

UC Berkeley

PaleoBios

Title

A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA

Permalink

<https://escholarship.org/uc/item/8x7767f8>

Journal

PaleoBios, 36(0)

ISSN

0031-0298

Authors

Gonçalves, Gabriel S.
Sidor, Christian A.

Publication Date

2019-12-15

DOI

10.5070/P9361046203

Copyright Information

Copyright 2019 by the author(s). This work is made available under the terms of a Creative Commons Attribution-NonCommercial-ShareAlike License, available at <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Peer reviewed

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



GABRIEL S. GONÇALVES & CHRISTIAN A. SIDOR (2019). A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA.

Cover: View of Kaye Quarry at Petrified Forest National Park, the site where the new drepanosauromorph genus and species, *Ancistronychus paradoxus*, was discovered.

Citation: Gonçalves, G.S. and C.A. Sidor. 2019. A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA. *PaleoBios*, 36. ucmp_paleobios_46203.

A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA

GABRIEL S. GONÇALVES^{1*} and CHRISTIAN A. SIDOR^{1,2}

¹Department of Biology, University of Washington, Box 351800 Seattle, WA 98195-1800; gabrig3@uw.edu

²Burke Museum, University of Washington, Box 353010 Seattle, WA 98195-3010; casidor@uw.edu

Drepanosauromorpha is an extinct group of reptiles known from the Middle Triassic to Late Triassic (237–212 Ma). The clade currently includes seven genera (*Avicranium*, *Dolabrosaurus*, *Drepanosaurus*, *Hypuronector*, *Kyrgyzsaurus*, *Megalancosaurus*, and *Vallesaurus*) that are known from fossils collected in Europe, North America, and Asia. These discoveries have helped shape our understanding of the biology and diversity of drepanosauromorphs. Here we describe *Ancistronychus paradoxus* n. gen. et sp. from the Chinle Formation in Petrified Forest National Park, Arizona based on the ungual phalanx of the second digit of the manus. A characteristic that this taxon shares with *Drepanosaurus unguicaudatus* is the pronounced size of the ungual relative to the penultimate element. It differs significantly from *D. unguicaudatus* and the Hayden Quarry *Drepanosaurus* in the shortened proximal dorsoventral height of the claw, its great transverse breadth, the presence of both a furrow on the midline of the extensor surface and a cleft on the apex, and a broad and flattened terminus. We suggest that *A. paradoxus* is likely closely related to *D. unguicaudatus* and the Hayden Quarry *Drepanosaurus*, but missing phylogenetic data precludes a more definitive assessment at this point. *Ancistronychus paradoxus* highlights unsuspected morphological variation within Drepanosauromorpha and suggests that different drepanosauromorphs used their enlarged second manual unguals for distinct functions enabling them to fill different ecological niches.

Keywords: Drepanosauromorpha, *Ancistronychus*, Triassic, Norian, ungual

INTRODUCTION

Tetrapods radiated after the Permo-Triassic mass extinction, with multiple reptilian lineages (e.g., Archosauromorpha von Huene, 1946, Lepidosauromorpha Gauthier et al., 1988) shaping terrestrial ecosystems for much of the Mesozoic (Benton et al. 2004, Evans and Jones 2010, Pritchard and Nesbitt 2017, Ezcurra and Butler 2018, Peacock et al. 2019). One of the best examples of this is seen in archosauromorphs, which were able to diversify within both terrestrial and marine ecosystems to occupy empty ecospace and niches left by the extinction of many non-mammalian synapsids and parareptiles (e.g., pareiasaurs) (Nesbitt et al. 2010, Brusatte et al. 2011, Sidor et al. 2013, Ezcurra and Butler 2018, Peacock et al. 2019). In North America,

large-bodied archosauriforms (e.g., phytosaurs, aetosaurs, rauisuchids, trilophosaurs, etc.) dominated Late Triassic terrestrial ecosystems, while many of the surviving non-mammalian therapsids were either the smaller cynodonts or herbivorous dicynodonts (Parker 2005). Much of the research over the past century has focused on these large archosauriforms, whereas study of the smaller-bodied tetrapods has lagged behind (Parker 2005, Lessner et al. 2018). One group, however, has been the focus of significant work in recent years, the drepanosauromorphs (Renesto et al. 2010, Pritchard et al. 2016, Pritchard and Nesbitt 2017).

Drepanosauromorpha Renesto et al. (2010) is a clade of diapsid reptiles known from the Middle to Late Triassic. The clade currently includes the following seven genera: *Avicranium* Pritchard and Nesbitt (2017), *Dolabrosaurus* Berman and Reisz (1992), *Drepanosaurus*

*author for correspondence

Citation: Gonçalves, G.S. and C.A. Sidor. 2019. A new drepanosauromorph, *Ancistronychus paradoxus* n. gen. et sp., from the Chinle Formation of Petrified Forest National Park, Arizona, USA. *PaleoBios*, 36. [ucmp_paleobios_46203](https://doi.org/10.21203/rs.3.rs-46203).

Permalink: <https://escholarship.org/uc/item/8x7767f8>

Copyright: Published under Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International (CC-BY-NC-SA) license.

LSID: [urn:lsid:zoobank.org:pub:3E1BA514-C21C-4DA1-94BF-64653E429F2F](https://zoobank.org/pub:3E1BA514-C21C-4DA1-94BF-64653E429F2F)

