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# DESCRIPTION OF A NEW UPPER TRIASSIC FOSSIL LUNGFISH (SARCOPTERYGII:DIPNOI) LOCALITY FROM THE GARITA CREEK FORMATION, EAST-CENTRAL NEW MEXICO, WITH A REEVALUATION OF LATE TRIASSIC LUNGFISH DIVERSITY IN THE AMERICAN SOUTHWEST

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ABSTRACT — Mesozoic lungfish fossils ordinarily consist of isolated tooth plates. Many tooth plates, typically assigned to *Arganodus*, are known from the Upper Triassic of the American Southwest. The new Homestead Site at Garita Creek is the most extensive vertebrate assemblage described from the Garita Creek Formation in east-central New Mexico. It has yielded enough new lungfish fossils (18 nearly complete-complete and 43 fragmentary tooth plates) to qualify as the second-richest Upper Triassic lungfish site in North America. We measured the tooth plates of Homestead and several others from the Chinle, identifying multiple tooth plate morphotypes, including ones with only 4–5 ridges that fall outside the diagnosis of *Arganodus*, suggesting that the Homestead assemblage preserves at least two taxa. Reevaluating 32 previously published PEFO tooth plates further supports the presence of two morphologies: a more common morph we assign to *Arganodus* sp., and a second morph that we assign to cf. *Ptychoceratodus*. *Ptychoceratodus* has a limited presence in North American strata, but is known from the Late Triassic of Greenland. A ptychoceratodontid in the Upper Triassic of western North America greatly increases their geographic range during the Triassic, and shows that they coexisted with *Arganodus* on at least three modern continents.

*Keywords*: Lungfish, *Arganodus*, *Ptychoceratodus*, Tooth Plate, Late Triassic, Chinle.

## INTRODUCTION

The Upper Triassic strata of the Colorado Plateau yield world-famous assemblages of vertebrate fossils, especially of archosaurian reptiles, including some of North America's oldest dinosaurs (Long and Murry, 1995; Heckert et al., 2005; Parker, 2005, 2006; Nesbitt et al., 2007; Marsh and Parker, 2020). These same strata also yield fossils of fishes, including dipnoans (Huber et al., 1993; Milner et al., 2006; Gibson, 2016; Kligman et al., 2017), but these are often more fragmentary and have historically not been afforded the same attention. While there are some assemblages of articulated fish from Upper Triassic strata in the American Southwest (Schaeffer, 1967; Johnson et al., 2002; Gibson, 2016, 2018), most fossil osteichthyans and chondrichthyans are found more incidentally, often as isolated and/or fragmentary fossils in microvertebrate assemblages (Murry, 1986

1989; Heckert, 2004; Kligman et al., 2017). Sarcopterygian fish, including coelacanths and lungfish, however, are sometimes recovered from larger, isolated fossils (Hunt, 1997; Milner et al., 2006). To date, Murry (1989) is the most recent author to document lungfish diversity and taxonomy from these strata, and in his analysis described a prolific site, the "lungfish locality" in Petrified Forest National Park (PEFO) that yielded 30 tooth plates, two vomerine teeth, and an additional 80 tooth plate fragments. While Polcyn et al. (2002) preliminarily described a site near Stinking Springs, Arizona, southeast of PEFO, that they said yielded approximately 700 tooth-plates, they did not illustrate or describe these fossils, thus Murry (1989) remains the most recent taxonomic treatment.

In this paper we describe a new assemblage of lungfish tooth plates from a site in east-central New Mexico and compare them to other lungfish tooth plates of similar age across the Colorado Plateau in New Mexico, Arizona, and Utah, including previously published specimens from the Petrified Forest National Park (PEFO), to expand upon the known diversity of Late Triassic lungfish in North America (Fig. 1). The new assemblage consists of 26 relatively complete tooth plates (Fig. 4) gathered from the Homestead Site at Garita Creek, located in the Garita Creek Formation of eastern New Mexico, as well as previously studied specimens from the Bluewater Creek Formation in New Mexico, Blue Mesa Member in Arizona, and Petrified Forest ("Painted Desert") Member in Utah (Fig. 1). As of now, Homestead is a largely unpublished assemblage, so we provide a brief summary of the stratigraphy, sedimentology, and taphonomy of the site, as the majority of the fossils used for this project were collected from it.

Upper Triassic lungfish from the American Southwest have long been considered to represent a single taxon, *Arganodus*, sometimes referred to the species *Arganodus dorotheae* (Murry, 1989; Hunt et al., 1989; Milner et al., 2006), which apparently replaced the Middle Permian sagenodontid taxa *Sagenodus* and gnathorhizid taxa *Gnathorhiza* (Pardo et al., 2010). The Ceratodontiformes were the only group of dipnoans that remained globally post-PTB (Kemp et al., 2017). Their diversity in the Mesozoic is still relatively poorly understood due to their mostly incidental occurrences worldwide as isolated tooth plates.

As with most vertebrates, cranial material is most taxonomically diagnostic in dipnoans down to the species level due to the unique structuring and fusion of bones in the calvarium (Kemp, 1998). However, reduced ossification of the skeleton in post-Paleozoic taxa has resulted in a near-total lack of fossil bone in the record of Mesozoic and Cenozoic lungfish (Cavin et al., 2007). Lungfish do, however, possess a dentition that is readily diagnostic to the genus level, and thus their tooth plates can be used as valid taxonomic indicators when identifying genera in the absence of cranial material (Kemp, 1998), though allometry, ontogenetic change, positional variation, and wear facets limit these assignments. Consequently, many species have been based on characters that may change over the course of ontogeny (Murry, 1989). Martin (1982) proposed a handful of phylogenetically informative characteristics for differentiating Mesozoic ceratodontoids, generally based solely on tooth plates, and specifically for identifying the four following families: Ceratodontidae, Ptychoceratodontidae, Arganodontidae, and the still extant Neoceratodontidae, all of which occur in Mesozoic strata.

In general, these diagnoses are based on the number, size, and shape of the ridges and intervening furrows (Fig. 2A–D, G).

Lungfish tooth plates form during development as rows of individual cusps that fuse together into a radiating, fan-shaped occlusal surface (Kemp, 2002). These plates continuously grow instead of undergoing continuous replacement as in most other fish (Kemp, 2002). Individual species may have uniquely shaped tooth plates, but features of these plates may change shape as the animal matures (Skrzycki, 2015). Although some morphological features change as a result of growth and wear, others remain unmodified (Kemp, 2005; Skrzycki, 2015). According to Skrzycki (2015), unmodified features include: the general shape of the tooth plates, position of palatal plates in relation to each other, the pattern of ridges (parallel or anterior/medial radiation), the shape of upper and lower symphyses, the morphology of the enamel to bone junction, the position of pterygopalatine ascending process, and form of prearticular sulcus. The origin of ridges, shape of first ridge crest, and relative length of first ridge to the lingual margin (ratio of anchor points $BC_1/BC_P$, Fig. 2E–F) may change slightly (Skrzycki, 2015). The most changeable characters are the size of the tooth plate, distinctiveness of inner angle tip (anchor points ABC, Fig. 2E-F), sharpness of ridges, morphology of the last ridge, the depth of furrows, the extent of the occlusal surface, the presence of denticles, and location of occlusal pits, most of which are clearly affected by wear facets (Skrzycki, 2015). Therefore, while tooth plates are useful for taxonomic identification, there are limitations.

While Kemp (1997) was skeptical of the taxonomic value for biometric measurements of isolated tooth plates, specifically the methods established by Vorob'yeva and Minikh (1968), there is no rigorous test of her hypothesis in the literature regarding these measurements offering insignificant taxonomic information. That is, neither Kemp (1997) nor other dipnoan workers have demonstrated that lungfish tooth plates, especially those of Triassic age sediments, yield ambiguous or spurious taxonomic assignments. Skrzycki (2015) has stated that sole application of these biometric plate measurements does not help to discriminate between morphologically similar species, which is why it can be used as independent support of morphological comparisons. Many have successfully used tooth plate characters in addition to biometric measurements to generate taxonomic hypotheses in the absence of cranial material (e.g., Martin et al., 1981; Martin, 1982; Murry, 1989; Milner and Kirkland, 2006; Soto and Perea, 2010; Skrzycki, 2015; Frederickson and Cifelli, 2017; Skrzycki et al., 2018), so we rely on those studies extensively here.

## MATERIALS AND METHODS

The motivation for this study stems from the "Homestead Site at Garita Creek Project," or Homestead site, of east-central New Mexico (Fig. 1, 3). This is a collaborative effort undertaken by personnel from ASU, the Lauer Foundation, VT, and NHMUK. The land and fossil assemblage are property of the Lauer Foundation and thus the specimens described here are available to qualified researchers per the earlier curation statement. A majority of Homestead fossils were collected by Larry and Betty Martin, with more recent samples collected by personnel from ASU, VT, NHMUK, and Lauer Foundation. The initial collection from the Martins is referred to as the “picked bags,” which are minimally sorted but contain most of the more complete specimens and/or material they considered more diagnostic. The rest of their collection is termed the “concentrate,” which includes all the material that did not make it into the picked bags. Of the 18 tooth plates found at Homestead (Fig. 1, 4A–R); 16 were recovered from the picked bags, another was found in the concentrate, and the last one was surface collected from the “wash” area in 2021. An additional 43 plate fragments were also recovered from Homestead.

The second and third localities, from the Bluewater Creek Formation of west-central New Mexico and Blue Mesa Member of east-central Arizona, have yielded two and three tooth plates respectively (Fig. 1, 4S–W). These sites are designated as NMMNH localities L-3380 and L-6818. Additionally, a fourth locality, in the Petrified Forest Member (Painted Desert equivalent) of southeastern Utah, yielded three tooth plates (Fig. 1, 4X–Z). This is the Four Aces mine locality of Parrish (1999), and is designated as UCM-97074. The tooth plates of these three localities were loaned to ASU for use in this project by NMMNH and UCM. Of the 32 tooth plates within Murry’s (1989) PEFO assemblage (Fig. 1), none of the fossils used within his original study were originally available for this project, as they remained in his possession. Only the figure and data tables provided in the original publication were utilized in this current study, although we have subsequently been in touch with personnel at PEFO to verify some observations of fossils that have since been returned to PEFO.

