PEFO 43703), being roughly triangular in transverse cross section with the ventral surface being the widest portion of the ungual along the entire body length. Uniquely among drepanosaurids, the definitively widest portion of the entire ungual of *U. onyx* is at the proximal cotyles. Similar to *S. skapter* (PEFO 43703), each cotyle is nearly as long in the proximo-ventral dimension as the ungual is deep. The cotyles are proximo-ventrally oriented in *U. onyx*, as in *Ancistronychus* and *Drepanosaurus*, creating another proximo-dorsal surface where the proximo-dorsal grooves are situated. This is unlike the condition of *S. skapter* (PEFO 43703), where there is no proximo-dorsal region distinct from the cotyles. The margins of the cotyles are cupped in lateral view in the holotype, as in other drepanosaurids, but some of the well-preserved paratypes, most notably LF 5351 and LF 5361, have cotylar margins that are approximately coplanar in lateral view. This may represent individual variation within the species or variable weathering patterns during fossilization and other taxonomic effects. The unguals have modest curvature compared with *Ancistronychus* and *Drepanosaurus*, with the holotype having curvature of 85° in lateral view and none in dorsal view. The holotype specimen is the largest, measuring 7.77 mm long and 4.42 mm wide, with the smallest specimens being just under half the lateral width of the holotype. It is possible that the holotype does not represent a skeletally mature individual, but LF 5575 represents the currently observable upper size limit of *U. onyx*. Throughout the size range, there is no clear morphological variation in the recovered sample aside from more pronounced flexor ridges in smaller specimens.

DREPANOSAURIDAE indet.
(Fig. 4)

Specimens—LF 5359 and LF 5576 (best preserved and primary references); LF 5350; LF 5353; LF 5360; LF 5378; LF 5379; LF 5393; LF 5394; LF 5395; LF 5577; LF 5578; LF 5585; LF 5586;

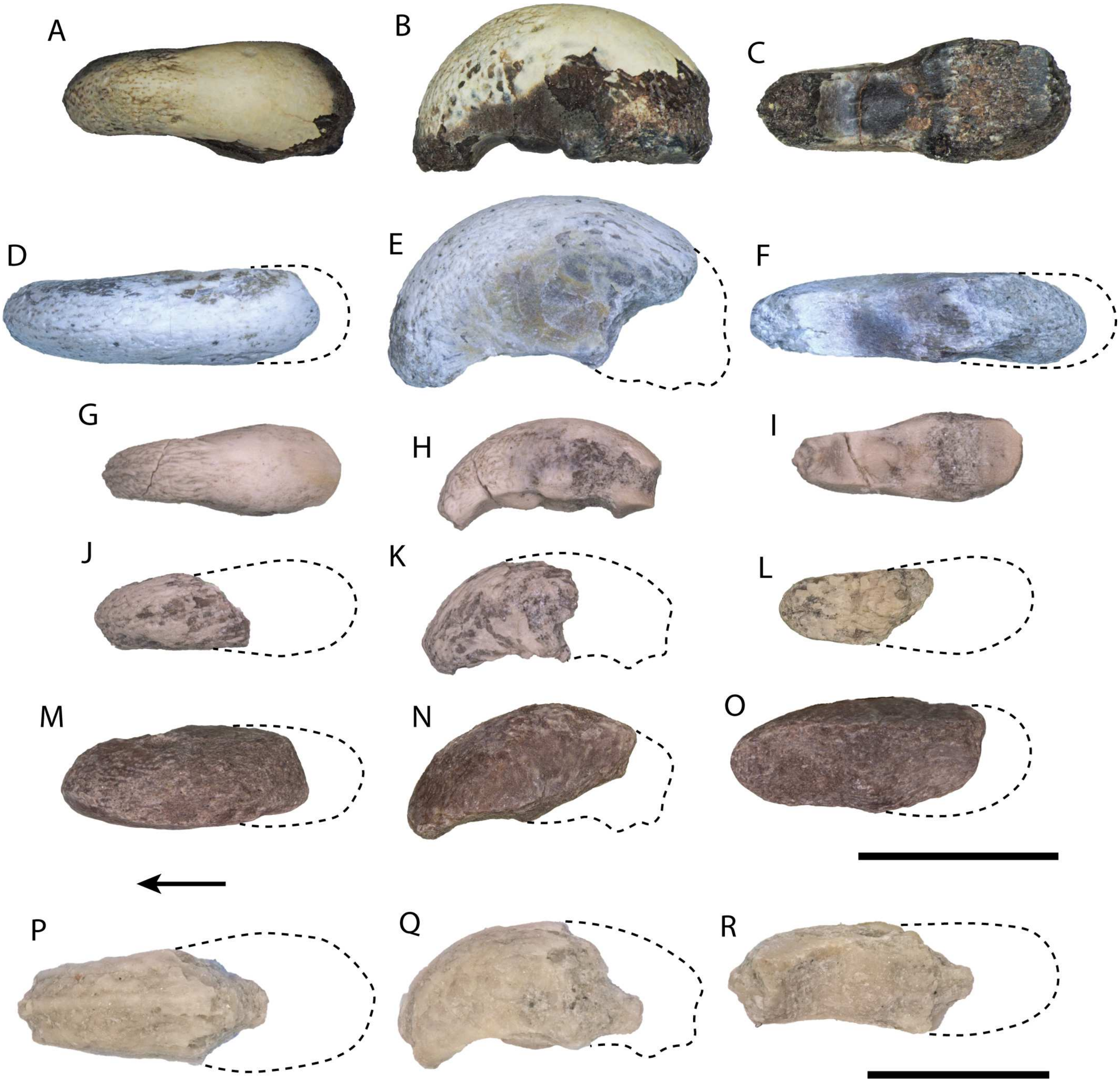

FIGURE 4. Specimens LF 5576, **A**–**C**, LF 5353, **D**–**F**, LF 5359, **G**–**I**, LF 5360, **J**–**L**, LF 5378, **M**–**O**, and LF 5379, **P**–**R**, are each shown, from left to right, in dorsal, left lateral, and ventral view. Dashed lines show predicted form for especially damaged specimens. Arrow points anteriorly. Top scale bar equals 10 mm and applies to **A**–**O**. Lower scale bar equals 2 mm and applies to **P**–**R**.

LF 5587, side unknown for all. We interpret these as enlarged manual unguals of digit II of the manus (Fig. 4).

Diagnosis—This ungual morphotype (Fig. 4) differs from all other drepanosauromorphs in the possession of the following combination of character states, with autapomorphies marked as *: nearly parallel lateral surfaces for most of its length (1); the proximal portion being approximately 50% wider than the distal portion, with an abrupt transition observed at about halfway down the ungual length (2); wrinkled dorsal texturing on the distal portion of the claw, with the proximal dorsal surface being smooth (3); *maximum lateral width over one half the maximum dorsoventral depth of the ungual but always less than the maximum depth (4); *and a relatively shallow articular cotyle (5).

LF 5359 differs from *Skybalonyx skapter* (Jenkins et al., 2020) by a ventrally angled proximal articulation, being dorsoventrally deeper, a hemispherical flexor tubercle, wrinkled dorsal texturing, and a constriction in lateral width approximately halfway along the proximodistal length.

LF 5359 differs from *Ancistronychus paradoxus* (Gonçalves & Sidor, 2019) by having a maximum dorsoventral depth greater than maximum lateral width, a non-elongated proximal region, a non-bifurcating distal tip, and constricting in lateral width near the proximodistal middle of the ungual.

LF 5359 differs from *Drepanosaurus unguicaudatus* (MCSNB 5728) and GR 697 in having a wrinkled dorsal texture, a maximum lateral width over half the maximum dorsoventral depth, and constricting in lateral width near the proximodistal middle of the ungual.