Pinna (1980), *Hypuronector* Colbert and Olsen (2001), *Kyrgyzsaurus* Alifanov and Kurochkin (2011), *Megalancosaurus* Calzavara et al. (1980), and *Vallesaurus* Renesto and Binelli (2006) that are known from fossils collected in Europe (Italy, United Kingdom), North America (Arizona, New Mexico, New Jersey), and Asia (Kyrgyzstan). The first described drepanosauromorph, *Drepanosaurus unguicaudatus* Pinna (1980) was based on a holotype preserving most of a complete flattened skeleton, including a peculiar tail claw and strongly modified forelimb featuring a crescent-shaped ulna, elongated proximal carpal, and massive ungual phalanx on the second digit (Pinna 1986, Renesto 1994, Renesto et al. 2010). As more drepanosauromorphs were discovered, they did not seem to possess the enlarged manual ungual phalanx of *D. unguicaudatus* either because of the lack of anatomical evidence (e.g., *Vallesaurus* and *Megalancosaurus*) or because of the lack of preservation of the entire manus (*Avicranium*, *Dolabrosaurus*, *Kyrgyzsaurus*, and *Hypuronector*, although the latter clearly lacks adaptations to scratching-digging in other parts of the forelimb). More recently, three-dimensionally preserved drepanosauromorph material from New Mexico was shown to possess similarly distinctive anatomy, with a forelimb containing a relatively enlarged manual ungual with a flattened, crescent-shaped ulna and elongated carpal bones (Pritchard et al. 2016). These discoveries suggest that drepanosauromorphs evolved a wide range of ecomorphologies, including likely arboreal and fossorial forms (due to the presence, for example, of an enlarged manual ungual in *Drepanosaurus*, or opposable digits and free rotating ankle and wrist bones in *Megalancosaurus*). Here we describe a new species of drepanosauromorph from the Late Triassic of Arizona. It features autapomorphic ungual morphology and broadens the stratigraphic and geographic sampling of the group.

MATERIALS AND METHODS

The holotype and referred specimens were collected during annual excavations at the Kaye Quarry, Petrified Forest National Park, Arizona (PEFO locality PFV 410) from 2014–2018. Both PEFO and University of Washington Burke Museum (UWBM) catalog numbers have been assigned, in order to comply with federal regulations. Except for the holotype, all the material is housed at the UWBM as a held-in-trust collection. The specimens were prepared with aircsribes, carbide needles, and B72 as a consolidant, as needed (preparation notes on file at the UWBM). The holotype was scanned on a Skyscan 1172 Microfocus X-radiographic Scanner, but no internal

structure was visible, despite several tests made with different settings. A digital surface reconstruction of the holotype is available on MorphoSource under Project 808.

Institutional Abbreviations—**GR**, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, New Mexico; **PEFO**, Petrified Forest National Park, Arizona; **MCSNB**, Museo Civico Scienzi Naturali Enrico Caffi, Bergamo, Italy; **UWBM**, University of Washington Burke Museum, Seattle, Washington.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA OSBORN, 1903

DREPANOSAURMORPHA RENESTO ET AL., 2010

ANCISTRONYCHUS N. GEN.

ANCISTRONYCHUS PARADOXUS N. GEN. ET SP.

FIGS. 1, 2C, 3

Diagnosis—Drepanosauromorph with autapomorphic ungual phalanx of the second digit, characterized by a broad distal tip with lack of transverse tapering and a cleft, presence of midline furrow on distal extensor surface, a ridge along the flexor surface, and a distal tip recurving strongly ventrally toward the proximal end. Distinct from *Vallesaurus*, *Dolabrosaurus*, *Megalancosaurus* based on the relative size of the claw and the orientation of the flexor tuberosities. Distinct from *Drepanosaurus unguicaudatus* and the Hayden Quarry *Drepanosaurus* (Pritchard et al. 2016) owing to its relatively short dorsoventral height proximally, asymmetrical flexor tubercle, and more medially located flexor pits. Similarities with both *D. unguicaudatus* and the Hayden Quarry *Drepanosaurus* (Pritchard et al. 2016) are based on the large size of the ungual relative to the actual or inferred size of the penultimate element (i.e., the unguals have a relatively small proximal cotyle for articulation with the penultimate element, suggesting that the latter was of normal size).

Holotype—PEFO 42805/UWBM 117331, an isolated manual ungual phalanx.

Paratypes—PEFO 39324/UWBM 108325, PEFO 39325/UWBM 108326, PEFO 39326/UWBM 108327, PEFO 39379/UWBM 108385, PEFO 39380/UWBM 108386, PEFO 42806/UWBM 117332, all isolated manual unguals.

Occurrence—All of the specimens come from the Kaye Quarry at Petrified Forest National Park, Arizona (locality PFV 410, locality UWBM C2226), which is predominantly composed of mottled purple mudstone with reduction halos commonly around fossils and occasional extra-basinal clasts. Stratigraphically, the quarry lies near the base of the Jim Camp Wash Beds (Sonsela Member,