Terminology of the morphological features on individual tooth plates (Fig. 2A–D) typically follows Kemp (2002), with some revisions for this study following Churcher et al. (2006). Additionally, the point formed by the mesial and lingual margins of tooth plates (anchor point B, Fig. 2E–F) is referred to by many names in publication, and is often considered synonymous with the angle that it forms (anchor points ABC, Fig. 2E–F). Some examples of these names include “inner angle” (e.g., Kemp, 1996; Cavin et al., 2007; Skrzycki, 2015), “angulus internus” (e.g., Murry, 1989), “mediolingual junction” (e.g., Vorob’yeva and Minikh, 1968; Kemp, 1996; Skrzycki, 2015; Pawlak, 2020), or “mesiointernal angle” (e.g., Churcher et al., 2006). While any of these terms are interchangeable, we prefer the name “mesiolingual corner,” following Frederickson and Cifelli (2017), as it most accurately represents the connection between the mesial and lingual margins (Fig. 2A–D). Ridges normally radiate from this corner, but this is not always the case for some species (Churcher et al., 2006). When referring specifically to angle ABC, we use the distinction “angle” rather than “corner,” following Soto and Perea (2010).

Here we analyze the morphology of each tooth plate, noting any differences that may indicate separate taxa. We follow the list of characters compiled by Skrzycki (2015). Here we emphasize the number of ridges present, as it is the character that most readily distinguishes between genera when fossil bone is not available. All fossils used in this project were photographed in occlusal view using a Keyence VHX 3D microscope. The length and width (in mm) of each tooth plate were measured using the ImageJ.JS web application v. 0.5.7 (Ouyang, 2024). Each tooth plate image was subsequently cropped and edited using Adobe Photoshop, with 15 having been tentatively reconstructed in Adobe Illustrator due to fractures or strong wear facets (proposed reconstructions shown by dotted lines, Fig. 4).

**Institutional Abbreviations** — **ASU**, Appalachian State University, Boone, NC, U.S.A.; **LF**, the Lauer Foundation for Paleontology, Science and Education, Wheaton, IL, U.S.A.; **NHMUK**, the Natural History Museum, London, England, United Kingdom; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, NM, U.S.A.; **PEFO**, Petrified Forest National Park, AZ, U.S.A.; **PFV**, Petrified Forest National Park fossil vertebrate locality; **UCM**, University of Colorado Museum of Natural History, Boulder, CO U.S.A.; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.; **VT**, Virginia Tech, Blacksburg, VA, U.S.A.

**Curation 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.

## PREVIOUS STUDIES

The first publication of Upper Triassic lungfish tooth plates now recognized as *Arganodus* from Upper Triassic strata in North America was by Case (1921), who described a singular tooth plate from the UMMP vertebrate paleontology collection ("geological collection" at the time of publication). This tooth plate, UMMP-7324, was collected from Upper Triassic beds of the Dockum Group in Crosby County, Texas (Case, 1921). The plate was assigned as the holotype for *Ceratodus dorotheae*, the first occurrence of "*Ceratodus*" from the Triassic of North America (Case, 1921). An additional tooth plate, UMMP-9634, from Upper Triassic beds of the Dockum Group at Walker's Tank, Crosby County, Texas, would later be described by Warthin (1928) as the holotype for *Ceratodus crosbiensis*, which was the second Triassic occurrence of "*Ceratodus*" in North America. However, "*C.*" *dorotheae* and other subsequently collected specimens would later be reassigned to a separate genus, *Arganodus*, as *Arganodus dorotheae* (Martin, 1982). Martin (1982) simultaneously established the new family, Arganodontidae (Martin 1982), and this taxonomy has generally been followed by other Triassic workers in the American Southwest (Murry, 1986, 1989; Huber et al., 1993; Milner et al., 2006). Murry (1986) considered Warthin's (1928) "*C.*" *crosbiensis* a junior subjective synonym of *A. dorotheae*, stating that it merely represented a "middle stage" ontogenetic variation within *A. dorotheae*.

In 1989, Murry described a new assemblage of 32 ceratodontoid lungfish tooth plates from Upper Triassic strata in the "upper Petrified Forest Member" (Painted Desert Member, of some usage) within PEFO (Fig. 1). These consisted of 30 plates from the Lungfish locality (PFV 190), and one additional tooth plate each from the Flattops (PFV 187) and Dinosaur Hill (PFV 040) localities. Murry (1989) utilized the method established by Vorob'yeva and Minikh (1968) as well as the phylogenetically informative characteristics of ceratodontoids proposed by Martin et al. 1981; Martin, 1982) to identify (the species of lungfish found within PEFO. The method first performed by Vorob'yeva and Minikh (1968) consists of measuring a series of angles formed by the ridges of ceratodontoid tooth plates. These angles are based on a set of anchor points placed on the origin of the ridges and distal ends of the ridges, or atop the crests (Fig. 2E-F). Murry (1989) assigned all 32 PEFO plates in his assemblage as *Arganodus* sp., and deemed them most similar to *A. dorotheae* and *A. atlantis*. He notes that the Chinle specimens are closely related to *A. dorotheae* and may be synonymous (Murry, 1986; 1989). Murry (1989: 269) also hinted at further diversity, stating that, "the variability of the internal angle is evidently unlike the condition seen in the arganodontids, and this character is somewhat reminiscent of the ptychoceratodontids." He (Murry, 1989: 269) also stated that, of the characters he used, "eight characters total are shared with at least some of the specimens Martin classifies as arganodontids, seven characters in common with at least some of the ptychoceratodontids…" Thus, while largely continuing to identify Triassic lungfish tooth plates from the American Southwest as *Arganodus*, he also acknowledged the possibility that there was more than one taxon represented in the assemblage.

More recently, Heckert et al. (2012) documented Upper Triassic lungfish tooth plates from the Cumnock Formation in the Newark Supergroup of North Carolina that they assigned to *Asiatoceratodus*, following Kemp (1998), who synonymized *Arganodus* with *Asiatoceratodus*, but many authors reject this hypothesis and instead retain *Arganodus* as a separate genus (Schultze, 2004; Cavin et al., 2007; Soto and Perea, 2010; Skrzycki 2015). Following this logic, essentially all Upper Triassic lungfish tooth plates from mainland North America have been assigned to *Arganodus* (=*Asiatoceratodus*), with *A. dorotheae* the nominal species, although authors such as Murry (1989) have suggested that some tooth plates are not readily assigned to *Arganodus* and thus there may be greater diversity.

## THE HOMESTEAD SITE: A NEW LUNGFISH LOCALITY

The Homestead Site at Garita Creek is located in the Upper Triassic Garita Creek Formation (Fig. 1, 3), which occurs in the middle of the Chinle Group of east-central New Mexico, following the stratigraphic terminology of workers in the region (Lucas et al., 2001; Lucas, 2004). During the Late Triassic, a continental river system drained northwest across the Four Corners region of North America into the Proto-Pacific Ocean (Dubiel, 1989; Lucas, 1993; Riggs et al., 1996; Fiorillo et al., 2000; Cleveland et al., 2008). This river system led to the deposition of Chinle sediments across the southern Colorado Plateau throughout the Norian and into the Rhaetian (Dubiel, 1989; Lucas, 1993; Cleveland et al., 2008; Martz and Parker, 2010; Martz et al., 2017). The Chinle, variously referred to as a formation (e.g., Stewart et al., 1972; Dubiel, 1989) or group (e.g., Lucas, 1993; Lucas et al., 2001), consists mainly of mudstone-dominated slopes and sandstone-dominated benches (Lucas et al., 2001). This is consistent with the lithology of the Garita Creek Formation, which is mostly silty/sandy mudstone slopes containing limestone nodules interrupted by massive, fine-grained sandstone-dominated benches with some laminations and ripples (Lucas and Hunt,