LF 5359 cannot be differentiated from *Avicranium renestoi* (Pritchard & Nesbitt, 2017) and other drepanosauromorph material from the *Coelophysis* Quarry (Renesto et al., 2010b; Nesbitt pers. obs.) or *Dolabrosaurus aquatilis* (Berman & Reisz, 1992) because of the lack of comparative elements. Nevertheless, *A. renestoi* and possibly *D. aquatilis* are likely younger in age based on stratigraphic and biostratigraphic correlations (Berman & Reisz, 1992; Heckert & Lucas, 2006; Lucas et al., 2001, 2005; Schwartz & Gillette, 1994). Though *D. aquatilis* lacks a complete manus, if the original interpretation of the manus preserving digits two through five is correct then an enlarged ungual would not be expected as in this morphotype (Berman & Reisz, 1992).

Locality, Horizon, and Age—All specimens are from the Homestead Site at Garita Creek of the lower Garita Creek Formation, and originate from the same horizon as *Unguinychus onyx* (see above).

Taxonomic Comments—This ungual morphotype is distinctive from all enlarged drepanosauromorph unguals primarily in its width to depth ratio and the mediolateral constriction along the midportion of the ungual. No other taxon identified from the Garita Creek Formation or the Homestead site has similar ungual morphology, though similar claw morphotypes are known from other sites (Sodano et al., 2022).

Taphonomic Comments—Weathering is extreme in the proximal portion of these specimens, with no proximal cortex surface in any but LF 5359 and LF 5576, though even they lack complete cotyles. LF 5350, LF 5360, and LF 5378 are similarly eroded across the entire element but share the general form and dorsal texturing of the other specimens. LF 5576 is the only specimen to preserve any form of innervation, with a pair of ventral foramina just proximal to the ventral tubercle. No specimen preserves any evidence of prominent lateral grooves, though some form of innervation or lateral grooves for blood circulation was likely present in all specimens in life. The shallow cotyles of LF 5359 and LF 5576 are likely a product of weathering, with the perimeter being potentially more pronounced in an unweathered specimen as in *Drepanosaurus* and *Ancistronychus*. With only two specimens preserving a partial articular end, this is difficult to determine. As such, a more complete description will be left to other active work on more abundant and better-preserved material from the Upper Triassic of Arizona (Sodano et al., 2022).

DESCRIPTION

Ungual—All unguals have a poorly preserved proximal portion, with the only specimens having any articular surface being LF 5359 and LF 5576, though LF 5576 preserves very little of the cotyles. Even in these specimens the proximal region is likely incomplete, as internal spongy textures are visible around the cotyles. The proximal articular facet is small relative to the dorsoventral depth of the ungual and lacks a midline ridge as seen in unguals of *Ancistronychus paradoxus* (PEFO 42805/UWBM 117331) and a *Drepanosaurus*-like taxon (GR 697). A near linear proximo-dorsal surface is present, much like in *Unguinychus onyx*, with sharp angles between the dorsal surface and cotyle when viewed laterally. This angle is sharper in LF 5359 (122°) than LF 5576 (141°). The interpretation of this shape should be considered with caution, as the more granular bone texture surrounding the cotyle indicates there is weathered, missing bone, and this likely extends to the cotyle in some capacity. However, a similar proximal linear surface is present in lateral view in the Hayden Quarry *Drepanosaurus*-like taxon (GR 697), so this interpretation is not unprecedented.

The ventral surface is smooth and flat, with the exception of a hemispherical tubercle positioned more than halfway along the proximodistal length of the ungual. Proximal to this tubercle there are ventrolaterally expanded flanges, though they are subtle. The lateral surfaces of the ungual are near parallel, excluding the width constriction in the midsection of the ungual. A smooth dorsal surface is present on the wider portion, and the distal portion has a wrinkled texturing on the dorsal surface. The dorsal surface of LF 5359 and LF 5379 preserve a midline ridge in the distal portion, somewhat similar to *Ancistronychus paradoxus* (PEFO 42805/UWBM117331). There is no clear variation with size in this ungual morphotype, as the smallest ungual, LF 5379, is similar to the much larger LF 5359. The largest specimen, LF 5353, lacks the proximal half of the ungual entirely, but is proportionally narrower and deeper than the smaller specimens. LF 5576, which is relatively complete, is also proportionally deeper than LF 5359 but not especially narrow. The narrowness of LF 5353 likely reflects it only being the distalmost portion of the ungual, lacking the laterally expanded proximal region. Whether the variation in dorsoventral depth is a result of ontogeny or individual variation is not clear, but it likely is not taphonomic given the lack of damage to the lateral surfaces of these specimens.

DREPANOSAURIDAE indet.
(Figs. 5–9)

Specimens—LF 5387 and LF 5579 (best preserved and primary references); LF 5580; LF 5592; LF 5593; LF 5594; LF 5595; LF 5596; LF 5597; LF 5598; LF 5599; LF 5600; LF 6301; LF 6302; LF 6303; LF 6304 (Fig. 5), fragments of drepanosaurid caudal unguals. LF 5357; LF 5373 (Fig. 6), fragments of cervical vertebrae. LF 5356; LF 5365; LF 5366; LF 5367 (Fig. 7), fragments of trunk vertebrae. LF 5355; LF 5368; LF 5369; LF 5370; LF 5371; LF 5372; LF 5581; LF 5582; LF 5583 (Fig. 8), fragments of caudal vertebrae. LF 5354; LF 5362; LF 5363; LF 5364; LF 5380; LF 5381; LF 5382; LF 5384; LF 5391; LF 5392; LF 6305; LF 6306; LF 6307; LF 6308; LF 6309; LF 6310; LF 6311; LF 6312; LF 6313; LF 6314; LF 6315 (Fig. 9), small claw morphotype.

Locality, Horizon, and Age—All specimens are from the Homestead Site at Garita Creek of the lower Garita Creek