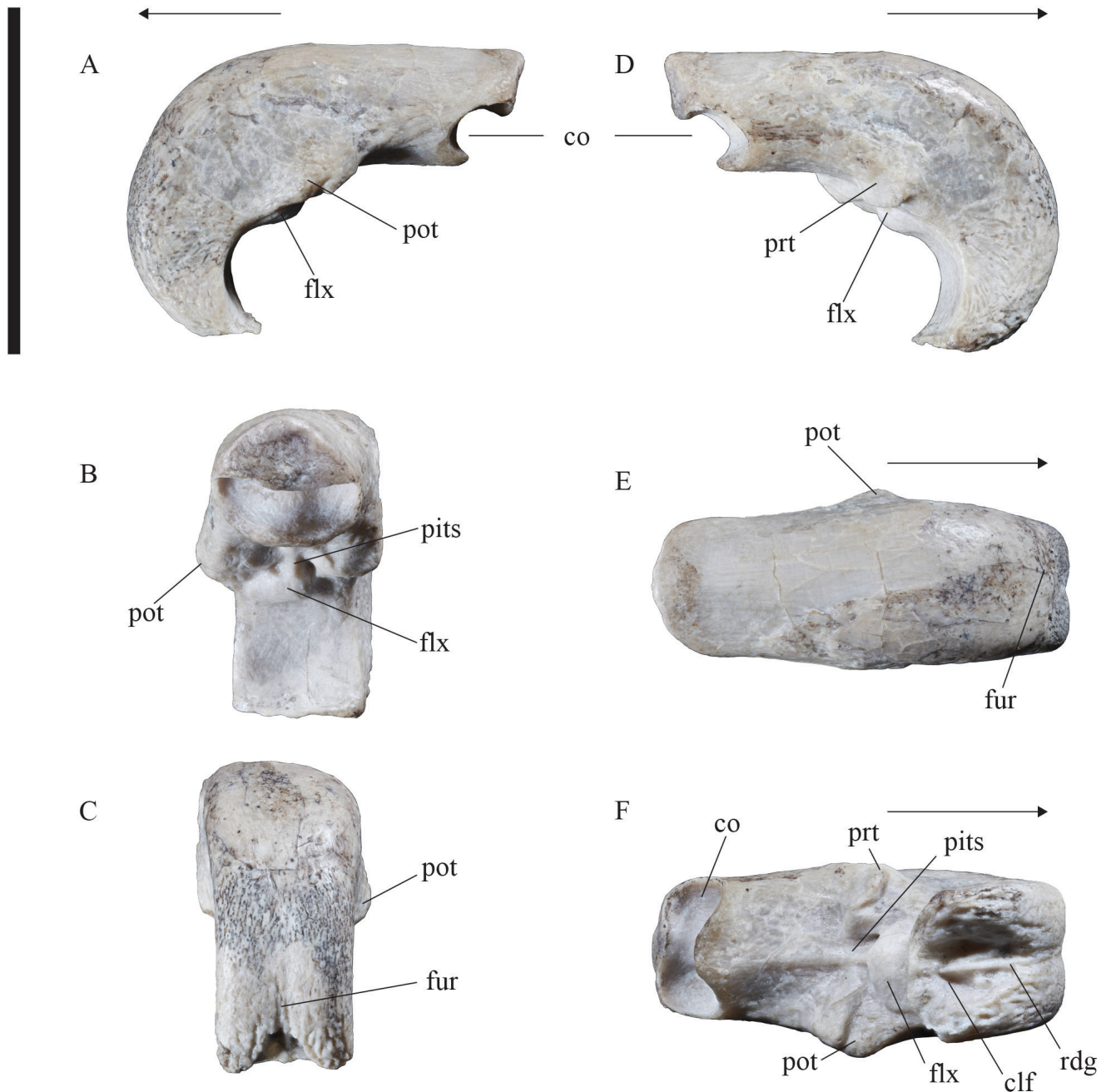


Figure 1. Holotype of *Ancistronychus paradoxus*, gen. et sp. nov. (PEFO 42805/UWBM 117331). **A.** Ungual phalanx in left lateral (postaxial) view. **B.** Proximal view. **C.** Distal view. **D.** Right lateral (preaxial) view. **E.** Dorsal view. **F.** Ventral view. Abbreviations: **pot**, postaxial tuberosity; **prt**, preaxial tuberosity; **flx**, flexor tubercle; **pits**, flexor pits; **co**, cotyle; **fur**, furrow; **rdg**, ridge. Arrow points distally. Scale bar=2 cm.

Chinle Formation) but its position relative to the "persistent red silcrete" approximating the Adamanian-Revueltian boundary has been difficult to establish. The vertebrate assemblage suggests that the site may be in the Adamanian land vertebrate holochronozone (Martz and Parker 2010, 2017, Sidor et al. 2018).

Etymology—The genus name combines the Greek

words for fishhook and claw and the species name is in reference to the unexpected nature of this taxon and other drepanosaurs, in general.

Description—We interpret PEFO 42805/UWBM 117331 as a left manual unguual phalanx from the second digit of a close relative of *D. unguicaudatus*. The specimen is morphologically distinct from other reptilian claws,

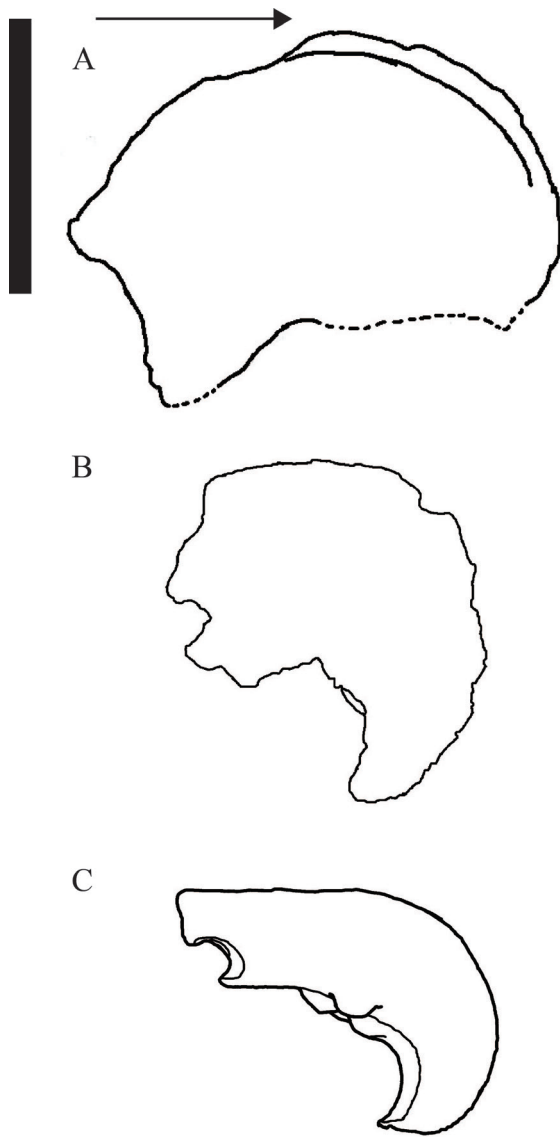


Figure 2. Comparison of the left manual unguals in *Drepanosaurus unguicaudatus* (A), GR 712 (B) and *Ancistronychus paradoxus*, gen. et sp. nov. (C). Scale bar=2 cm.

with a more fishhook-like appearance that has laterally oriented flexor tuberosities (Fig. 1 B, F), a cotyle located posteroventrally (Fig. 1 A, D), two facets within the cotyle for a tight connection with the more proximal element (Fig. 1 B, F), as well as the combination of both flexor pits and a flexor tubercle (Fig. 1 B, F). In medial and lateral view (Fig. 1A, D), the specimen has a flat dorsal (i.e., extensor) surface proximally that then arcs nearly 180° to its tip. A straight line from the dorsal edge of the cotyle to the distal edge of the apex of the phalanx is 2.23 cm long. The same measurement in *D. unguicaudatus* (MCSNB 5728) is 2.88 cm and the Hayden Quarry *Drepanosaurus* (GR 712) is 2.07 cm (Fig. 2). The ungual curves ventrally near the proximal margin of the lateral tuberosities 1.0

cm from the proximal end dorsally and 1.2 cm from the proximal end ventrally. This contrasts with the condition in the Hayden Quarry *Drepanosaurus* (GR 712) and *D. unguicaudatus* (MCSNB 5728), in which the curvature occurs throughout the entire length of the element or occurs much further distally, respectively.