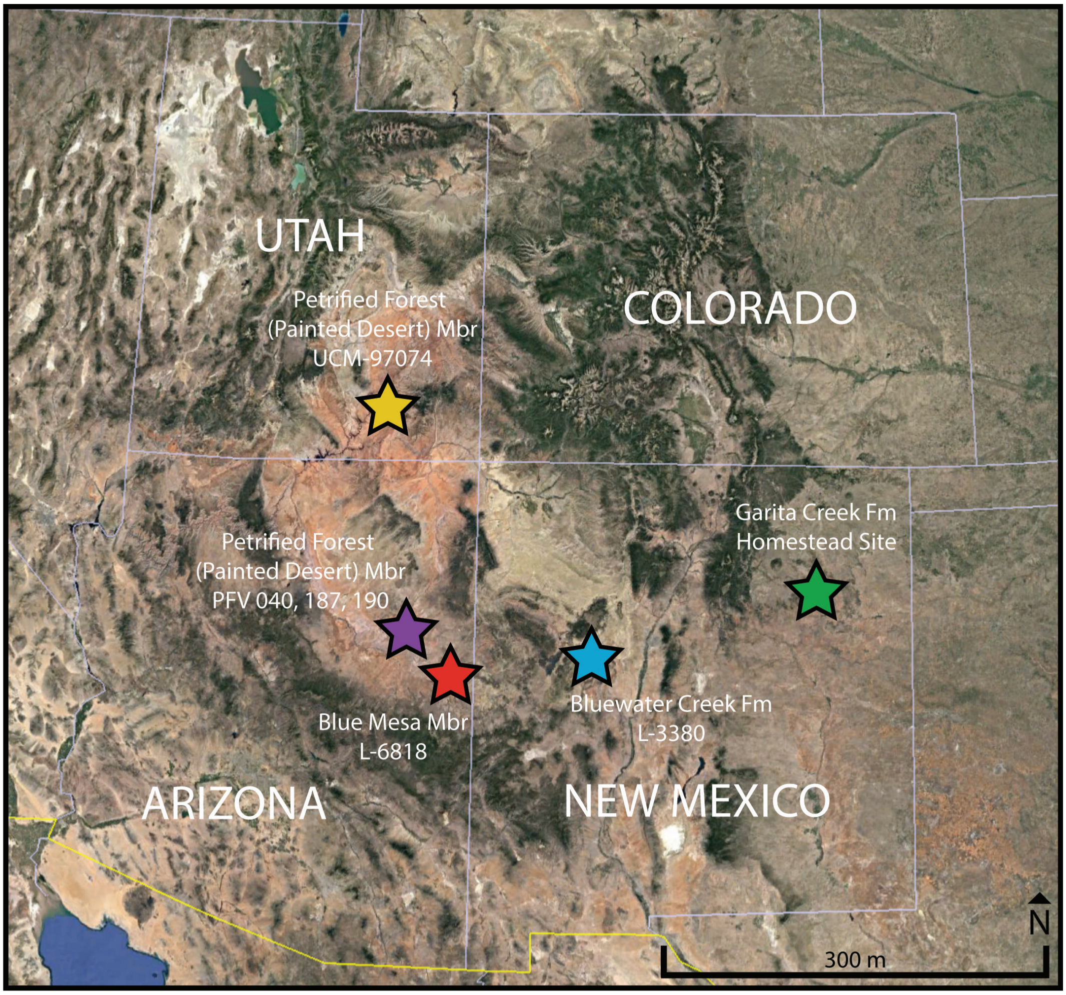

FIGURE 1. Map of the Four Corners region in the southwestern United States, showing the location of Upper Triassic lungfish localities used in this study. Includes the new locality, the Homestead Site of the Garita Creek Formation; NMMNH L-3380 of the Bluewater Creek Formation; NMMNH L-6818 of the Blue Mesa Member; and UCM-97074 of the Petrified Forest Member. PEFO localities PFV 040 (Dinosaur Hill), PFV 187 (Flattops), and PFV 190 (Lungfish Locality) used by Murry (1989) indicated as well. Image captured via Google Earth.

1989; Fig. 3). Lucas et al. (2001) provided a detailed review of the history of stratigraphic nomenclature in the region.

**Local Stratigraphy.** — The exposed section of Homestead is only 7.45 m thick, with a 0.35 m thick fossiliferous horizon found at the base of the section; it is located 7.2 km northwest from the type section of Garita Creek and less than 4.8 km southwest from the Mouth of Garita Creek (MoGC) section (Fig. 3). The type section of the Garita Creek Formation is 71 m thick and the MoGC section is 88 m thick, the latter of which is located approximately 13 km northwest of the type section (Fig. 3). The Homestead site is hypothesized to correlate 14-24 m above the base of the type section and 6 m above the base of the MoGC section, based on correlation of the local section near the site to a persistent bench-forming sandstone (Fig. 3). This puts the Homestead site approximately 70 m below the top of the Garita Creek Formation locally.

**Biostratigraphy and Age.** — Lucas and Hunt (1989) named the Garita Creek Formation, and shortly thereafter Hunt et al. (1989) reported a fragmentary assemblage of vertebrate fossils from this outcrop belt. Thus far, this remains the only published vertebrate assemblage from the outcrop belt associated with the type section, although there are some other incidental fossil occurrences in the eastern Garita Creek Formation (Lucas et al., 2001). Based on these fossils and others farther to the west, Lucas et al. (2001; Lucas, 2004) considered the Garita Creek Formation to be of Adamanian (early Norian) age.

Farther to the west, the Garita Creek Formation hosts the world-famous Lamy metoposaur mass death assemblage (see Lucas et al., 2010; Hegrón et al., 2020). Until discovery of the Homestead site, the Lamy quarry and other nearby localities yielded the only fossils of the Garita Creek Formation that are age-diagnostic beyond “Late Triassic.” Lucas et al. (2001, 2010) considered the Garita Creek Formation to be Adamanian based on this assemblage, a conclusion echoed by Martz and Parker (2017). Hegrón et al. (2020) similarly considered the Garita Creek Formation to be Adamanian in age, although their argument was based on the presence of azendohsaurids and tanystropheids, and thus was more of a stage of evolution argument. However, Pritchard et al. (2015) recorded the presence of tanystropheids in the Revueltian-aged Hayden Quarry of Ghost Ranch in northern New Mexico, thus casting doubt on using the presence of tanystropheids for differentiating between the Adamanian and Revueltian. Previously Hunt et al. (2005) coined the term “Lamyan” to indicate that the quarry’s assemblage represented a younger interval of Adamanian time, based on fossils from the stratigraphically lower Tres Lagunas Member of the Santa Rosa Formation (assigned by them to the aetosaur *Typothorax antiquum* and the phytosaur *Pseudopalatus* sp.), and proposed a tentative correlation to strata now identified as the Jim Camp Wash beds of the Sonsela Member in PEFO.

We note that the Adamanian age for the Garita Creek Formation is thus established based on fossils low in the formation from the western edge of its recognized outcrop belt. With many thousands of microvertebrate and some larger fossils available, we tentatively consider the Homestead site to be of Revueltian (early-mid Norian; Revueltian teilzone of Martz and Parker, 2017). We base this argument principally on the presence of the index fossil *Reticulodus synergus*, a

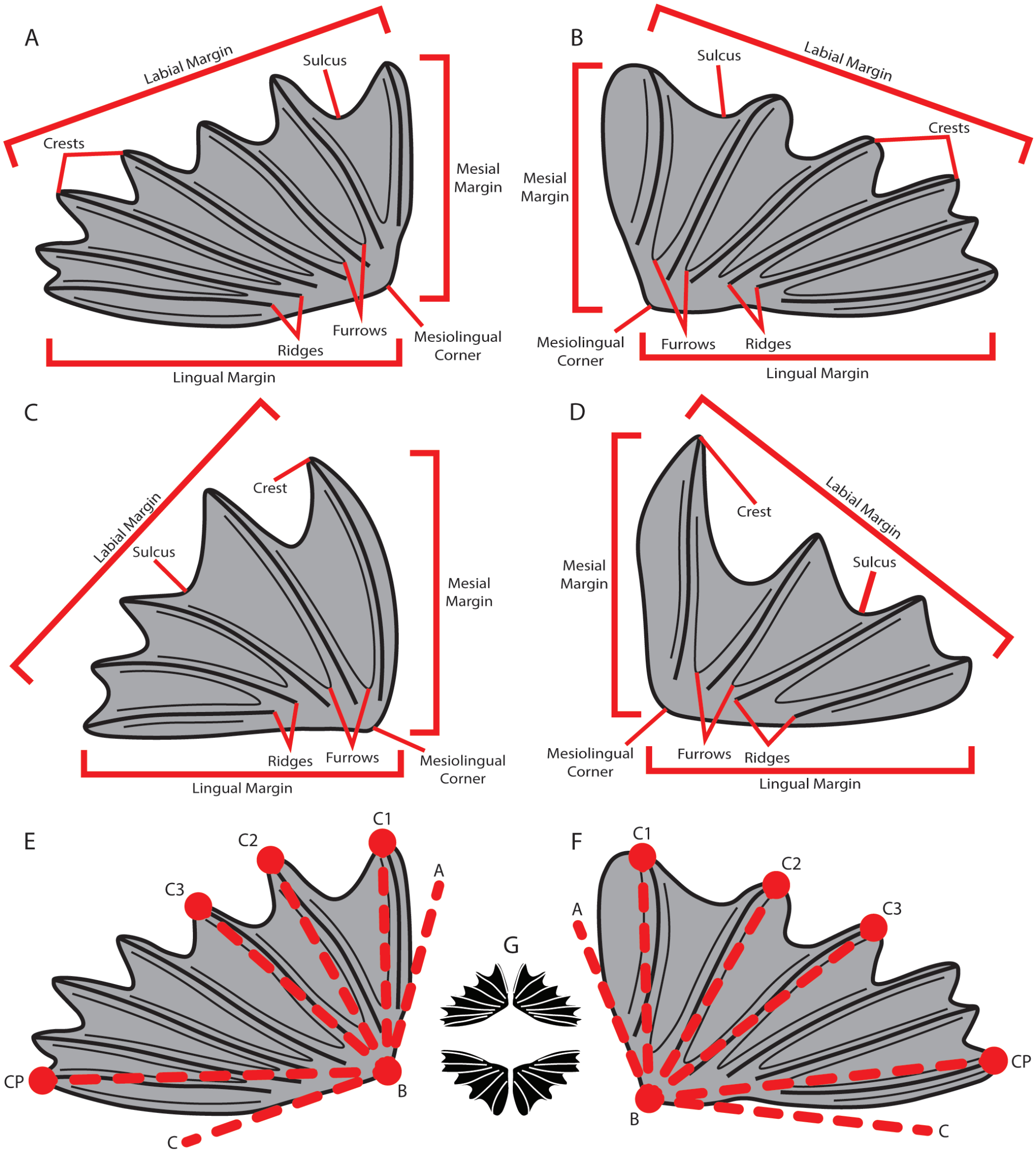

FIGURE 2. Lungfish tooth plate orientation and nomenclature. A–B: *Arganodus* right palatal (A) and right splenial (B) tooth plates based on Murry (1989, fig. 6). C–D: *Ptychoceratodus* right palatal (C) and right splenial (D) tooth plates based on Skrzycki et al. (2018, fig. 3). Terminology associated with the different margins and morphological features based on Kemp (2002) and Churcher et al. (2006). "Mesiolingual corner" follows Frederickson and Cifelli (2017). E–F: Schematics showing the orientation of specific crests and other features as measured in *Arganodus* by Murry (1989). G: 180° view of *Arganodus* palatal and splenial plates oriented within the mouth, based on Murry (1989, fig. 6).

durophagous hybodont shark with superficially batoid-like teeth known primarily from strata of Revueltian age in the American Southwest (Murry and Kirby, 2002; Heckert and Lucas, 2006; Voris and Heckert, 2017). Voucher specimens of *Reticulodus* from the Homestead Site include LF 5513-17 and LF 5535. We also note that, while there are many thousands of microvertebrate fossils still undergoing organization and curation, thus far we have not identified any characteristically Adamanian microvertebrates, such as *Triodus moorei*, *Colognathus*, *Crosbysaurus*, or *Krzyzanowskisaurus* (e.g., Heckert and Lucas, 2006) from the assemblage. Presently, all larger tetrapods from the assemblage are fragmentary, but osteoderm fragments of aetosaurs from the site (e.g., LF 5536) are more consistent with assignment to *Typothorax*, which may occur in the uppermost strata of Adamanian age (e.g, Parker and Martz, 2011), but is more characteristic of Revueltian assemblages.