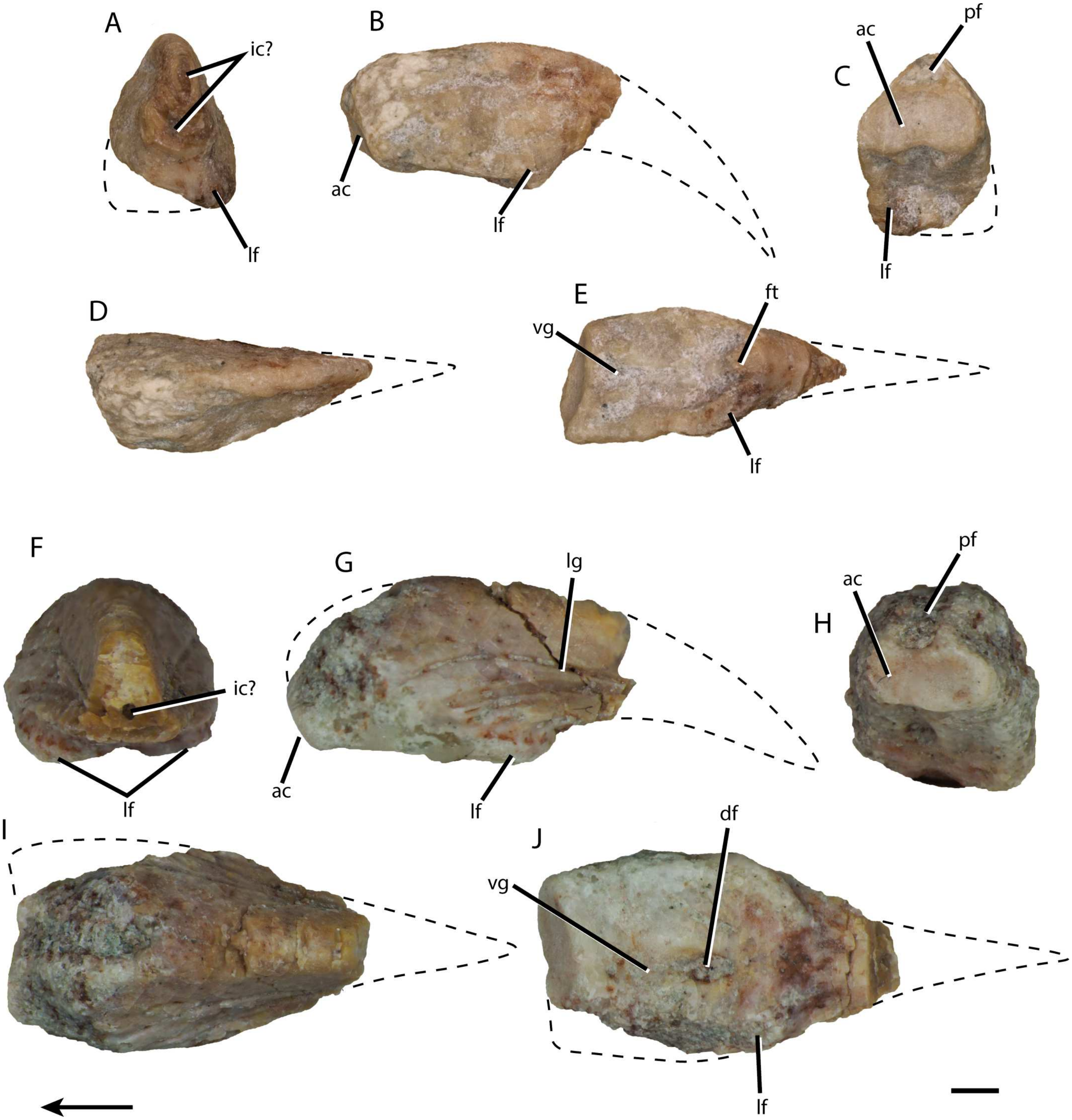

FIGURE 5. Fragmentary tail claws from Homestead, LF 5387, **A**–**E**, and LF 5579, **F**–**J**. Shown in distal, **A** and **F**, left lateral, **B** and **G**, articular, **C** and **H**, dorsal, **D** and **I**, and ventral, **E** and **J** views. Arrow points anteriorly and applies to **B**, **D**, **E**, **G**, **I**, and **J**. **Abbreviations**: **ac**, articular cotyles; **df**, distal foramen; **ft**, flexor tubercle; **ic?**, possible innervating channels; **lf**, lateral flange; **lg**, lateral groove; **pf**, proximo-dorsal foramen; **vg**, ventral groove. Dashed lines show predicted form for damaged portions. Scale bar equals 1 mm.

Formation, and presumably originate from the same horizon as *Unguinychus onyx* (see above).

Taxonomic Comments—All of these specimens share some similarities, but not necessarily apomorphies, to previously described drepanosaurid material, including *Drepanosaurus*, *Megalancosaurus*, *Vallesaurus*, and *Dolabrosaurus*. They cannot currently be assigned to any named drepanosaur.

Taphonomic Comments—Originating from the same horizon as *Unguinychus onyx*, these specimens share weathering patterns consistent with the enlarged claw morphotypes. Several elements have weathered edges, especially the left side of LF 5387. The majority of specimens are broken in some location, though enough of each element remains to make tentative identifications.

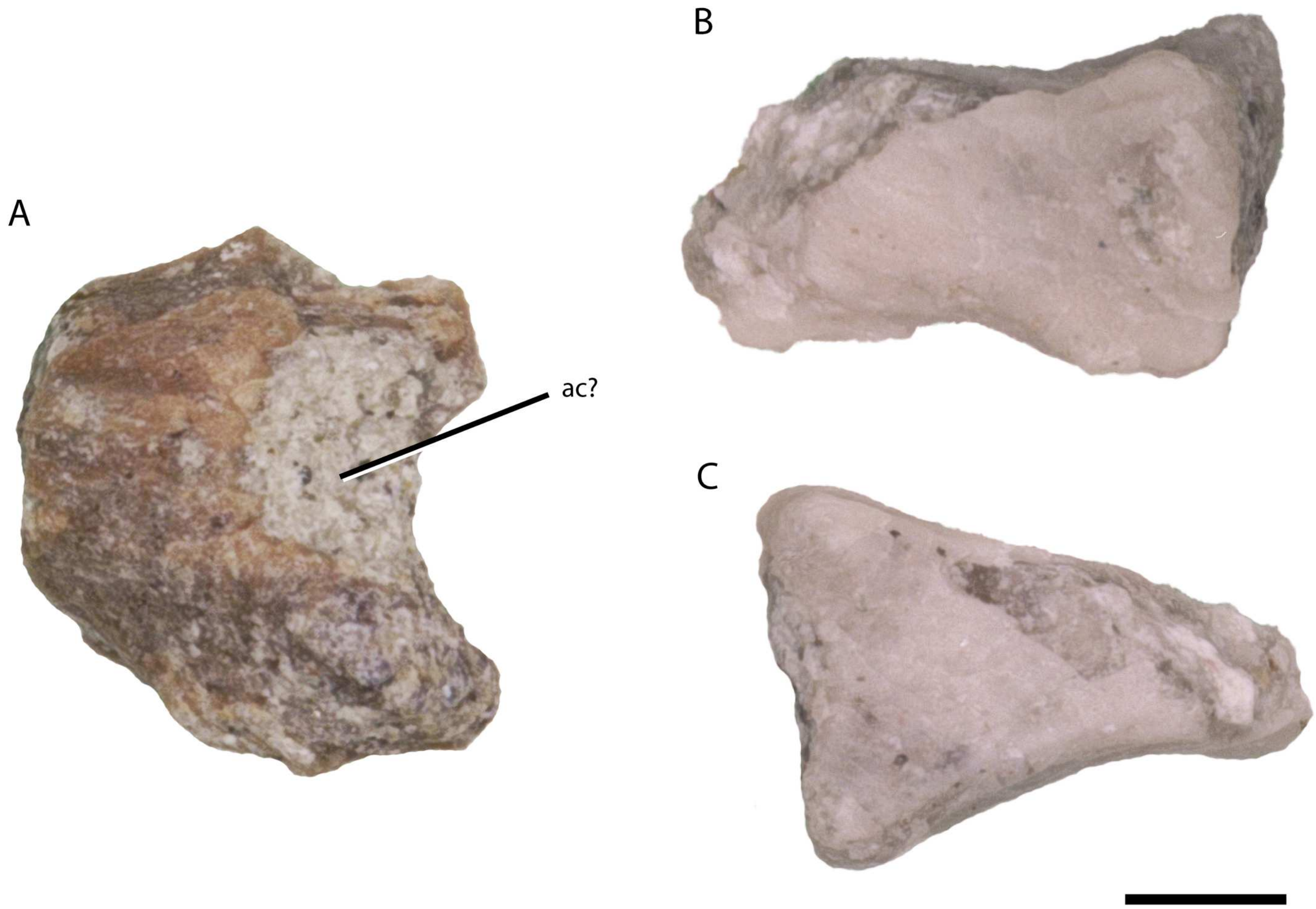

FIGURE 6. Possible drepanosauromorph cervical vertebrae from Homestead. LF 5357 in lateral view, **A**, and LF 5373 in lateral, **B**, and dorsal?, **C** view. **Abbreviation**: **ac?**, possible anterior cotyle. Scale bar equals 1 mm.