The ventral (i.e., flexor) surface (Fig. 1F) has a deep articular cotyle proximally and bilateral pairs of pits and tuberosities near the midline. In flexor view, the outline of the cotyle is hourglass shaped, with the lateral (i.e., postaxial) facet slightly larger (Fig. 1F). The articular surface is concave and deep, with sharp-rimmed edges suggesting a tight articulation with the more proximal element. Near the middle of the articular surface is a low ridge that runs proximodistally and divides the cotyle into two facets. When compared to the ungual phalanges of most reptiles [e.g., *Iguana Laurenti* (1768), *Alligator Cuvier* (1807)], the articular surface in *Ancistronychus paradoxus* is displaced ventrally on the proximal end of the bone and faces more proximoventrally than proximally (Renesto 1994). These characteristics are shared with the enlarged manual unguals in *D. unguicaudatus* and the Hayden Quarry *Drepanosaurus*. As is found in the other manual unguals of *Megalancosaurus*, *Vallesaurus*, and *Dolabrosaurus*, and except for the second ungual in *D. unguicaudatus*, all the manual ungual phalanges have the articular surface located proximally rather than proximoventrally (Spielmann et al. 2005, Renesto et al. 2010). Distal to the cotyle, the ventral surface of the specimen bears a pronounced ridge along its midline that connects to the proximal edge of the flexor tubercle.

In ventral view, the center of the ungual features a complicated array of pits, grooves, and tuberosities (Fig. 1F) that have not been previously reported in a drepanosauromorph. The midline ridge is paralleled by shallow troughs on either side, which each end distally at a small pit. It is unclear if these pits represent foramina, but as currently prepared the preaxial pit is slightly deeper. Three rounded tuberosities surround the flexor pits: one distally and one to either side. The preaxial and postaxial tuberosities bulge laterally as opposed to the relatively straight sides of the ungual (Fig. 1). A prominent postaxial tuberosity that is larger than the preaxial tuberosity is also present in GR 712 and PEFO 42805/UWBM 117331, which identifies each specimen as a left second manual ungual (Pritchard 2015). Slightly distal to the flexor pits and centered on the ungual is the flexor tubercle. This structure is suboval in outline and oriented transversely. It is smooth and rounded, likely as the result of the insertion of muscles and tendons. In the

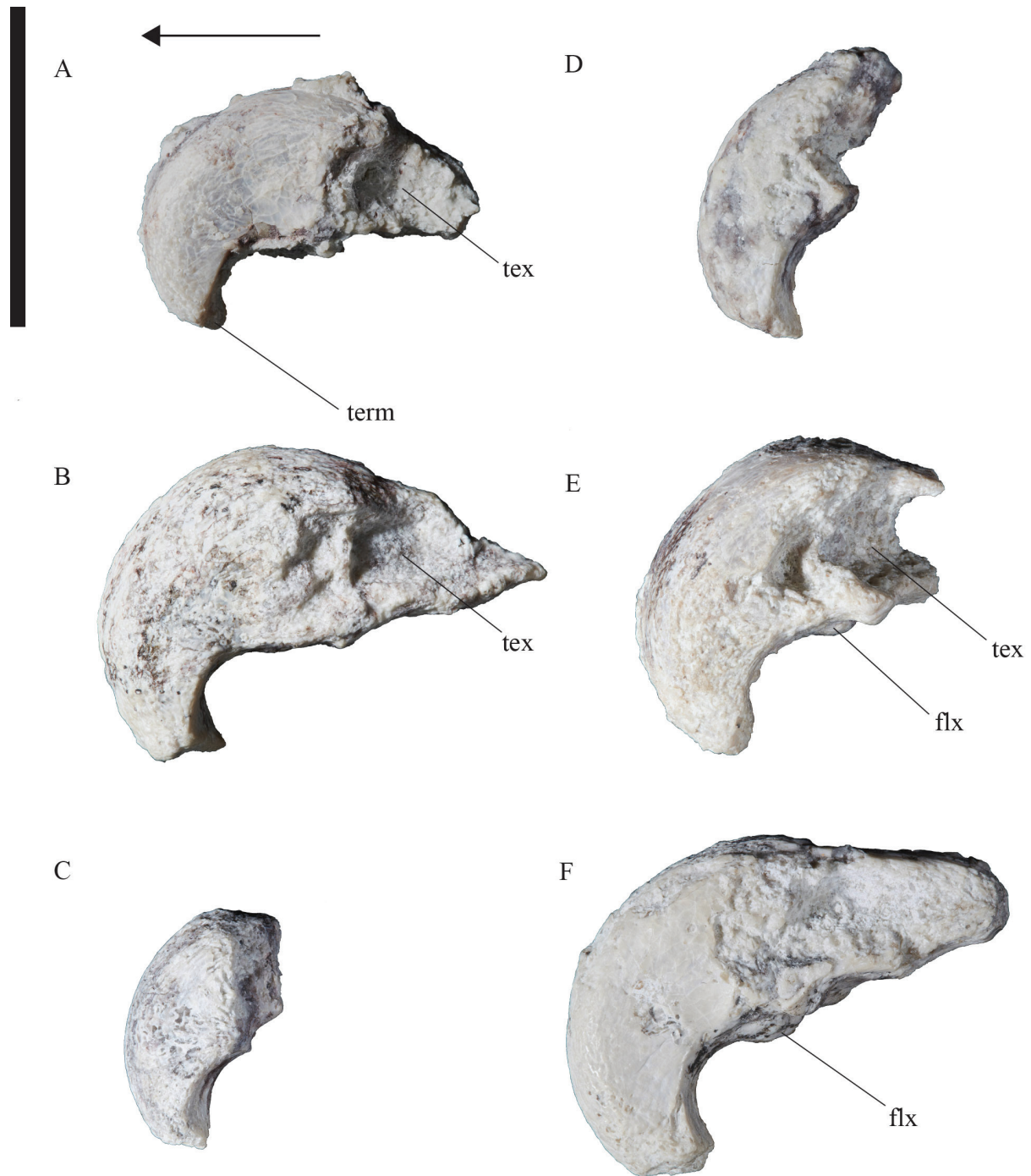


Figure 3. Paratypes of *Ancistronychus paradoxus*, gen. et sp. nov., in left lateral (postaxial) view that show varying degrees of completeness. **A.** PEFO 42806/UWBM 117332. **B.** PEFO 39324/UWBM 108325. **C.** PEFO 39325/UWBM 108326. **D.** PEFO 39326/UWBM 108327. **E.** PEFO 39379/UWBM 108385. **F.** PEFO 39380/UWBM 108386. Abbreviation: **tex**, triangular excavation on side of unguis; **flx**, flexor tubercle; **term**, terminus. Arrow points distally. Scale bar=2 cm.