**Sedimentology.** — Based on the fine-grained, predominantly dark, but somewhat color-mottled strata, we hypothesize that Homestead was an oxbow lake or other ephemeral water body that filled in with sediment and underwent soil formation (Dubiel, 1989; Fiorillo et al., 2000). The majority of sediments that make up the fossiliferous interval are fine-grained silts and clays. This fine-grained matrix, along with the color mottling of the mudstone, implies there were many periods of seasonal drought within a low energy depositional environment (Dubiel, 1991; Firoillo et al., 2000; Therrien and Fastovsky, 2000; Cleveland et al., 2008). Intermittent drought would have caused the water table to fluctuate, resulting in alternating anoxic and aerobic conditions that produce reduced and oxidized iron compounds, which is represented by the greenish-gray and reddish-brown mudstone (Dubiel, 1991; Fiorillo et al., 2000; Therrien and Fastovsky, 2000; Cleveland et al., 2008).

**Taphonomy.** — A wide variety of microvertebrate fossils are preserved within the fossiliferous bed at Homestead. These fossils range from <0.5 mm to >4 mm in size, though the majority found are 1–2 mm. Few fossils are actually found *in situ*, as the fossiliferous bed weathers out into a shallow slope called the “wash.” This “wash” extends out beyond the exposed section into an area called the “South Mesquite,” which contains some stratigraphically lower, but *in situ* fossils in a sandy siltstone/fine-grained sandstone. These fragile elements are disarticulated but undistorted, preserving a great amount of detail that aids in taxonomic identification. There are many specimens from Homestead diagnostic to at least the genus level, such as the aforementioned *Reticulodus synergus*, the lungfish described here (Fig. 4A–H), but the site is dominated by diverse tetrapods (Heckert et al., 2023).

The most common fossils found at Homestead are coprolites. Some of these coprolites contain fish scales, or on rare occasions, bone and teeth. The picked bag collection is heavily biased against coprolites as well as fish material. It was not until the concentrate was provided that most of the coprolites and fish fossils were accounted for. However, due to the diagnostic shape and texture of lungfish tooth plates, most lungfish material at Homestead was recovered from the picked bags. The large number of fish fossils preserved at Homestead suggests that a stable body of water must have been present, at least temporarily, and assuming that Homestead was part of an oxbow lake based on our sedimentological observations, the vast number of tetrapods that are preserved here may have been attracted to the ephemeral nature of this lacustrine region due to the fluctuating water table resulting from seasonal drought (Dubiel, 1991; Fiorillo et al., 2000). Periodic flooding may explain how many of the principally non-aquatic tetrapods were preserved at Homestead (Dubiel, 1991; Fiorillo et al., 2000; Therrien and Fastovsky, 2000), but we are not able to support any of these suggestions without further study.

## SITE COMPARISONS

The Homestead site is now the second most prolific lungfish tooth plate site in the Upper Triassic of North America of which we are aware, following Murry's (1989) "lungfish locality" (PFV 190, Fig. 1). Thus, in studying the tooth plates here, we relied on first-hand comparison to tooth plates from other sites in New Mexico, Arizona, and Utah, as well as comparisons to the specimens described and illustrated by Murry (1989).

The other New Mexico locality is in the Lucero uplift of central New Mexico and is NMMNH locality 3380 (NMMNH L-3380, Fig. 1). This and two other nearby localities are in low exposures of the Bluewater Creek Formation. The vertebrate assemblage from these localities was previously described by Heckert (1997) and Zeigler et al. (2002), who considered them to be Adamanian (early Norian) in age. The tooth plates from Arizona were collected from a region known as the "Blue Hills," slightly northeast of St. Johns. This area is well known for its tetrapod fossils, dating back to Charles L. Camp's collections in the 1920s (Long et al., 1989; Long and Murry, 1995; Heckert et al., 2005).

The lungfish fossils described here were collected from NMMNH locality 6818 (NMMNH L-6818, Fig. 1), low in the Blue Mesa Member amongst many other fossils of well corroborated Adamanian (early Norian) age (Heckert et al., 2005). The three localities in Arizona that were sampled by Murry (1989, Fig. 1) are all located in the Petrified Forest Member (Woody, 2006; Martz et al., 2012), also referred to as the Painted Desert Member by some (Lucas, 1993; Heckert and Lucas, 2002), and are stratigraphically above the other Adamanian localities (Martz and Parker, 2017, fig. 14). The Petrified Forest Member in PEFO, including all of Murry's (1989) sites is of well-corroborated Revueltian age (Heckert and Lucas, 2002; Parker and Martz, 2011; Martz and Parker, 2017). The Utah fossils were collected from strata exposed in the Red Canyon area and originally described by Parrish and Good (1987) and Parrish (1999). This particular locality is known as the Four Aces Mine, reposited at UCM, and the site is designated as UCM-97074 (Fig. 1). This locality also lies in the Petrified Forest Member (Painted Desert Member of some usage), which is probably stratigraphically equivalent to the Petrified Forest Member in PEFO and also considered to be Revueltian in age (e.g., Martz et al., 2017). All three specimens from this locality were cataloged under a single number (UCM 76502) so we distinguish between them as 76502-A, 76502-B, and 76502-C.

## SYSTEMATIC PALEONTOLOGY

### OSTEICHTHYES Huxley, 1880

### SARCOPTERYGII Romer, 1955

### DIPNOI Müller, 1844

### CERATODONTIFORMES Berg, 1940

**Description**. — Within the assemblage of 18 tooth plates from Homestead (Fig. 4A–R; Appendix 1), we identify a total of nine palatal tooth plates (six left, three right) and four splenial tooth plates (two left, two right). Five of the 18 plates have an unclear palatal/splenial position due to strong wear, fracturing, or lack of attached bone, and thus are considered positionally "ambiguous;" tentatively two are splenial and three are palatal. Palatal and splenial tooth plates can be distinguished based on several characteristics. In palatal plates, the mesial margin is not "inflated" outward from the anteriormost ridge in occlusal view, the lingual and labial profile declines posteriorly, and/or remnants of the pterygopalatine bone/ascending process can be seen (Murry, 1989; Fig. 2A, C). In splenial plates, the mesial margin is "inflated" outward from the anteriormost ridge in occlusal view, the lingual and labial profile is concave or straight, and/or remnants of the prearticular bone/sulcus is present (Murry, 1989; Skrzycki, 2015; Fig. 2B, D). The total ridge count may also be used to distinguish between palatal and splenial plates, with *Arganodus* specifically ranging from 6-8 for palatal and 6-7 for splenial (Skrzycki, 2015).

The tooth plates from Homestead (Fig. 4A–R) are relatively typical of Upper Triassic lungfish tooth plates from the American Southwest, having a morphology that would traditionally be classified as *Arganodus* sp. The ridges originate anteriorly and radiate outwards, forming a fan-like occlusal surface, the ridges are all roughly similar in how slender and acute they are, unlike in some taxa where they are much more robust, and are generally triangular in overall shape (Skrzycki, 2015; Skrzycki et al., 2018). 16 of the 18 plates have 5-7 total ridges, which historically was considered to align with *Arganodus* (Murry, 1989), however, a total of five ridges is no longer considered a feature of *Arganodus* (Skrzycki, 2015), suggesting another taxa is present. This will be explained in further detail in the following section.

We have identified a total of nine different morphologies based on the positioning (palatal vs splenial) and total ridge count of the tooth plates: 1) 8-ridged palatal (LF 5726; e.g., Fig. 4G); 2) 7-ridged palatal (LF 5720, 5721, 5724, 5725; e.g., Fig. 4A); 3) 7-ridged splenial (LF 5722, 6272; e.g., Fig. 4H); 4) 6-ridged palatal (LF 5723; e.g., Fig. 4D); 5) 6-ridged splenial (LF 6273; e.g., Fig. 4R); 6) 6-ridged ambiguous (LF 5728, 5729; e.g., Fig. 4J); 7) 5-ridged palatal (LF 5731, 5732, 5733; e.g., Fig. 4N); 8) 5-ridged ambiguous (LF 5727, 5734, 5735; e.g., Fig. 4I); 9) 4-ridged splenial (LF 5730; e.g., Fig. 4L).