DESCRIPTION AND RATIONALE FOR ASSIGNMENT

Caudal Ungual

These "unguals" (Fig. 5) possesses a unique combination of character states that distinguish them from manual and pedal elements, including: lateroventrally expanded flanges approximately halfway along the proximodistal length; a concave proximo-ventral surface; a proximo-dorsal foramen; ventral groove leading to a ventral foramen; a rounded ventral surface along the main body of the spike in LF 5387; and no tubercle on the main spike (see Fig. 5). *Drepanosaurus unguicaudatus* (MCSNB 5728) and *Megalancosaurus* (MFSN 18443a) preserve a caudal ungual articulated with the caudal series, though both specimens are crushed. The flanges of LF 5387 and LF 5579 are likely equivalent to the ventrally expanded knob on each of these specimens (see Fraser & Renesto, 2005:fig. 4 and Renesto et al., 2010b:figs. 2b and 15b). In lateral view and anterior to this expanded region, is a concave surface in both LF 5387 and the slab specimens. UMZC 2004.8 has also been identified as an isolated and three-dimensional caudal ungual (Fraser & Renesto, 2005). Its expanded ventral region is shelf-like, as in LF 5387 and LF 5579, and it too has a concave ventral surface anterior to this expansion. In addition, Fraser and Renesto (2005) reported the articulation to be similar to notochordal amphicoelous vertebrae with a clear opening. LF 5387 also has a clear opening on the proximal surface, though it is separate from the cotyles and does not greatly resemble notochordal vertebrae. LF 5579 has two ridges forming the base of what would be a similar proximo-dorsal opening. Given the similarities of LF 5387 and LF 5579 to each of these specimens, we consider them to also be caudal unguals. The remaining specimens are less complete, but preserve portions of the ventral shelf or innervating channels throughout the spike and as such are tentatively considered to be caudal ungual fragments.

Though unusual in tetrapods, "tail claws" are common among drepanosaurids. The distal region, or the main "spike," is mostly absent in LF 5387 and the leftmost margins of the cotyles and proximo-ventral surface protrude less than their right mirror counterparts (Fig. 5). This asymmetry is more likely a result of taphonomic influence than original shape. The proximal region differs notably from most manual and pedal unguals, bearing a distinct double lobed articulation on a slight proximal protrusion. Ventral to the protrusion is a concave surface, much like the profile of the caudal ungual in *Drepanosaurus unguicaudatus* (MCSNB 5728). There is a bony knob on the midline of the distal rim of this surface that is grossly similar to the hemispherical tubercles of drepanosauromorph manual unguals (GR 697 and PEFO 42805/UWBM 117331), though proportionally much smaller than tubercles of the smaller ungual morphotypes and more proximally oriented than enlarged unguals. A groove extends along the proximo-ventral concave surface and leads to a partially obscured ventral foramen (Fig. 5). Little can be determined about the full width or length of the spike region of the caudal ungual, but in the small preserved portion it is narrow with a rounded ventral surface. There is a small foramen filled in with matrix dorsal to the articular surface, and this foramen

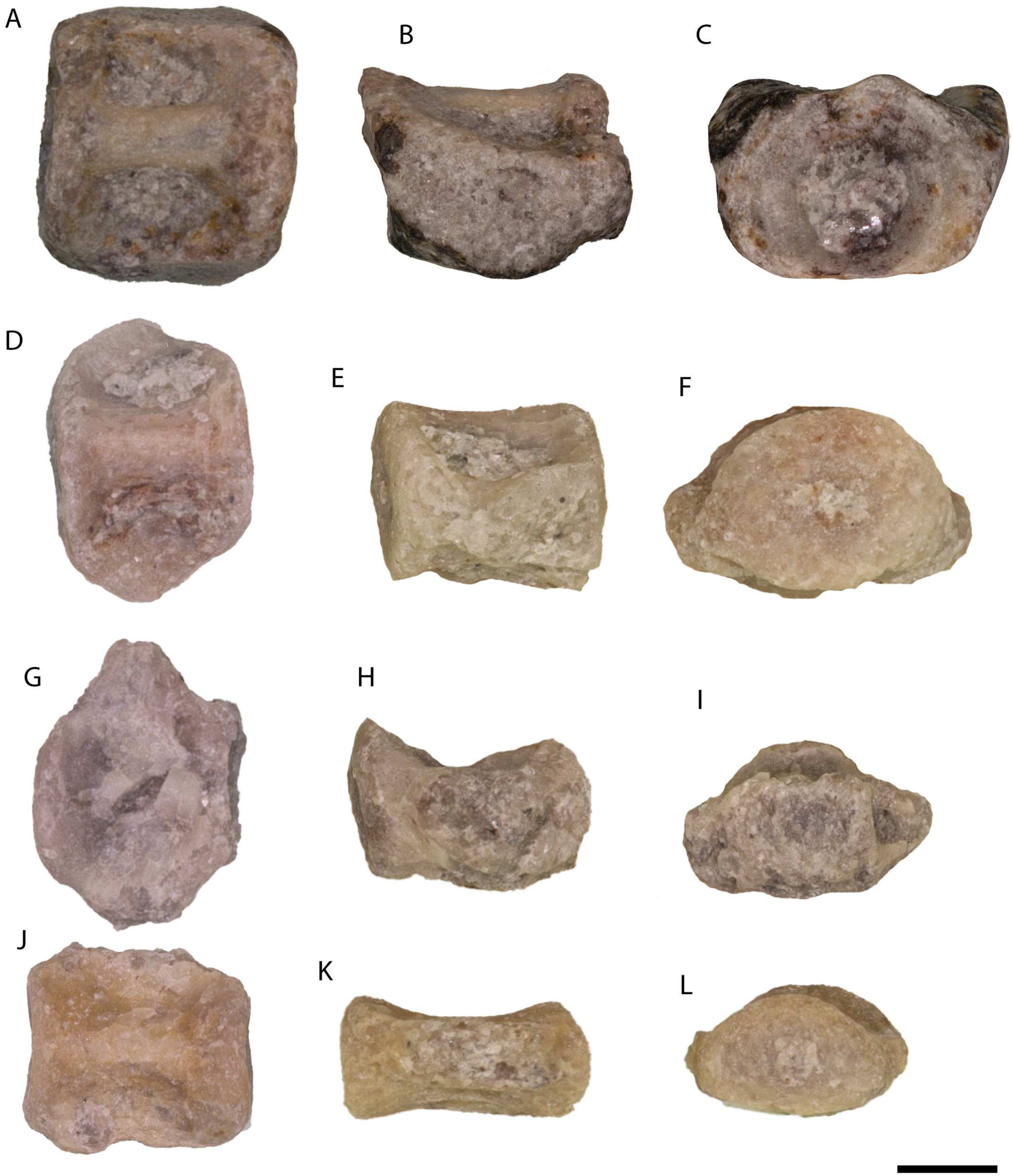

FIGURE 7. Drepanosaur trunk vertebrae known from Homestead. Specimens LF 5356, **A**-**C**, LF 5365, **D**–**F**, LF 5366, **G**–**I**, and LF 5367, **J**–**L** are each shown, from left to right, in dorsal, lateral, and articular view. Scale bar equals 1 mm.

as well as the ventral foramen likely extend for some length, as the broken distal portion displays two potentially connected tube-like ovular shapes.