Hayden Quarry *Drepanosaurus*, the flexor tubercle of the second manual unguis (GR 712) is hemispherical. This difference in morphology could be owing to taphonomic processes that distorted the original morphology of the tubercle in the holotype of *A. paradoxus*, but we believe it more likely indicates a somewhat different function of the

unguis in each taxon because in some of the paratypes the flexor tubercle is present (Fig. 3A, B, E, F) and is similar in morphology to the holotype (see Discussion).

Distal to the flexor tubercle, the flexor surface of the unguis curves strongly ventrally, such that the tip of the unguis points nearly proximally. Uniquely among

drepanosaurs, the distal half of the holotype retains a wide transverse breadth in both flexor and extensor views. This contrasts with what is seen in GR 712, which is more similar to a typical reptilian unguis in which the bone tapers distally in both mediolateral and dorsoventral planes. Also, uniquely among drepanosaurs, a furrow is present on the extensor surface of the holotype that gradually becomes deeper distally and a narrow ridge along the midline becomes more prominent (Fig. 1C). Eventually, the ventral furrow divides the tip of the unguis to form a V-shaped cleft, with the ridge present within the cleft terminating 3 mm before the distal end of specimen (Fig. 1F). Within the cleft, both sides of the ridge are marked by deep oval fossae. The distal extremity of the holotypic unguis of *A. paradoxus* is very broad and flat in proximal and distal view (resembling a shovel), which contrasts with most reptilian claws (including drepanosaurs) in which the unguis tapers distally to a sharply pointed apex.

DISCUSSION

Ecomorphology of Drepanosauromorphs

Interpretations of the ecology of drepanosauromorphs have changed substantially over the past few decades, with many hypotheses proposed. For example, *Megalancosaurus preonensis* was first described as being an arboreal climber owing to the presence of opposable digits on its hand (Calzavara et al. 1980). In contrast, Berman and Reisz (1992) argued that *Dolabrosaurus aquatilis* was an aquatic swimmer based on: 1) the presence of a dorsoventrally elongated tail that could have been used for carangiform locomotion (Kambe 1978) within the water; 2) the paddle-shaped manus and pes; and 3) a barrel-shaped chest possibly adapted for diving in deep water in order to counteract high pressures at those depths. *Hypuronector limnaios* was also argued as representing an aquatic swimmer based on the presence of elongated chevrons on the caudal vertebrae, making for a very flattened and large tail, which the authors compared to living aquatic tetrapods such as crocodilians and newts (Colbert and Olsen 2001). *Vallesaurus cenensis* was considered to be scansorial owing to the presence of modifications on the wrists and ankles for the ability of a wider range of motion, as is found in *Megalancosaurus*, which also had a prehensile manus and pes with opposable digits, a *Drepanosaurus*-like tail claw, dorsoventrally elongated caudal neural spines for a muscular tail, restricted motion of the tail along the ventral plane and the morphology of the phalanges, among other features

(Renesto and Binelli 2006). Pritchard and Nesbitt (2017) considered the orbital anatomy and braincase of *Avicranium renestoi* to be consistent with an arboreal habitat. However, the most recent hypothesis is that all of these taxa were scansorial, with the aquatic hypothesis for some taxa having been rejected due to the inferred lack of mediolateral flexibility of the tail (Renesto et al. 2010).

Drepanosaurus unguicaudatus was initially considered to have fossorial habits owing to the presence of a large manual unguis phalanx (Pinna 1986), but most recent researchers agree that this species was most likely an arboreal scratch digging organism (Renesto et al. 2010, Pritchard et al. 2016). The latter interpretation is supported by features indicative of a prehensile tail such as: 1) vertically oriented zygapophyses constraining any lateral movement, and 2) haemapophyseal connections positioned posteriorly along the ventral margin of the caudal vertebrae (Renesto et al. 2010). Other traits, such as the presence of a large manual unguis phalanx, as well as a crescent-shaped ulna for the attachment of flexor and extensor muscles, are suggestive of scratch-digging or hook-and-pull digging in *D. unguicaudatus* (Pritchard et al. 2016, 2018). These functional interpretations are primarily based on comparisons with the silky anteater, *Cyclopes didactylus* Linnaeus (1758), which has a large manual unguis phalanx and uses it forelimb for hook-and-pull digging, as well as to sloths, *Manis* Linnaeus (1758) (pangolin), *Myrmecophaga* Linnaeus (1758) (anteater), *Priodontes* F. Cuvier (1825) (armadillo), and the pterosaur *Peteinosaurus* Wild (1978) (Renesto 1994, Renesto et al. 2010, Pritchard et al. 2016). Arboreal anteaters, such as the silky anteater *Cyclopes didactylus*, have strongly curved claws used for climbing along branches as well as piercing the nests of ants, while the giant anteater, *Myrmecophaga tridactyla* Linnaeus (1758), has longer, less recurved claws that are used primarily to dig into the nests of termites and ants (Desbiez and Medri 2010, Hayssen et al. 2012).