There is a wide variety of minor character variations preserved within the Homestead assemblage. These may include the distinctiveness of the mesiolingual corner (anchor point B) or ridge crests, how obtuse the mesiolingual angle (anchor points ABC) is, curvature of the mesial and lingual margins, declination of the labial margin, width or depth of the sulci, depth of the furrows, height and length of the ridges, radiation of the

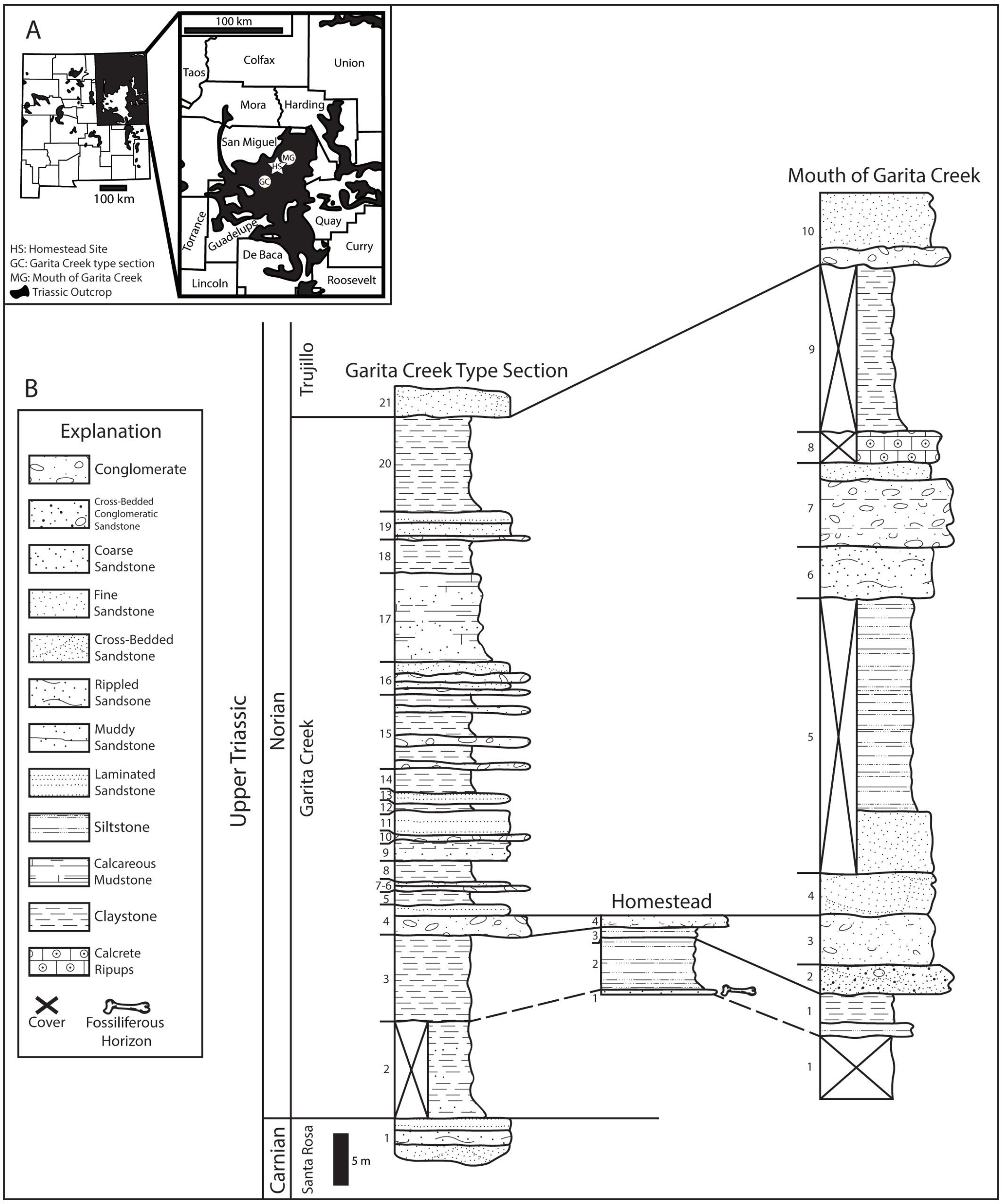

FIGURE 3. A: Index map of New Mexico, United States, showing the location of the Homestead Site stratigraphic section (**HS**), Garita Creek type section (**GC**), and Mouth of Garita Creek section (**MG**). B: Stratigraphic correlation of the Homestead Site to the Garita Creek type section and Mouth of Garita Creek section. Lithological explanation shown on left-side, along with columns representing the geologic epoch, age, and formation for the correlations. Representative lithologies sampled in largely covered intervals are shown to the right side of the column.

ridges, length of the anteriormost ridge compared to the second, inflation of the anteriormost ridge, definition of the posteriormost ridge, and the presence of ridge denticles, as well the color preserved in the tooth plate (Fig. 2, 4). Many of these variations in the plates are affected by the number of ridges, preservation, and wear facets. In terms of size, the 18 total tooth plates range from 2.2 to 23.1 mm in length and 1.8 to 13.4 mm in width. Notably, specimens LF 5728-35 (Fig. 4J-Q) from Homestead are distinctively smaller than the rest of the assemblage, ranging from 2.2 to 6.1 mm in length and 1.8 to 3.5 mm in width. Additionally, LF 5720 (Fig. 4A) from Homestead, while not as small, is still only 8.5 mm long and 4.7 mm wide; all others are at least 11.1 mm long and 6.9 mm wide.

The total number of ridges preserved in the tooth plates ranges from 4-8. Only one specimen, LF 5730 (Fig. 4L) bears four ridges, and only one specimen, LF 5726 (Fig. 4G) bears eight ridges. The majority of plates in the assemblage possess either seven or five ridges. Specimens LF 5720-22, LF 5724-25, and LF 6272 (Fig. 4A-C, E-F, H) have seven ridges. Specimens LF 5727, and LF 5731-35 (Fig. 4I, M-Q), have five ridges. The rest of the plates, LF 5723, LF 5728-29, and LF 6273 (Fig. 4D, J–K, R) have six ridges. Due to wear or fracturing, many of the plates have a poorly defined posteriormost ridge. LF 5721 (Fig. 4B) is counted as having seven ridges, though there appears to be remnants of what looks like an additional 8th ridge. LF 5727 (Fig. 4I), which has a peculiar morphology overall, with its broadly curved mesial/lingual margins and near-flat ridges, may possess a 6th ridge. LF 5735 (Fig. 4Q) has the most wear of the plates in the assemblage, and combined with its near-flat ridges, may also possess a 6th ridge.

**Comparisons**. — Specimens LF 5720-26 and LF 6272 (Fig. 4A–H) from Homestead appear to more closely resemble the eight non-Homestead tooth plates from localities L-3380, L-6818, and UCM-97074. NMMNH P-90530 (Fig. 4S) resembles the 7-ridged palatal morph; NMMNH P-90532 and UCM-76502-B (Fig. 4U, Y) resemble the 7-ridged splenial morph; NMMNH P-90533 (Fig. 4V) resembles the 6-ridged palatal morph; NMMNH P-90531, P-90534, and UCM-76502-A, C (Fig. 4T, W–X, Z) resemble the 6-ridged splenial morph. Out of these 16 tooth plates, they range from 8.5 to 23.1 mm in length and 4.7 to 13.4 mm in width, and consist of 6–8 total ridges.

Specimens LF 5727-35 and LF 6273 (Fig. 4I–R) from Homestead, when compared to the 16 other tooth plates in the Chinle assemblage, have differences from the rest of the assemblage that indicate a separate taxa present at Homestead, which we interpret to be a ptychoceratodontid. Species of *Arganodus* and *Ptychoceratodus* share many overlapping morphological features in their tooth plates that make distinguishing between them difficult (Murry, 1989; Skrzycki, 2015). According to Skrzycki (2015), a tooth plate bearing fewer than six ridges cannot be assigned to the genus *Arganodus*. Specimens LF 5727 and LF 5731-35 (Fig. 4I, M–Q) have five total ridges, and LF 5730 (Fig. 4L) has four total ridges. Individuals of *Ptychoceratodus* have 5–6 ridges for their palatal tooth plates and 4–6 for their splenial tooth plates, while individuals of *Arganodus* have 6–8 ridges for their palatal tooth plates and 6–7 for their splenial tooth plates (Skrzycki, 2015).

Because the Homestead assemblage includes tooth plates with as few as 4–5 ridges, it almost certainly includes an additional dipnoan taxon besides *Arganodus*. All other specimens within the Chinle assemblage range from 6-8 total ridges, which does align with the number of ridges present among arganodontids (Skrzycki, 2015). These include LF 5728-29 (Fig. 4J–K) and LF 6273 (Fig. 4J–K, R) from Homestead, which have six ridges. LF 5728-29 (Fig. 4J–K) are more similar to LF 5730-35 (Fig. 4L-Q) due to their smaller size compared to the rest of the assemblage. LF 5728 (Fig. 4J) has a broadly curved mesial/lingual margin similar to LF 5727 (Fig. 4I), and LF 6273 (Fig. 4R) has a noticeably longer, inflated first ridge, much like LF 5730 (Fig. 4L).

Additionally, LF 5726 (Fig. 4G) has eight total ridges, which is an atypical feature of lungfish known from the Upper Triassic of North America (along with the four total seen in LF 5730, Fig. 4I); these tooth plates commonly have 5–7 ridges preserved (Case, 1921; Warthin, 1928; Huber et al., 1993; Murry, 1989; Heckert, 2004; Milner et al., 2006). While eight ridges still aligns with *Arganodus*, it is typically seen in individuals of *A. atlantis* known from the Late Triassic of northern Africa, whose palatal plates may possess eight ridges, compared to *A. dorotheae*, which normally has seven (Case, 1921; Skrzycki, 2015; Skrzycki et al., 2018).

### ARGANODONTIDAE Martin, 1982

### *ARGANODUS* Martin, 1979

### *ARGANODUS* sp.

Figure 4A–H

**Diagnosis**. — The following diagnosis is based on the tooth plate characters presented by Skrzycki (2015, table 5). Tooth plates triangular and high-crowned with wide pulp cavity; limited mantle dentine visible on occlusal surface; short radiating ridges originate anteriorly; six to eight ridges on upper tooth plate, six to seven on lower; upper tooth plates contiguous in the midline, lower close or in contact; upper symphysis oval, lower linear; ascending process of pterygopalatine bone originating between second and third ridges; petrodentine absent.