LF 5579 represents a second morphotype of caudal ungual. Though in most respects it is similar to LF 5387, it has a triangular spike in cross section, is proportionally wider, has a slightly larger

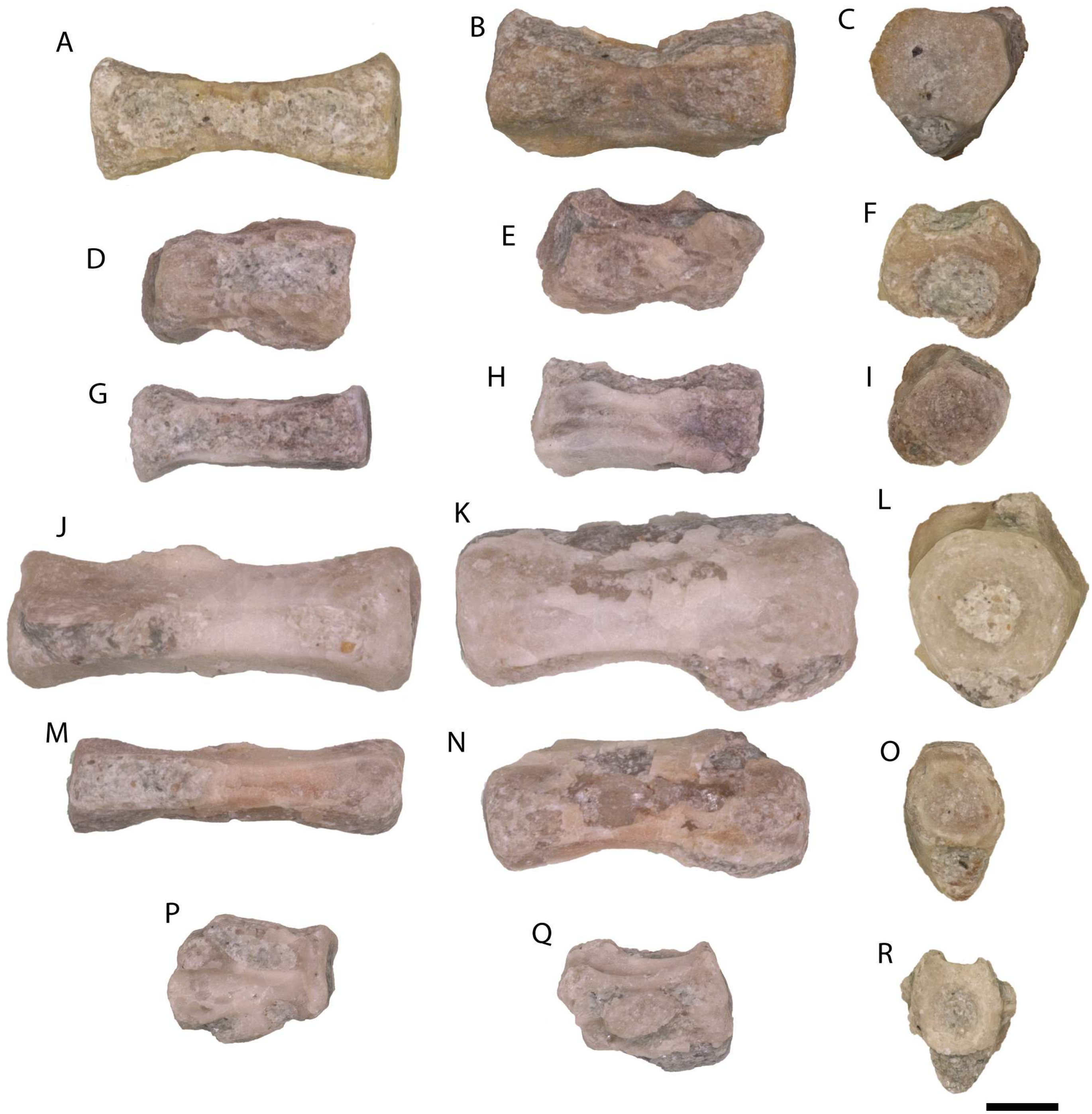

FIGURE 8. Drepanosaur caudal vertebrae known from Homestead. Specimens LF 5355, **A**–**C**, LF 5368, **D**–**F**, LF 5369, **G**-**I**, LF 5370, **J**–**L**, LF 5371, **M**–**O**, and LF 5372, **P**–**R** are each shown, from left to right, in dorsal, lateral, and articular view. Scale bar equals 1 mm.

protruding proximal region, and a more defined ventral foramen. It also has much more defined lateral grooves, granted this was possibly modified through taphonomic processes. In cross section, LF 5579 has only one apparent channel. Most caudal ungual fragments with spikes also appear to have triangular cross sections with only one channel. Assuming that the break on LF 5387 accurately represents the cross section of the entire spike length, this second morphotype is more common at Homestead, though the presence of only one channel throughout the length of the spike may be common to both morphotypes.

Vertebrae

General Comments—The vertebrae are the most difficult specimens to assign to Drepanosauromorpha. Vertebral processes and articulations have been treated as diagnostic character states for drepanosauromorphs (see Fraser & Renesto, 2005; Renesto & Fraser, 2003; Senter, 2004), but Homestead specimens are comprised almost entirely of centra. Even so, a few features are shared with articulated slab specimens. All drepanosauromorph vertebrae from the Homestead Site at Garita Creek are non-notochordal and amphicoelous (except for cervical

FIGURE 9. Small manual/pedal morphotype unguals from Homestead. Specimens LF 5363, **A**–**C**, LF 5364, **D**–**F**, LF 5354, **G**–**I**, LF 5362, **J**–**L**, LF 5380, **M**–**O**, LF 5381, **P**–**R**, LF 5382, **S**–**U**, and LF 5384, **V**–**X** are each shown, from left to right, in dorsal, right lateral, and ventral view. Scale bar equals 1 mm.

vertebrae), as in *Drepanosaurus unguicaudatus* (MCSNB 5728), *Megalancosaurus preonensis* (MFSN 1769), and *Hypuronector limnaios* (AMNH 7759), though notochordal amphicoelous vertebrae have been reported in the group (Renesto et al., 2010a, b).

Cervical Vertebrae—Drepanosauromorph cervical vertebrae have neural arches laterally wider than the centrum, are heterocoelous with a cotyle and condyle, have a relatively short and anteriorly inclined neural spine, and keeled hypapophyses (Colbert & Olsen, 2001; Renesto, 1994; Renesto & Binelli, 2006; Renesto & Fraser, 2003; Renesto et al., 2010b). Though these features are largely absent in the fragmentary specimens from Homestead, LF 5357 has a potential posterior articular cotyle, whereas LF 5373 is strongly flared at one end, indicating it supported the wide neural arch, and has a much narrower midsection similar to the centrum and hypapophysis seen in drepanosauromorph cervical vertebrae from the Cromhall Quarry (Renesto & Fraser, 2003, see Fig. 6).

Trunk Vertebrae—The trunk vertebrae are dorsoventrally low, with nearly equal transverse and anteroposterior dimensions (Fig. 7). Near equal transverse and anteroposterior lengths can also be observed in disarticulated and rotated vertebrae of *Drepanosaurus unguicaudatus* (MCSNB 5728), as can the low lateral profile when the neural arch processes are not included. Some trunk vertebrae preserve part of lateral processes and fusion points to support a large neural arch, and large neural arches and processes are typical in drepanosauromorphs. Currently, we are not sure these character states are diagnostic only to drepanosauromorphs given uncertainty in their phylogenetic position and the lack of other comparative articulated material. We do note that these character states are common to drepanosauromorphs that we can compare with.

Caudal Vertebrae—Most caudal vertebrae are notably more elongate than trunk vertebrae or cervical vertebrae, though not all are (Fig. 8). Centrum shape is generally similar to that reported in drepanosauromorph caudal vertebrae by Fraser and Renesto (2005), sharing a midline constriction, a large broken posteroventral surface that would have supported the large chevron, and deeply cupped articular facets. More elongate caudal vertebrae likely correspond to the midsection of the tail, whereas the more compact centra better align with the most distal and proximal vertebrae of the tail, as observed in the caudal series of *Drepanosaurus*, *Megalancosaurus*, *Dolabrosaurus*, and *Vallesaurus*. Determining anterior versus posterior orientation of all centra is somewhat difficult, but is possible in some more elongate caudal vertebrae where the chevron fusion is evident, marking the posterior end. Drepanosauromorphs with presumably prehensile tails (e.g., Drepanosauridae and close relatives) shift the fusion point for the chevron in the posterior portion of the caudal series, with more anterior vertebrae fusing the chevron to the posterior of the centrum and the most posterior vertebrae fusing the chevron to the anterior of the centrum. Hence, orientation of the more compact (such as LF 5372, Fig. 8P–R) and presumably more posteriorly or anteriorly oriented vertebrae from Homestead is difficult to determine.