We expect that the pronounced differences in the shape of the unguis in *Ancistronychus paradoxus* and *D. unguicaudatus* connote ecological differences between these two taxa. The main morphological difference between these two taxa, in terms of their hypertrophied manual unguis that might have corresponded to ecological differences, is the shape of the distal terminus and the transverse breadth of the whole unguis. In *D. unguicaudatus*, the claw comes to a sharpened apex (Renesto et al. 2010), while in *A. paradoxus*, the distal terminus has a broad and flattened shape in proximal and distal view (resembling a shovel). The morphology of the

distal terminus in *A. paradoxus* is similar to that found in the fossorial taxon *Philodota* Weber (1904) (pangolin), in which the unguals bifurcate into two distinct distal processes and a fissure exists in between the processes (Gaudin et al. 2009). In frogs that dig with their forelimbs (i.e., head-first burrowers) both the whole manus and the phalanges of each digit are wide and stout, giving the manus a spatulate (i.e., shovel-like) shape that can be used to excavate into a substrate. Taxa like the Namibian web-footed gecko have feet that have a large surface area that can be used to dig through sand. Manual unguals that are wide and spatulate in shape occur in other taxa like moles and pangolins, with the later being the best comparison to *A. paradoxus* because of morphological similarities between the claws (e.g., fissured ungual phalanges) (Kley and Kearney 2007, Gaudin et al. 2009). In the fossorial taxon *Gopherus Rafinesque* (1832), all of the manual unguals are flattened along the flexor surface and marginally curved on the extensor surface (Fowler and Hall 2011). Bramble (1982) describes the manual morphology of *Gopherus* in some detail and demonstrates that, due to the flattened and wide nails with a manus that is short and large, the manus of *Gopherus* is well suited for digging through soft and easily friable sandy soils. Taxa like the *Tamandua* Gray (1825) have large claws that are similar in shape to *A. paradoxus* (i.e., spatulate in shape) and use their claws to tear into the nests of insects or to tear through insect infested soft wood (Taylor 1978). Sloths have claws that taper towards a sharp apex and recurve at an obtuse angle throughout their entire length in order to bring down and hold fruit suspended from trees (Britton 1941). Regarding *A. paradoxus*, we suggest that because of the distinct morphology of the distal terminus of the enlarged manual ungual, this taxon was possibly an arboreal/fossorial organism, similar to modern day pangolins, that either used its claw to dig into soft substrates (e.g., soft soil, rotten wood, etc.) or to help climb through trees in order to search for food. However, without more complete skeletal material, the ecology of *A. paradoxus* is difficult to evaluate further.

Ungual Taphonomy

Based on their distinctive broad distal tip with a central furrow and lack of lateral compression, we interpret the specimens shown in Figure 3 as second manual ungual phalanges of *Ancistronychus paradoxus* that are missing some to all of their proximal portion. These specimens vary in size from being proportionately larger than the holotype to subequal in size. Some of these specimens are highly incomplete, preserving just the distal tip of

the phalanx (Fig. 3A–F). Several of the more complete specimens display a characteristic triangular excavation on either side of the ungual. The symmetry of these excavations and their occurrence on four specimens suggests that they represent real anatomy and not a taphonomic artifact (Fig. 3A, B, E, F). We are unaware of previous reports of this type of feature but suggest that they could represent planes of weakness where two elements fused to form the complete ungual phalanx. Unfortunately, CT scans of the holotype were unsuccessful at visualizing internal morphology that could support the hypothesis of an internal plane of weakness, possibly due to high iron content within the fossil. However, in the anteater *Tamandua*, the joint between the penultimate phalanx and the ungual phalanx has a semi-lunate shape in flexor view, much like what is visible in some of the unguals described here (Taylor 1978).

Although ontogeny seems like a reasonable explanation for the variation in preservation seen in this sample of unguals (i.e., the least complete unguals represent the youngest individuals that did not have the entire ungual ossified), there are problems with this interpretation. Namely, while some of the incomplete unguals are relatively small, unguals that are proportionately larger than the holotype are also incompletely preserved (Fig. 3A–F).

Using the fusion of structures in a specimen and the size of the individual as a proxy for understanding of the ontogeny of a species is not always the most reliable assumption (Griffin and Nesbitt 2016). An alternative explanation is that the paratypic specimens vary in completeness due simply to differing degrees of preservation. For example, there are several shuvosaurid limb bones from the Kaye Quarry that are perfectly preserved at one end but are shattered or incomplete at the other end. In addition, though some work has been done to better understand the ontogeny of basal reptiles, it is still poorly constrained in the skeletal system and more work on other taxa needs to be done in the future (Barta et al. 2018, Griffin 2018). More work on the taphonomy of the Kaye Quarry will be required to more completely understand the preservation of the unguals shown in Figure 3.

Phylogenetic Position of *Ancistronychus*

Establishing the phylogenetic position of *Ancistronychus paradoxus* among drepanosauromorphs is difficult because of the limited anatomical information available from the holotype and paratypes. However, several derived features suggest that *Ancistronychus paradoxus* is likely closely related to *Drepanosaurus*

unguicaudatus and the Hayden Quarry *Drepanosaurus* discussed by Pritchard et al. (2016). In particular, the shared presence of an enlarged manual ungual phalanx with flexor pits and flexor tubercle, lateral tuberosities and a proximoventrally located cotyle, argues that *A. paradoxus*, *D. unguicaudatus*, and the Hayden Quarry *Drepanosaurus* form a clade. Sister-taxon relationships within that hypothesized clade are difficult to determine. *Drepanosaurus unguicaudatus* and the Hayden Quarry *Drepanosaurus* share a number of features of the ungual (e.g., transverse compression, proportionally deeper) that *A. paradoxus* lacks, but some of these features are likely plesiomorphies (Pritchard 2015). The lack of articulated material for *A. paradoxus* and several other drepanosauromorphs (e.g., *Avicranium renestoi*) suggests that establishing a comprehensive phylogeny for the clade will be problematic and plagued by missing data. Excavations at the Kaye Quarry have yielded additional cranial and postcranial material that is likely drepanosauromorph in origin (Goncalves et al. 2018), but until articulated material demonstrates that they can be referred to *A. paradoxus*, they are currently of limited phylogenetic utility.

The recognition of *A. paradoxus* as a previously unrecognized species of drepanosauromorph from the Norian of North America demonstrates unsuspected morphological (and likely ecological) variation existed within the clade and helps to reconstruct its evolutionary history. Future studies and discoveries of drepanosauromorphs will help researchers to understand the biology of these organisms more in depth and their roles within Late Triassic ecosystems.