**Referred Specimens**. — LF 5720-26, LF 6272.

Fossils we are comfortable assigning to *Arganodus* here have 6-8 ridges on their palatal tooth plates and 6-7 on their splenial tooth plates (Skrzycki, 2015). Comparisons of these plates to other “typical” Upper Triassic lungfish tooth plates (Fig. 4S-Z) show relatively consistent proportions, ridge counts, and other features.

### PTYCHOCERATODONTIDAE Martin, 1982

### *PTYCHOCERATODUS* Jaekel, 1926

### cf. *PTYCHOCERATODUS*

Figure 4I–R

**Diagnosis**. — The following diagnosis is restricted to tooth plate characters and was presented by Skrzycki (2015: e964357-3). “...tooth plates triangular and high-crowned with wide pulp cavity; limited mantle dentine visible on occlusal surface; short radiating ridges originate anteriorly; five to six ridges on upper tooth plate, four to six on lower; upper tooth plates close or contiguous in the midline, lower close; upper symphysis oblong, lower linear; ascending process of pterygopalatine bone originating

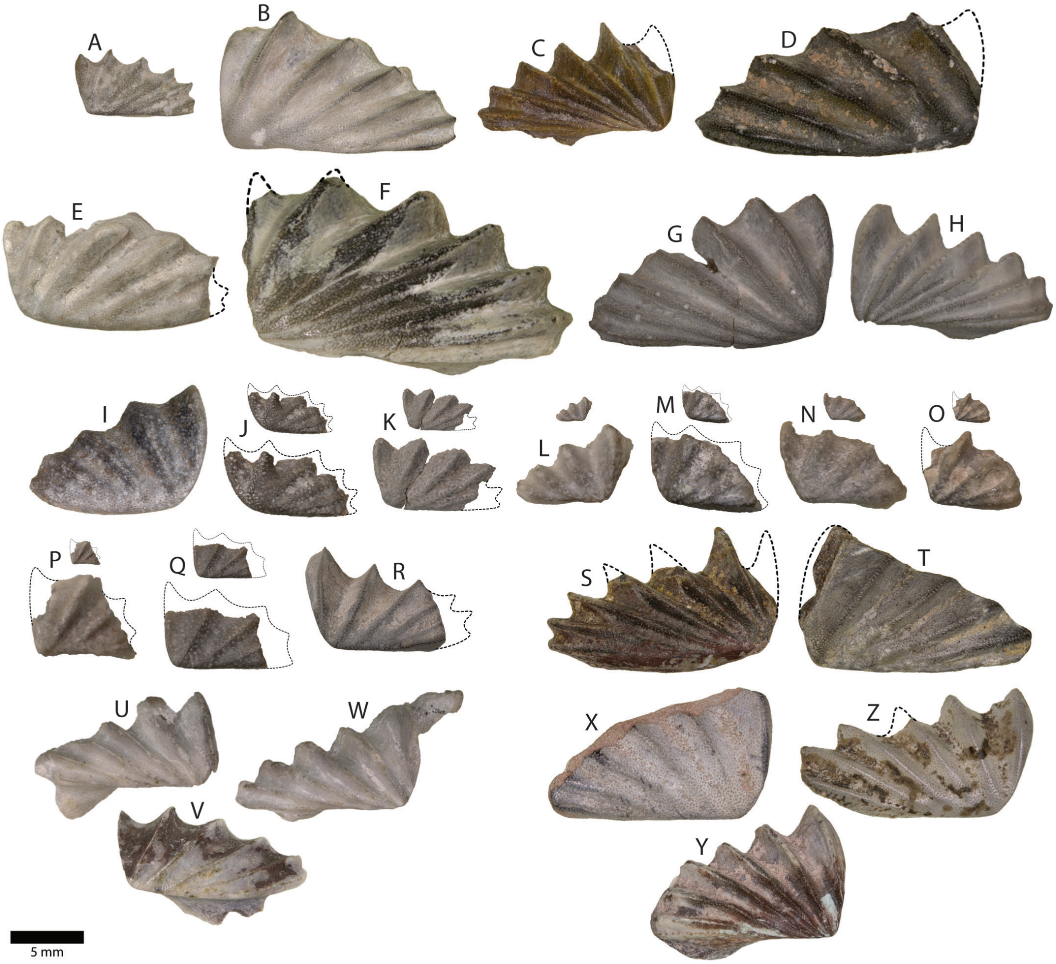

FIGURE 4. Assemblage of 26 lungfish tooth plates from four Upper Triassic Chinle localities. All tooth plates pertain to *Arganodus* sp. unless specified. LF 5720-26, LF 6272 (A–H): Homestead Site, Garita Creek Formation; NMMNH P-90530, P-90531 (S–T): NMMNH L-3380, Bluewater Creek Formation; NMMNH P-90532, P-90533, P-90534 (U–W): NMMNH L-6818; Petrified Forest Formation; UCM-76502-A, B, C (X–Z): UCM-97074, Petrified Forest Formation. Specimens LF 5727, 5728, 5729, 5730, 5731, 5732, 5733, 5734, 5735, and LF 6273 (I–R) belong to the cf. *Ptychoceratodus* morphology of Homestead; LF 5728-35 showcase original size and upscaled version to show detail. Dashed outlines represent proposed reconstructions. See Appendix 1 for details of positional assignments.

above the second ridge of upper tooth plate or between second and third ridges; petrodentine absent."

**Referred Specimens**. — LF 5727-35, LF 6273.

Specimens possessing only 4–5 ridges fall outside the currently accepted range of variation for *Arganodus*, and instead most closely resemble *Ptychoceratodus* (Skrzycki, 2015). Due to the similar morphology in the plates of *Arganodus* and *Ptychoceratodus* (Fig. 2, 4), the main distinguishing character is the total number of ridges present, although there is some overlap, as both genera may have six ridges per plate (Skrzycki, 2015). The lack of cranial material prevents any species assignments from being made, so tentatively, we consider the larger morph as still representing *Arganodus* sp., while the generally smaller morph is best designated as cf. *Ptychoceratodus*. The possibility remains that some six-ridged individuals of the second morph may be smaller individuals of the first morph in actuality. Using these same criteria, we recognize two taxa in the sample described by Murry (1989). While the vast majority of the specimens he (Murry, 1989) described and illustrated are best assigned to *Arganodus*, those with only six ridges could conceivably be assigned to either *Arganodus* or *Ptychoceratodus*.

Importantly, Murry (1989) illustrated two tooth plates that have five or fewer ridges (PEFO 3860; Murry, 1989, fig. 6g-h; PEFO 3864, Murry, 1989, fig. 6j) that he assigned to "*Arganodus*?." Another three reported in his dataset (PEFO 3852, PEFO 3881, PEFO 3885; Murry, 1989, table 1) also only have five ridges. LF-5727 (Fig. 4I) from Homestead bears a striking resemblance to PEFO 3860 (Murry, 1989, fig. 6g-h), while NMMNH P-90530 (Fig. 4S) from L-3380 resembles PEFO 3857 (Murry, 1989, fig. 6c). Based on subsequent work, especially that of Kemp (1998), Cavin et al. (2007), Soto and Perea (2010), Skrzycki (2015), and sources cited therein, we tentatively consider these teeth to also represent a taxon more closely related to *Ptychoceratodus* than *Arganodus*.

## CONCLUSIONS

For decades essentially all lungfish tooth plates recovered from Upper Triassic strata in North America were assigned to *Arganodus*. Detailed examination of specimens from prolific sites, such as Murry's (1989) lungfish locality and the Homestead site fossils documented here indicates that, while the majority of fossil tooth plates from the Upper Triassic of North America can be assigned to *Arganodus*, there is likely at least one additional taxon present, one best considered as cf. *Ptychoceratodus*.

The genus *Ptychoceratodus* has a limited record within North America. A single occurrence of *P. rectangulus* is known from the Upper Triassic Fleming Fjord Formation of east Greenland, a taxon first described from the middle-upper Norian of Germany (Pawlak et al., 2020). *Ptychoceratodus* was abundant during the Late Triassic, occupying an extensive geographic range across Pangea where it inhabited a variety of climatic settings (Skrzycki et al., 2018). Multiple species are known from various localities across the southern Central European Basin, Argentina, Brazil, Madagascar, Turkey, and India (Schultze, 2004; Skrzycki, 2015; Skrzyckiet al., 2018). Occurrences of *Ceratodus guentheri*, a species compared favorably to *Ptychoceratodus* by Martin (1982), are known from the Jurassic Morrison Formation of the U.S.A.

(Milner and Kirkland, 2006; Frederickson and Cifelli, 2017), but was later assigned to the genus *Potamoceratodus* by Pardo et al. (2010). Additionally, some lungfish tooth plates with a "ptychoceratodont" morphology are known from Cretaceous deposits of the western U.S.A. (Frederickson and Cifelli, 2017; Skrzycki et al., 2018). The presence of a ptychoceratodontid within the Chinle Group would help explain the multiple appearances of these ptychoceratodontids in post-Triassic strata of North America. As suggested by Skrzycki et al. (2018), representatives of *Ptychoceratodus* likely expanded westward from Great Britain to reach North America, possibly starting from Greenland, as there was some connection between Europe and North America until the Jurassic.

The geographic range of both *Arganodus* and *Ptychoceratodus* are quite extensive throughout the Mesozoic, occurring across Pangea (Skrzycki et al., 2018; Pawlak et al., 2020). Both genera are known to have coexisted with each other in the Early Triassic of Russia and Australia (Skrzycki et al., 2018). The occurrence of cf. *Ptychoceratodus* in the Upper Triassic Chinle Group would extend the range of the "ptychoceratodont" morphology into the southwest U.S.A., and shows that they coexisted with *Arganodus* in basins that are now on at least three modern continents. Therefore, *Arganodus* would no longer be the solely represented genus within the Late Triassic U.S.A.