Small Ungual Morphotype

These unguals (Fig. 9) are tentatively assigned to Drepanosauromorpha based on the large hemispherical flexor tubercles they have in common with the larger unguals, with all being nearly as dorsoventrally deep and/or transversely wide as the main ungual. All unguals of this morphotype lack an articular face, making it impossible to compare the structure of the cotyles and any proximal channels with LF 5359 and *Unguinychus onyx*. However, the remainder of the elements are fairly well preserved. There is a variety of forms between the unguals, ranging from relatively robust specimens (LF 5384) to longer, more delicate forms (LF 5380), with some specimens (LF 5363) exhibiting a relatively flat, wide form (Fig. 9). The primary unifying feature is the large hemispherical tubercle in all specimens, often making up at least one third of the dorsoventral depth of the ungual as commonly observed in articulated drepanosauromorphs (see *Drepanosaurus unguicaudatus*, *Megalancosaurus preonensis*, *M. endennae*, *Vallesaurus zorzinensis*, *V. cenensis*, and *Dolabrosaurus aquatilis*). In specimens with lower tubercles, the tubercle is still nearly as wide as the ungual. In specimens that have lateral grooves, they are oriented closer to the dorsal surface than the ungual midline, a structural feature comparable to enlarged drepanosauromorph unguals (Jenkins et al., 2020; Pritchard et al., 2016). A few specimens have a wrinkled dorsal texturing similar to LF 5359 and *Ancistronychus paradoxus*. All specimens also exhibit a distinct flat ventral surface forming a sharp angle with the lateral surface, similar to LF 5359, *A. paradoxus*, *Skybalonyx skapter*, GR 697, and *Unguinychus onyx*.

This ungual morphotype is difficult to see in crushed, articulated specimens, so a detailed comparison is challenging. The flat ventral surface has not been reported in other smaller drepanosauromorph unguals, though most other examples are from crushed slab specimens. NMMNH P-57651, an articulated hindlimb from Ghost Ranch, preserves some three-dimensionality but lacks any dorsal texturing and does not have a flat ventral surface. Hence, the Homestead morphotype, though united with other drepanosauromorph unguals by the large tubercle and with larger Homestead unguals by dorsal texturing and lateral groove orientation, may represent a unique form within the clade.

DISCUSSION

The Homestead Site at Garita Creek preserves a remarkable collection of isolated drepanosauromorph elements. Most importantly, all elements are preserved in three dimensions, which is uncommon among drepanosauromorphs that are documented from articulated skeletons that have been crushed and preserved on rock slabs. As such, Homestead specimens offer a look at morphology rarely observed in the clade at other sites. Furthermore, the use of explicit synapomorphies to identify isolated drepanosauromorph elements is improving (Lessner et al., 2018; Pritchard et al., 2023), but many drepanosauromorph element identifications have not gone through this rigorous, apomorphy-based assignment process; here we add to this effort by identifying further drepanosauromorph bones including cervical, trunk, and caudal vertebrae, manual ungual morphotypes and other non-hypertrophied manual or pes unguals.

Rigorous application of apomorphies shows that two species of drepanosauromorph with distinct manual unguals coexisted at the Homestead Site at Garita Creek in the Late Triassic and, consequently, this is the first time at least two drepanosauromorphs of differing life modes have been confirmed to be in the same vertebrate community in North America. It is difficult to determine with certainty whether the variability of smaller ungual morphotype could be the result of unguals from two different species, manual vs pedal variation within a single species, ontogenetic or individual variation, or some combination of these factors. However, the relatively large ventral tubercle, distinctively flat ventral surface, and dorsal textures comparable to larger ungual morphotypes imply that these represent drepanosauromorph unguals from digits other than II of the manus. Diagnostic morphotypes are only apparent in the unguals, so it is unclear which postcranial remains (vertebrae and tail claws) go with each taxon. LF 5359 and LF 5576 are similar to *Drepanosaurus* and *Ancistronychus*, but are proportionately not as dorsoventrally tall as the unguals of *Drepanosaurus*, as *Drepanosaurus* unguals are very laterally narrow in comparison to all other drepanosauromorphs (Pinna, 1980; Pritchard et al., 2016; Renesto et al., 2010b). *Ancistronychus paradoxus* is known to have a prominent flat ventral surface on its enlarged unguals and a small ventral tubercle, but its unguals are far more recurved, have an elongate proximal portion, and a spade-like tip (Gonçalves & Sidor, 2019). The Homestead unguals lack these features, though the proximal portion is not well preserved in any specimen. As such, LF 5359 and LF 5576 likely represent a new species of arboreal drepanosauromorph with a life mode similar to *D. unguicaudatus*, though work on more abundant and better-preserved material from the Petrified Forest area is ongoing.

Unguinychus onyx is most similar to *Skybalonyx skapter* among drepanosauromorphs, although it is not as proportionally wide as the *S. skapter* holotype (PEFO 43703) at any point along its length. However, the paratypes of *S. skapter* (PEFO 43704–PEFO 4370) are notably narrower than the holotype, but are still regarded as representative of a fossorial lifestyle. *Unguinychus* unguals are approximately as laterally wide as dorsoventrally deep, similar to both *Skybalonyx* and *Ancistronychus*, both hypothesized burrowers (Jenkins et al., 2020). Hence, we hypothesize *Unguinychus onyx* to also be a fossorial taxon. The articular morphology of *Unguinychus onyx* is unusual, even among drepanosauromorphs, with two distinct articular facets and two innervating channels along the midline. *Skybalonyx* shares these features, though in *Skybalonyx* the two articular facets are fully separated.

The morphology of the manual unguals indicates niche partitioning of Homestead drepanosauromorphs, with the LF 5359 and LF 5576 best matching *Drepanosaurus* as an arboreal hook-and-pull insectivore, comparable to living tree-dwelling anteaters, and *Unguinychus onyx* likely representing a fossorial insectivore similar to modern moles. The two caudal ungual morphotypes also reflect two contemporary taxa, although which species had which caudal morphotype is speculative. The enlarged manual unguals reveal dozens of individuals are represented in the assemblage so far, as none have an obvious twin of closely matching size and shape from the mirror limb. The occurrence of multiple drepanosauromorph species and life modes at one site is not unheard of but remains unpublished for other microvertebrate localities. The number and variety of three-dimensional elements found at Homestead makes this a unique opportunity to study drepanosauromorph morphology and ecology. Regardless of the exact life mode for these drepanosauromorphs, their presence and morphology is largely consistent with other Upper Triassic sites and suggests that the environment maintained enough water to support at least some trees and vegetation, as well as abundant insects, to support at least one arboreal and fossorial insectivorous species.

The ability to deduce ecological inferences from isolated unguals is remarkable. Without the 2D articulated specimens, these identifications and interpretations from isolated material would be extremely difficult. However, without three-dimensional material to reference, the form and function of the articulated specimens would also be difficult to determine, demonstrating the usefulness of combining data from both types of preservation. These preservation patterns are not limited to drepanosauromorphs, so combining data from variable preservations across different taxonomic groups is not only possible but potentially very insightful. The fossil record does not typically provide fully articulated and three-dimensional specimens, but the drepanosauromorphs of Homestead offer a useful case study in using diverse preservation to assess diversity, ecology, and anatomy within an enigmatic clade.