ACKNOWLEDGEMENTS

First and foremost, we thank Tom Kaye for discovering the locality that produced all of the fossils of *Ancistronychus* discussed here. Since 2014, annual field teams have helped to excavate the Kaye Quarry and we acknowledge all of the participants, including Chuck Beightol, Jon Graff, Adam Huttenlocker, Carol Kaye, Zoe Kulik, Gary Livingston, Jackie Lungmus, Larry Mose, Savannah Olroyd, Brandon Peacock, Natalie Toews, Athena Tse, Luke Weaver, Megan Whitney, and Brenen Wynd. Kelsie Abrams did an exceptional job preparing the holotype. We thank Craig Abramson, Bruce Crowley, and Gary Livingston for preparation of other drepanosaur material. Additionally, we thank Adam Marsh for reading through the manuscript and giving helpful suggestions. Finally, we thank our colleagues at PEFO (Bill Parker, Adam Marsh, Matt Smith, Chuck Beightol) and Jon Graff

and Pam Proske for supporting the UWBM-PEFO project, as well as the anonymous reviewers for their important edits and Christian Kammerer for taxonomic suggestions.

LITERATURE CITED

- Alifanov, V.R., and E.N. Kurochkin. 2011. *Kyrgyzsaurus bukhanchenkoi* gen. et sp. nov., a new reptile from the Triassic of southwestern Kyrgyzstan. *Paleontological Journal* 45:639–647. [<https://doi.org/10.1134/S0031030111060025>]
- Barta, D.E., S.J. Nesbitt, and M.A. Norell. 2018. The evolution of the manus of early theropod dinosaurs is characterized by high inter- and intraspecific variation. *Journal of Anatomy* 232:80–104.
- Benton, M.J., V.P. Tverdokhlebov, and M.V. Surkov. 2004. Ecosystem remodeling among vertebrates at the Permo-Triassic boundary in Russia. *Nature* 432:97–100. [<https://doi.org/10.1038/nature02950>]
- Berman, D.S., and R.R. Reisz. 1992. *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. *Journal of Paleontology* 66:1001–1009. [<https://doi.org/10.1017/S0022336000020928>]
- Britton, W.S. 1941. Form and function in the sloth (concluded). *The Quarterly Review of Biology* 16:190–207. [<http://www.jstor.org/stable/2809209>]
- Bramble, D.M. 1982. *Scaptochelys*: Generic revision and evolution of gopher tortoises. *Copeia* 1982:852–867.
- Brusatte S.L., M.J. Benton, G.T. Lloyd, M. Ruta, and S.C. Wang. 2011. Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101(3–4):367–382. [<https://doi.org/10.1017/S1755691011020056>]
- Calzavara, M., G. Muscio, and R. Wild. 1980. *Megalancosaurus preonensis* n.g., n.sp., a new reptile from the Norian of Friuli, Italy. *Gortania*. 2:59–64.
- Colbert, E.H., and P.E. Olsen. 2001. A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). *American Museum Novitates* 3334:1–24. [<http://hdl.handle.net/2246/2887>]
- Cuvier, G. 1807. Sur les différentes especes de crocodiles vivans et sur leurs caracteres distinctifs. *Annales du Muséum d'Histoire Naturelle*, Paris. 10:8–66.
- Cuvier, F. 1825. Des Dentes des Mammifères, Considérées Comme Caractères Zoologiques. Strasbourg and Paris, 275 pp.
- Desbiez, A.L.J., and Í.M. Medri. 2010. Density and habitat use by giant anteaters (*Myrmecophaga tridactyla*) and southern tamanduas (*Tamandua tetradactyla*) in the Pantanal wetland, Brazil. *Edentata* 11:4–10. [<https://doi.org/10.1896/020.011.0102>]
- Evans, S.E., and M.E. Jones. 2010. The origin, early history and diversification of Lepidosauromorph reptiles, in S. Bandyopadhyay (ed.). New aspects of Mesozoic biodiversity. *Lecture Notes in Earth Sciences* 132:27–44. [https://doi.org/10.1007/978-3-642-10311-7_2]
- Ezcurra, M.D., and R.J. Butler. 2018. The rise of the ruling reptiles and ecosystem recovery from the Permo-Triassic mass extinction. *Proceedings of the Royal Society B: Biological Sciences* 285. [<https://doi.org/10.1098/rspb.2018.0361>]
- Fowler, D.W., and L.E. Hall. 2011. Scratch-digging sauropods, revisited. *Historical Biology* 23:27–40. [<http://doi.org/10.1080/08912963.2010.504852>]
- Gaudin, T.J., R.J. Emry, and J.R. Wible. 2009. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated

- taxa: a morphology based analysis. *Journal of Mammalian Evolution* 16:235–305. [<https://doi.org/10.1007/s10914-009-9119-9>]
- Gauthier, J., R.D. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15–98 in R.D. Estes, and G.K. Pregill (eds.). *Phylogenetic relationships of the lizard families: Essays commemorating Charles L. Camp*. Stanford University Press, California.
- Goncalves, G.S., B.R. Peacock, and C.A. Sidor. 2018. Three-dimensionally preserved drepanosauromorph remains from the Sonsela Member (Chinle Formation, Norian) of Petrified Forest National Park, Arizona. *Journal of Vertebrate Paleontology* 38 (electronic supplement):135.
- Gray, J.E. 1825. An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera. *Annals of Philosophy* 10:337–344.
- Griffin, C.T., and S.J. Nesbitt. 2016. The femoral ontogeny and long bone histology of the Middle Triassic (?late Anisian) dinosauriform *Asilisaurus kongwe* and implications for the growth of early dinosaurs. *Journal of Vertebrate Paleontology* 36. [<https://doi.org/10.1080/02724634.2016.1111224>]
- Griffin, C.T. 2018. Developmental patterns and variation among early theropods. *Journal of Anatomy* 232:604–640.
- Hayssen, V., F. Miranda, and B. Pasch. 2012. *Cyclopes didactylus* (Pilosa: Cyclopedidae). *Mammalian Species* 44(895):51–58.
- von Huene, F. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologische Zentralblatt* 65:268–275.
- Kambe, T. 1978. The dynamics of carangiform swimming motions. *Journal of Fluid Mechanics* 87:533–560. [<https://doi.org/10.1017/S0022112078001755>]
- Kley, N.J. and M. Kearney. 2007. Adaptations for digging and burrowing. Pp. 284–309 in B.K. Hall (ed.). *Fins Into Limbs*. University of Chicago Press, Chicago
- Laurenti, J.N. 1768. Specimen medicum : exhibens synopsis reptilium emendatum cum experimentis circa venena et antidota reptilium austriacorum. 234 pp. [<https://doi.org/10.5962/bhl.title.5108>]
- Lessner, E.J., W.G. Parker, A.D. Marsh, S.J. Nesbitt, R.B. Irmis, and B.D. Mueller. 2018. New insights into Late Triassic dinosauriform-bearing assemblages from Texas using apomorphy-based identifications. *PaleoBios* 35:1–41. [<https://escholarship.org/uc/item/4ht19712>].
- Linnæus, C. 1758. *Systema Naturae*. 10th Edition. Volume 1, Salvii, Stockholm, 824 pp.
- Martz, J.W., and W.G. Parker. 2010. Revised lithostratigraphy of the Sonsela Member (Chinle Formation, Upper Triassic) in the southern part of Petrified Forest National Park, Arizona. *PLoS ONE* 5(2):e9329. [<https://doi.org/10.1371/journal.pone.0009329>]
- Martz, J.W., and W.G. Parker. 2017. Revised formulation of the Late Triassic land vertebrate “Faunachrons” of Western North America: recommendations for codifying nascent systems of vertebrate biochronology. Pp. 39–125 in K.E. Zeigler, and W.G. Parker (eds.). *Terrestrial depositional systems: Deciphering complexities through multiple stratigraphic methods*. Elsevier, Amsterdam, Netherlands. [<https://doi.org/10.1016/B978-0-12-803243-5.00002-9>]
- Nesbitt, S.J., C.A. Sidor, R.B. Irmis, K.D. Angielczyk, R.M.H. Smith, and L.A. Tsuji. 2010. Ecologically distinct dinosaurian sister-group demonstrates early diversification of Ornithodira. *Nature* 464:95–98. [<https://doi.org/10.1038/nature08718>]
- 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-b>]
- Parker, W.G. 2005. Faunal review of the Upper Triassic Chinle Formation of Arizona. *Mesa Southwest Museum Bulletin* 11:34–54.
- Peacock, B.R., R.M.H. Smith, and C.A. Sidor. 2019. A novel archosauromorph from Antarctica and an updated review of a high-latitude vertebrate assemblage in the wake of the end-Permian mass extinction. *Journal of Vertebrate Paleontology* 38. [<https://doi.org/10.1080/02724634.2018.1536664>]
- Pinna, G. 1980. *Drepanosaurus unguicaudatus*, nuovo genere nuova specie di Lepidosauro del Trias Alpino (Reptilia). *Atti della Societh Italiana di Scienze Naturali* 121:181–192.
- Pinna, G. 1986. On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. *Journal of Paleontology* 60:1127–1132.
- Pritchard, A.C. 2015. The early evolution of diapsid reptiles and the origin of Sauria. Stony Brook, New York, Stony Brook University, Ph.D. dissertation.
- Pritchard, A.C., A.H. Turner, R.B. Irmis, S.J. Nesbitt, and N.D. Smith. 2016. Extreme modification of the tetrapod forelimb in a Triassic diapsid reptile. *Current Biology* 26: 2779–2786. [<https://doi.org/10.1016/j.cub.2016.07.084>]
- Pritchard, A.C., and S.J. Nesbitt. 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). [<https://doi.org/10.1098/rsos.170499>]
- Pritchard, A.C., E. Clark, K. Walls, and B.S. Bhullar. 2018. Testing functional hypotheses in a Triassic diapsid reptile—3D modeling of modern muscles and range-of-motion modeling inform digging in *Drepanosaurus*. *Journal of Vertebrate Paleontology*. 38 (electronic supplement):199.
- Rafinesque, C.S. 1832. *Zoology. Atlantic Journal, and Friend of Knowledge: A Cyclopedic Journal and Review of Universal Science and Knowledge: Historical, Natural, and Medical Arts and Sciences: Industry, Agriculture, Education, and Every Useful Information*. 1(2): 39–82.
- Renesto, S. 1994. The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. *Zoological Journal of the Linnean Society* 111:247–264.
- Renesto, S., and G. Binelli. 2006. *Vallesaurus cenensis* Wild, 1991, a drepanosaurid (Reptilia, Diapsida) from the Late Triassic of northern Italy. *Rivista Italiana Di Paleontologia e Stratigrafia* 112:77–94. [<https://www.doi.org/10.13130/2039-4942/5851>]
- Renesto S., J.A. Spielmann, S.G. Lucas, and G.T. Spagnoli. 2010. The taxonomy and paleobiology of the Late Triassic (Carnian-Norian: Adamanian-Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). *Bulletin of the New Mexico Museum of Natural History and Science* 46:1–92.
- Sidor, C.A., D.A. Vilhena, K.D. Angielczyk, A.K. Huttenlocker, S.J. Nesbitt, B.R. Peacock, J.S. Steyer, R.M.H. Smith, and L.A. Tsuji. 2013. Provincialization of terrestrial faunas following the end-Permian mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* 110: 8129–8133. [<https://doi.org/10.1073/pnas.1302323110>]
- Sidor, C.A., B.R. Peacock, C.V. Beightol, T. Kaye, G. Livingston, W.G. Parker, S.L. Olroyd, and M.R. Whitney. 2018. A multitaxic bonebed featuring a new shuvosaurid (Archosauria: Popsauroidae) from the Sonsela Member of the Chinle Formation at Petrified

- Forest National Park. *Journal of Vertebrate Paleontology* 38 (electronic supplement):216.
- Spielmann, J.A., A.B. Heckert, and S.G. Lucas. 2005. The Late Triassic archosauromorph *Trilophosaurus* as an arboreal climber. *Rivista Italiana Di Paleontologia e Stratigrafia* 111:395–412.
- Taylor, B.K. 1978. The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. *Journal of Morphology* 157:347–367.
- Weber, M.W.C. 1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. 890 pp.
- Wild, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Bollettino della Societa Paleontologica Italiana* 17:176–256.