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## REFERENCES

Berg, L.S. 1940. Classification of fishes both recent and fossil: Transactions of the Zoological Academy of Sciences, U.S.S.R., v. 5, p. 85–517.

Case, E.C. 1921. A new species of *Ceratodus* from the Upper Triassic of western Texas: Occasional Papers of the Museum of Zoology, v. 101, p. 1–2.

Cavin, L., Suteethorn, V., Buffetaut, E., and Tong, H. 2007. A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution: Zoological Journal of the Linnean Society, v. 149, p. 141–177.

Churcher, C.S., De Iuliis, G., and Kleindienst, M.R. 2006. A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Paleozoic dipnoan evolution: Zoological Journal of the Linnean Society, v. 149, p. 147–177.

Cleveland, D.M., Nordt, L.C., and Atchley, S.C. 2008. Paleosols, trace fossils, and precipitation estimates of the uppermost Triassic strata in northern New Mexico: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 257, no. 4, p. 421–444.

Dubiel, R.F. 1989. Depositional and climatic setting of the Upper Triassic Chinle Formation, Colorado Plateau in Lucas, S.G. and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 171–188.

Dubiel, R.F. 1991. The Pangaean megamonsoon: Evidence from Upper Triassic Chinle Formation, Colorado Plateau: PALAIOS, v. 6, p. 347–370.

Fiorillo, A.R., Padian, K., and Musikasinthorn, C. 2000. Taphonomy and depositional setting of the *Placerias* Quarry (Chinle Formation: Late Triassic, Arizona): PALAIOS, v. 15, no. 5, p. 373–386.

Frederickson, J.A., and Cifelli, R.L. 2017. New Cretaceous lungfishes (Dipnoi, Ceratodontidae) from western North America: Journal of Paleontology, v. 91, no. 1, p. 146–161.

Gibson, S.Z. 2016. Redescription and phylogenetic placement of †*Hemicalypterus weiri* Schaeffer, 1967 (Actinopterygii, Neopterygii) from the Triassic Chinle Formation, southwestern United States: new insights into morphology, ecological niche, and phylogeny: PLOS ONE, v. 11, no. 9, p. e0163657.

Gibson, S.Z. 2018. A new species of *Lasalichthys* (Actinopterygii, Redfieldiiformes) from the Upper Triassic Dockum Group of Howard County, Texas, with revisions to the genera *Lasalichthys* and *Synorichthys*: Journal of Vertebrate Paleontology, p. 1–17.

Heckert, A.B. 1997. The tetrapod fauna of the Upper Triassic lower Chinle Group (Adamanian:latest Carnian), of the Zuni Mountains, west-central New Mexico, in Lucas, S.G., Estep, J.W., Williamson, T.E., and Morgan, G.S., eds., New Mexico's Fossil Record 1.: New Mexico Museum of Natural History and Science Bulletin, v. 11, p. 29–39.

Heckert, A.B. 2004. Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern U.S.A.: New Mexico Museum of Natural History and Science Bulletin, v. 27, p. 1–170.

Heckert, A.B., and Lucas, S.G. 2002. Revised Upper Triassic stratigraphy of the Petrified Forest National Park, Arizona, U.S.A., in Heckert, A.B., and Lucas, S.G., eds., Upper Triassic Stratigraphy and Paleontology: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 1–36.

Heckert, A.B., and Lucas, S.G. 2006. Micro-and small vertebrate biostratigraphy and biochronology of the Upper Triassic Chinle Group, southwestern USA, in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., and Kirkland, J.I., eds., The Triassic-Jurassic Terrestrial Transition: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 94–104.

Heckert, A.B., Crothers, J.P., Rose, L.J., Nesbitt, S.N., Pugh, I., Stocker, M.R., Barrett, P.M., Wills, S., Ward, D., Lauer, B., and Lauer, R. 2023. An exceptionally rich Upper Triassic microvertebrate site from the ?Early Revueltian (mid-Norian) Garita Creek Formation of east-central New Mexico, USA.: The Anatomical Record, v. 306, no. S1, p. 129–131.

Heckert, A.B., Lucas, S.G., and Hunt, A.P. 2005. Triassic vertebrate fossils in Arizona, in Heckert, A.B., and Lucas, S.G., eds., Vertebrate Paleontology in Arizona: New Mexico Museum of Natural History and Science Bulletin, v. 29, p. 16-44.

Heckert, A.B., Mitchell, J.S., Schneider, V.P., and Olsen, P.E. 2012. Diverse new microvertebrate assemblage from the Upper Triassic Cumnock Formation, Sanford Subbasin, North Carolina, USA: Journal of Paleontology, v. 86, no. 2, p. 368–390.

Hégron, A., Stocker, M.R., Marsh, A.D., and Nesbitt, S.J. 2020. Archosauromorphs (Reptilia: Diapsida) from the Lamy Quarry, Garita Creek Formation (Adamanian, Late Triassic), New Mexico, USA: Palaeodiversity, v. 13, no. 1, p. 135–149.

Huber, P., Lucas, S.G., and Hunt, A.P. 1993. Late Triassic fish assemblages of the North American Western Interior and their biochronological significance, in Morales, M., ed., Aspects of Mesozoic Geology and Paleontology of the Colorado Plateau: Museum of Northern Arizona Bulletin, v. 59, p. 51–66.

Hunt, A.P. 1997. A new coelacanth (Osteichthyes: Actinistia) from the continental Upper Triassic of New Mexico, in Lucas, S.G., Estep, J.W., Williamson, T.E., and Morgan, G.S., eds., New Mexico's Fossil Record 1.: New Mexico Museum of Natural History and Science Bulletin, v. 11, p. 25–28.

Hunt, A.P., Lucas, S.G., and Heckert, A.B. 2005. Definition and correlation of the Lamyan: A new biochronological unit for the nonmarine Late Carnian (Late Triassic), in Lucas, S.G., Ziegler, K.E., Lueth, V.W., and Owen, D.E., eds., Geology of the Chama Basin: New Mexico Geological Society Guidebook, 56th Field Conference, p. 357–366.

Hunt, A.P., Lucas, S.G., and Sealey, P.L. 1989. Paleontology and vertebrate biochronology of the Upper Triassic Garita Creek Formation, east-central New Mexico: New Mexico Journal of Science, v. 29, no. 2, p. 61–68.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia: Zoological Society of London, Scientific Memoirs, v. 4, p. 457–472.

Jaekel, O. 1926. Zur Morphogenie der Gebisse und Zähne: Vierteljahrs-schrift Zahnheilkunde, v. 42, p. 217–242.

Johnson, S.C., Lucas, S.G., and Hunt, A.P. 2002. Macro-fish fauna of the Upper Triassic (Apachean) Redonda Formation, eastern New Mexico, in Heckert, A.B., and Lucas, S.G., eds., Upper Triassic Stratigraphy and Paleontology: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 107–114.

Kemp, A. 1996. Triassic lungfish from Gondwana, in Arratia, G., and Viohl, G., eds., Mesozoic Fishes—

Systematics and Paleoecology: München, Verlag Dr. Friedrich Pfeil, p. 409–416.

Kemp, A. 1997. A revision of Australian Mesozoic and Cenozoic lungfish of the family Neoceratodontidae (Osteichthyes: Dipnoi), with a description of four new species: Journal of Paleontology, v. 71, no. 4, p. 713–733.

Kemp, A. 1998. Skull structure in post-Paleozoic lungfish: Journal of Vertebrate Paleontology, v. 18, no, 1, p. 43–63.

Kemp, A. 2002. Unique dentition of lungfish: Microscopy Research and Technique, v. 59, p. 435–448.

Kemp, A. 2005. New insights into ancient environments using dental characters in Australian Cenozoic lungfish: Alcheringa, v. 29, no. 1, p. 123–149.

Kemp, A., Cavin, L., and Guinot, G. 2017. Evolutionary history of lungfishes with a new phylogeny of post-Devonian genera: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 471, p. 209–219.

Kligman, B.T., Parker, W.G., and Marsh, A.D. 2017. First record of *Saurichthys* (Actinopterygii) from the Upper Triassic (Chinle Formation, Norian) of western North America: Journal of Vertebrate Paleontology, v. 37, no. 5, e1367304.

Long, R.A., and Murry, P.A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: New Mexico Museum of Natural History and Science Bulletin, v. 4, p. 1–254.

Long, R.A., Lucas, S.G., Hunt, A.P., and McCrea, R.T. 1989. Charles Camp: Collecting Late Triassic vertebrates in the American Southwest during the 1920’s and 1930’s, in Lucas, S.G., and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 65–71.

Lucas, S.G. 1993. The Chinle Group: Revised stratigraphy and biochronology of the Upper Triassic nonmarine strata in the western United States, in Morales, M., ed., Aspects of Mesozoic Geology and Paleontology of the Colorado Plateau: Museum of Northern Arizona Bulletin, v. 59, p. 27–50.

Lucas, S.G. 2004. The Triassic and Jurassic systems in New Mexico, in Mack, G.H., and Giles, K.A., eds., The Geology of New Mexico: A Geologic History: Socorro, New Mexico Geological Society, p. 137–152.

Lucas, S.G. and Hunt, A.P. 1989. Revised stratigraphy in the Tucumcari basin, east-central New Mexico, in Lucas, S.G. and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 150–170.

Lucas, S.G., Heckert, A.B., and Hunt, A.P. 2001. Triassic stratigraphy, biostratigraphy and correlation in east-central New Mexico, in Lucas, S.G. and Ulmer-Scholle, D., eds., Geology of the Llano Estacado: New Mexico Geological Society Guidebook, 52nd Field Conference, p. 85–102.

Lucas, S.G., Rinehart, L. F., Krainer, K., Spielmann, J. A., and Heckert, A. B. 2010. Taphonomy of the Lamy amphibian quarry: A Late Triassic bonebed in New Mexico, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 298, p. 388–398.