ACKNOWLEDGMENTS

The Lauer Foundation for Paleontology, Science, and Education has generously provided access to the Homestead Site at Garita Creek and the existing collections from it. The Lauer Foundation (PSE) is proud to demonstrate the benefits that can be achieved through the cooperative and cooperative efforts between avocational paleontologists, private collectors, the Lauer Foundation, and academic institutions and museums to advance our understanding of the fossil record. We also thank L. and B. Martin for collection and preliminary identification of specimens. Michelle Stocker of Virginia Tech has provided valuable aid in identification of elements from Homestead. We thank S. Wills, P. Barrett, and D. Ward of the Natural History Museum in London for collaboration throughout the Homestead project. AppPaleo's Finding Fossils on Friday group has been particularly helpful in sorting and identifying specimens, notably J. Crothers, L. Rose, S. Ahmed, J. Meyer, S. Randleman, Z. Ore, A. Wurtz, R. Dunn, J. Crouch, J. Heidenfelder, T. Walker II, and many more. The VT Paleobiology research group has also provided valuable feedback during this project, especially Megan Sodano and Ben Kligman (who provided scans of *Skybalonyx skapter*). We additionally thank R. Mueller and J. Socha for facilitating μCT scanner access at Virginia Tech for scanning of *S. skapter* specimens and PEFO staff and interns for their field and lab efforts that led to the existence and availability of these fossils. Funding for undergraduate research (IP) was provided by the L. Raymond fund and Triassic Trip Scholarship for fieldwork, the Appalachian State University Office of Student Research for travel, the Appalachian Department of Geological and Environmental Sciences in the form of an Undergraduate Research Assistantship, and the National Science Foundation through the S-STEM program. Additional graduate funding (IP) has been provided by the National Science Foundation Graduate Research Fellowship Program. Additionally, we thank the Museo di Scienze Naturali Bergamo for allowing study of the holotypes of *Drepanosaurus unguicaudatus* and *Vallesaurus cenensis*. Lastly, we greatly thank our reviewers and handling editors for valuable feedback. This is contribution 9 from the Homestead at Garita Creek project.

AUTHOR CONTRIBUTIONS

IP designed the project and drafted the manuscript. SJN provided preliminary identifications and numerous suggestions for descriptions and figures. ABH established initial contacts with Larry Martin and the Lauer Foundation for Paleontology, Science, and Education, aided with early project organization, and coordinated and/or conducted relevant fieldwork. RL and BL provided a specimen repository, institution catalog numbers, and drafted provenance information, with additional information added by ABH. All authors edited the manuscript.

DATA AVAILABILITY STATEMENT

The raw and segmented CT data for *Skybalonyx skapter* holotype PEFO 43703 and *Skybalonyx skapter* specimens PEFO 44760 and PEFO 44761 referenced in this study are available on MorphoSource: https://www.morphosource.org/projects/000580888?locale=en.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

ORCID

Sterling J. Nesbitt http://orcid.org/0000-0002-7017-1652

LITERATURE CITED

Berman, D. S., & Reisz, R. R. (1992). *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. *Journal of Paleontology*, *66*(6), 1001–1009. doi:10.1017/S0022336000020928

Carroll, R. L. (1988). *Vertebrate paleontology and evolution*. W.H. Freeman and Company, New York, 566.

Colbert, E. H., & Olsen, P. E. (2001). A New and Unusual Aquatic Reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). *American Museum Novitates*, *3334*, 1–24. doi:10.1206/0003-0082(2001)334<0001:ANAUAR>2.0.CO;2

Dilkes, D. W. (1998). The early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1368), 501–541. https://doi.org/10.1098/rstb.1998.0225

Fraser, N. C. (2006). *Dawn of the dinosaurs: Life in the Triassic*. Indiana University Press.

Fraser, N. C., & Renesto, S. (2005). Additional Drepanosaur elements from the Triassic Fissure Infills of Cromhall Quarry, England. *Jeffersoniana*, *15*, 1–16.

Gonçalves, G. S., & Sidor, C. A. (2019). A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA. *PaleoBios*, *36*, 1–10. doi:10.5070/P9361046203

Harris, J. D., & Downs, A. (2002). A drepanosaurid pectoral girdle from the Ghost Ranch (Whitaker) *Coelophysis* Quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. *Journal of Vertebrate Paleontology*, *22*(1), 70–75. doi:10.1671/0272-4634(2002)022[0070:ADPGFT]2.0.CO;2

Heckert, A. B., Crothers, J. P., Rose, L. J., Nesbitt, S. J., Pugh, I., Stocker, M. R., Barrett, P. M., Wills, S., Ward, D., Lauer, B., & Lauer, R. (2023). An exceptionally rich microvertebrate site from the ?early Revueltian (mid-Norian) Garita Creek Formation of east-central New Mexico, USA. *The Anatomical Record: Special Issue; The 14th Symposium on Mesozoic Terrestrial Ecosystems and Biota: v*, *306*(S1), 129–131. https://d oi.org/1 0.1002.ar/25/219

Heckert, A. B., & Lucas, S. G. (2006). Micro- and small vertebrate biostratigraphy and biochronology of the Upper Triassic Chinle Group, southwestern USA. *New Mexico Museum of Natural History and Science Bulletin*, *37*, 94–104.

Hunt, A. P., Lucas, S. G., & Heckert, A. B. (2005). Definition and correlation of the Lamyan: A new biochronological unit for the nonmarine late Carnian (late Triassic). *Geology of the Chama Basin*, *56*, 357–366. doi:10.56577/FFC-56.357

Hunt, A. P., Lucas, S. G., & Sealey, P. L. (1989). Paleontology and vertebrate biochronology of the Upper Triassic Garita Creek Formation, east-central New Mexico. *New Mexico Journal of Science*, *29*, 61–68.

Irmis, R. B., Mundil, R., Martz, J. W., & Parker, W. G. (2011). High-resolution U–Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. *Earth and Planetary Science Letters*, *309*(3–4), 258–267. https://doi.org/10.1016/j.epsl.2011.07.015

Irmis, R. B., Nesbitt, S. J., Padian, K., Smith, N. D., Turner, A. H., Woody, D., & Downs, A. (2007). A Late Triassic Dinosauromorph Assemblage from New Mexico and the Rise of Dinosaurs. *Science*, *317*(5836), 358–361. https://doi.org/10.1126/science.1143325

Jenkins, X. A., Pritchard, A. C., Marsh, A. D., Kligman, B. T., Sidor, C. A., & Reed, K. E. (2020). Using Manual Ungual Morphology to Predict Substrate Use in the Drepanosauromorpha and the Description of a New Species. *Journal of Vertebrate Paleontology*, *40*(5), e1810058. doi:10.1080/02724634.2020.1810058

Lauer, R., Lauer, B., Ward, A., & Ward, D. (2023). Acquiring the Homestead Upper Triassic Site: An international collaboration that provides educational, research and publication opportunities. *The Anatomical Record: Special Issue; The 14th Symposium on Mesozoic Terrestrial Ecosystems and Biota: v*, *306*(S1), 163–164. D OI: 1 0.1002.ar/25/219

Lessner, E. J., Parker, W. G., Marsh, A. D., Nesbitt, S. J., Irmis, R. B., & Mueller, B. D. (2018). New insights into Late Triassic dinosauromorph-bearing assemblages from Texas using apomorphy-based identifications. *PaleoBios*, *35*, 1–41. doi:10.5070/P9351039960

Lucas, S. G., Heckert, A. B., & Hunt, A. P. (2001). Triassic stratigraphy, biostratigraphy and correlation in east-central New Mexico. In S. G. Lucas, & D. Ulmer-Scholle. *Geology of the Llano Estacado: New Mexico Geological Society, Guidebook, 52nd Field Conference* (pp. 85–102). New Mexico Geological Society. https://doi.org/10.56577/ffc-52.85

Lucas, S. G., & Hunt, A. P. (1989). *Dawn of the Age of Dinosaurs in the American Southwest*. New Mexico Museum of Natural History and Science.

Lucas, S. G., Rinehart, L. F., Krainer, K., Spielmann, J. A., & Heckert, A. B. (2010). Taphonomy of the Lamy amphibian quarry: A Late Triassic bonebed in New Mexico, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *298*(3-4), 388–398. doi:10.1016/j.palaeo.2010.10.025

Lucas, S. G., K. E. Zeigler, A. B. Heckert, A. P. Hunt. (2005). Review of Upper Triassic stratigraphy and biostratigraphy in the Chama Basin, northern New Mexico. In S. G. Lucas, K. E. Zeigler, V. W. Lueth, & D. E. Owen. *Geology of the Chama Basin, New Mexico Geological Society Guidebook, 56th Field Conference* (pp. 170–181). New Mexico Geological Society.

Mirzaei, M., Housen, B. A., Burmester, R. F., & Foreman, B. Z. (2021). Paleomagnetic results from Upper Triassic and Middle Jurassic strata of east-central New Mexico, and implication for North American apparent polar wander path. *Tectonophysics*, *811*, 228872. https://doi.org/10.1016/j.tecto.2021.228872

Muttoni, G., Kent, D. V., Olsen, P. E., Di Stefano, P., Lowrie, W., Bernasconi, S. M., & Hernández, F. M. (2004). Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and correlation to the Late Triassic Newark astrochronological polarity time scale. *Geological Society of America Bulletin*, *116*(9), 1043. doi:10.1130/B25326.1

Osborn, H. F. (1903). On the Primary Division of the Reptilia into Two Sub-Classes, *Synapsida* and *Diapsida*. *Science*, *17*(424), 275–276. https://doi.org/10.1126/science.17.424.275.c

Padian, K. (1989). The Origin of Dinosaurs and the Beginning of the Age of Dinosaurs. *Short Courses in Paleontology*, *2*, 7–21. doi:10.1017/S2475263000000817

Padian, K. (2012). The problem of dinosaur origins: Integrating three approaches to the rise of dinosauria. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *103*(3–4), 423–442. doi:10.1017/S1755691013000431

Padian, K., & Sues, H. D. (2015). The age of transformation: The Triassic Period and the rise of today's land vertebrate fauna. In K. P. Dial, N. Shubin, & E. L. Brainerd (Eds.), *Great transformations: major events in the history of vertebrate life* (pp. 351–374). University of Chicago Press.

Pinna, G. (1980). *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di Lepriosauro del Trias Alpino. *Atti della Societa Italiana di Scienze Naturali*, *121*, 181–192.

Pinna, G. (1984). Osteologia di *Drepanosaurus unguicaudatus*, lepdiosauro Triassico del Sottordine Lacertilia. *Memorie della Societa Italiana di Scienze Naturali*, *24*, 1–28.

Pinna, G. (1986). On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. *Journal of Paleontology*, *60*(5), 1127–1132. doi:10.1017/S0022336000022654

Pinna, G. (1987). Un nuovo esemplare giovanile di *Drepanosaurus unguicaudatus* del Norico di Val Preone (Udine). *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, *128*, 80–84.

Pritchard, A. C., Irmis, R. B., Olori, J. C., Nesbitt, S. J., Smith, N. D., Stocker, M. R., & Turner, A. H. (2023). The femora of Drepanosauromorpha (Reptilia : Diapsida): Implications for the functional evolution of the thigh of Sauropsida. *The Anatomical Record*, *306*(8): https://doi.org/10.1002/ar.25160

Pritchard, A. C., & Nesbitt, S. J. (2017). A bird-like skull in a Triassic diapsid reptile increases heterogeneity of the morphological and phylogenetic radiation of Diapsida. *Royal Society Open Science*, *4*(10), 170499–170499. https://doi.org/10.1098/rsos.170499

Pritchard, A. C., Sues, H.-D., Scott, D., & Reisz, R. R. (2021). Osteology, relationships and functional morphology of *Weigeltisaurus jaekeli* (Diapsida, Weigeltisauridae) based on a complete skeleton from the Upper Permian Kupferschiefer of Germany. *PeerJ*, *9*, e11413. https://doi.org/10.7717/peerj.11413

Pritchard, A. C., Turner, A. H., Irmis, R. B., Nesbitt, S. J., & Smith, N. D. (2016). Extreme Modification of the Tetrapod Forelimb in a Triassic

Diapsid Reptile. *Current Biology*, *26*(20), 2779–2786. https://doi.org/10.1016/j.cub.2016.07.084
Renesto, S. (1994). *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. *Journal of Vertebrate Paleontology*, *14*(1), 38–52. https://doi.org/10.1080/02724634.1994.10011537
Renesto, S., & Binelli, G. (2006). *Vallesaurus cenensis* Wild, 1991, A drepanosaurid (Reptilia, Diapsida) from the Late Triassic of Northern Italy. *Rivista Italiana Di Paleontologia E Stratigrafia*, *112*(1), 77–94. https://doi.org/10.13130/2039-4942/5851
Renesto, S., & Fraser, N. C. (2003). Drepanosaurid (Reptilia: Diapsida) remains from a Late Triassic fissure infilling at Cromhall Quarry (Avon, Great Britain). *Journal of Vertebrate Paleontology*, *23*(3), 703–705. doi:10.1671/A1101
Renesto, S. C., Spielmann, J. A., & Lucas, S. G. (2010a). The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian *Placerias* Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, *252*(3), 315–325. https://doi.org/10.1127/0077-7749/2009/0252-0315
Renesto, S., Spielmann, J. A., Lucas, S. G., & Spagnoli, G. T. (2010b). The taxonomy and paleobiology of the Late Triassic (Carnian-Norian: Adamanian-Apachean) drepanosaurs (Diapsida:Archosauromorpha: Drepanosauromorpha). *New Mexico Museum of Natural History and Science Bulletin*, *46*, 81.
Schwartz, H. L., & Gillette, D. D. (1994). Geology and taphonomy of the Coelophysis quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. *Journal of Paleontology*, *68*(5), 1118–1130. doi:10.1017/S0022336000026718
Senter, P. (2004). Phylogeny of Drepanosauridae (Reptilia: Diapsida). *Journal of Systematic Palaeontology*, *2*(3), 257–268. doi:10.1017/S1477201904001427
Simões, T. R., Kammerer, C. F., Caldwell, M. W., & Pierce, S. E. (2022). Successive climate crises in the deep past drove the early evolution and radiation of reptiles. *Science Advances*, *8*(33), eabq1898. https://doi.org/10.1126/sciadv.abq1898
Sodano, M. P., Kligman, B., Stocker, M., Marsh, A., Parker, W. G., & Nesbitt, S. J. (2022). A new drepanosaur ungual morphotype from the Sonsela Member of Petrified Forest National Park. *Journal of Vertebrate Paleontology, Program and Abstracts*, *2022*, 327–328.
Sues, H. D., & Fraser, N. C. (2010). *Triassic life on land—the great transition*. Columbia University.
Voris, J. T., & Heckert, A. B. (2017). Ontogenetic heterodonty in *Reticulodus synergus* (Chondrichthyes, Hybodontiformes) from the Upper Triassic of the southwestern U.S.A., with a redescription of the genus. *Journal of Vertebrate Paleontology*, *37*(4), e1351980–e1351980. https://doi.org/10.1080/02724634.2017.1351980

Handling Editor: Hans-Dieter Sues.