Marsh, A.D., and Parker, W.G. 2020. New dinosauromorph specimens from

Petrified Forest National Park and a global biostratigraphic review of Triassic dinosauromorph body fossils: PaleoBios, v. 37, p. 1–56.

Martin, M. 1979. *Arganodus atlantis* et *Ceratodus arganensis*, deux nouveaux Dipneustes du Trias supérieur continental marocain: Comptes Rendus de l'Académie des Sciences à Paris, Série D, v. 289, p. 89–92.

Martin, M. 1982. Nouvelles données sur la phylogénie et la systématique des Dipneustes postpaléozoiques, conséquences stratigraphiques et paléogéographiques: Geobios, mémoire spécial, v. 6, p. 53–64.

Martin, M., Sigogneau-Russel, D., Coupatez, P., and Wouters, G. 1981. Les Cératodontidés (Dipnoi) du Rhétien de Saint-Nicolas-de-Port (Meurthe-et-Moselle): Geobios, v. 14, no. 6, p. 773–791.

Martz, J.W., and Parker, W.G. 2010. Revised lithostratigraphy of the Sonsela Member (Chinle Formation, Upper Triassic) in the southern part of Petrified Forest National Park, Arizona: PLOS ONE, v. 5, no. 2, e9329.

Martz, J.W., and Parker, W.G. 2017. Revised formulation of the Late Triassic land vertebrate "faunachrons" of western North America: Recommendations for codifying nascent systems of vertebrate biochronology, in Zeigler, K.E., and Parker W.G., eds., Terrestrial Depositional Systems: Deciphering Complexities Through Multiple Stratigraphic Methods: Elsevier Science, p. 39–125.

Martz, J.W., Kirkland, J.I, Milner, A.R.C., Parker, W.G., and Santucci, V.L. 2017. Upper Triassic lithostratigraphy, depositional systems, and vertebrate paleontology across southern Utah: Geology of the Intermountain West, v. 4, p. 99–180.

Martz, J.W., Mueller, B., and Nesbitt, S.J. 2012. A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 103, no. 3-4, p. 339–364.

Milner, A.R.C., and Kirkland, J.I. 2006. Preliminary review of the Early Jurassic (Hettangian) freshwater Lake Dixie fish fauna in the Whitmore Point Member, Moenave Formation in southwest Utah, in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., and Kirkland, J.I., eds., The Triassic-Jurassic Terrestrial Transition: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 510–521.

Milner, A.R.C., Kirkland, J.I., and Birthisel, T.A. 2006. The geographic distribution and biostratigraphy of Late Triassic-Early Jurassic freshwater fish faunas of the southwestern United States, in Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., and Kirkland, J.I., eds., The Triassic-Jurassic Terrestrial Transition: New Mexico Museum of Natural History and Science Bulletin, v. 37, p. 522–529.

Müller, J. 1844. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. Abhandlungen der Akademie des Wissenschaften, Physische-Mathematische Klasse, v. 11, p. 119–216.

Murry, P.A. 1986. Vertebrate paleontology of the Dockum Group, western Texas and eastern New Mexico, in Padian, K., ed., The Beginning of the Age of the Dinosaurs: Faunal Change

Across the Triassic-Jurassic Boundary: Cambridge, Cambridge University Press, p. 109–138.

Murry, P.A. 1989. Microvertebrate fossils from the Petrified Forest and Owl Rock Members (Chinle Formation) in Petrified Forest National Park and vicinity, Arizona, in Lucas, S.G and Hunt, A.P., eds., Dawn of the Age of Dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 249–277.

Murry, P.A., and Kirby, R.E. 2002. A new hybodont shark from the Chinle and Bull Canyon Formations, Arizona, Utah and New Mexico, in Heckert, A.B., and Lucas, S.G., eds., Upper Triassic Stratigraphy and Paleontology: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 87–106.

Nesbitt, S.J., Irmis, R.B., and Parker, W.G. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America: Journal of Systematic Palaeontology, v. 5, no. 2, p. 209–243.

Ouyang, W. 2024. Imjoy-team/imagej.js: ImageJ.JS, Version 0.5.7: Zenodo, https://ij.imjoy.io/., doi://10.5281/zenodo.4944985.

Pardo, J.D., Huttenlocker, A.K., Small, B.J., and Gorman II, M.A. 2010. The cranial morphology of a new genus of lungfish (Osteichthyes: Dipnoi) from the Upper Jurassic Morrison Formation of North America: Journal of Paleontology, v. 30, no. 5, p. 1352–1359.

Parker, W.G. 2006. The stratigraphic distribution of major fossil localities in Petrified Forest National Park, Arizona, in Parker, W.G., Ash, S.R., and Irmis, R.B., eds., A Century of Research at Petrified Forest National Park: Museum of Northern Arizona Bulletin, v. 62, p. 46–61.

Parker, W.G., and Martz, J.W. 2011. The Late Triassic (Norian) Adamanian-Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 101, no. 3-4, p. 231–260.

Parrish, J.M., and Good, S.C. 1987. Preliminary report on vertebrate and invertebrate fossil occurrences, Chinle Formation (Upper Triassic), southeastern Utah: Four Corners Geological Society, v. 10, p. 109–118.

Parrish, J.M. 1999. Small fossil vertebrates from the Chinle Formation (Upper Triassic) of southern Utah, in Gillette, D.D., ed.,Vertebrate Paleontology in Utah: Miscellaneous Publication 99-1, Utah Geological Survey, p. 45–50.

Pawlak, W., Tałanda, M., Sulej, T., and Niedźwiedzki, G. 2020. Dipnoan from the Upper Triassic of East Greenland and remarks about palaeobiogeography of *Ptychoceratodus*: Acta Palaeontologica Polonica, v. 65, no. 3, p. 561–574.

Polcyn, M.J., Winkler, D.A., Jacobs, L.L., and Newman, K. 2002. Fossil occurrences and structural disturbance in the Triassic Chinle Formation at North Stinking Springs Mountain near St. Johns, Arizona, in Heckert, A.B., and Lucas, S.G., eds., Upper Triassic stratigraphy and paleontology: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 43–50.

Pritchard, A.C., Turner, A.H., Nesbitt, S.J., Irmis, R.B., and Smith, N.D. 2015. Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae:

Journal of Vertebrate Paleontology, v. 35, no. 2, e911186.

Riggs, N.R., Lehman, T.M., Gehrels, G.E., and Dickinson, W.R. 1996. Detrital zircon link between headwaters and terminus of the Upper Triassic Chinle-Dockum paleoriver system: Science, v. 273, p. 97–100.

Romer, A.S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii: Nature, v. 176, p. 126.

Schaeffer, B. 1967. Late Triassic fishes from the western United States: Bulletin of the American Museum of Natural History, v. 135, p. 287–342.

Schultze, H. 2004. Mesozoic sarcopterygians, in Arratia, G., and Tintori, A., eds., Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity: München, Verlag Dr. Friedrich Pfeil, p. 463–492.

Skrzycki, P. 2015. New species of lungfish (Sarcopterygii, Dipnoi) from the Late Triassic Krasiejów site in Poland, with remarks on the ontogeny of Triassic dipnoan tooth plates: Journal of Vertebrate Paleontology, v. 35, no. 5, e964357.

Skrzycki, P., Niedźwiedzki, G., and Tałanda, M. 2018. Dipnoan remains from the Lower-Middle Triassic of the Holy Cross Mountains and northeastern Poland, with remarks on dipnoan palaeobiogeography: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 496, p. 332–345.

Soto, M., and Perea, D. 2010. Late Jurassic lungfishes (Dipnoi) from Uruguay, with comments on the systematics of Gondwanan Ceratodontiformes: Journal of Vertebrate Paleontology, v. 30, no. 4, p. 1049–1058.

Stewart, J.H., Poole, F.G., and Wilson, R.F. 1972. Stratigraphy and origin of the Chinle Formation and related Upper Triassic strata in the Colorado Plateau region: U.S. Geological Survey Professional Paper, v. 690, p. 1–336.

Therrien, F., and Fastovsky, D.E. 2000. Paleoenvironments of early theropods, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona: PALAIOS, v. 15, no. 3, p. 194–211.

Voris, J.T., and 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, v. 37, no. 4, e1351980.

Vorob'yeva, E.I., and Minikh., M.G. 1968. An attempt at a biometrical study of the tooth plates of ceratodontids: Paleontological Journal, v. 2, p. 76–87.

Warthin Jr., A.S. 1928. Fossil fishes from the Triassic of Texas: Contributions from the Museum of Paleontology, v. 3, no. 2, pp. 15–18.

Woody, D.T. 2006. Revised stratigraphy of the Lower Chinle Formation (Upper Triassic) of Petrified Forest National Park, Arizona, in Parker, W.G., Ash, S.R., and Irmis, R.B., eds., A Century of Research at Petrified Forest National Park: Museum of Northern Arizona Bulletin, v. 62, p. 17–45.

Zeigler, K.E., Heckert, A.B., and Lucas, S.G. 2002. A tale of two sites: a taphonomic comparison of two Late Triassic (Chinle Group) vertebrate fossil localities from New Mexico, in Heckert, A.B., and Lucas, S.G., eds., Upper Triassic Stratigraphy and Paleontology: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 285–290.

APPENDIX 1. Details of the new lungfish tooth plates described and illustrated in this paper.

| Fig. 4 | Catalog Number | Locality | Proposed Identification | Position | Ridge Count | Length (mm) | Width (mm) |
|---|---|---|---|---|---|---|---|
| A | LF 5720 | Homestead | *Arganodus* sp. | Left Palatal | 7 | 8.500 | 4.711 |
| B | LF 5721 | Homestead | *Arganodus sp.* | Left Palatal | 7? | 16.923 | 10.022 |
| C | LF 5722 | Homestead | *Arganodus sp.* | Left Splenial | 7 | 14.183 | 7.763 |
| D | LF 5723 | Homestead | *Arganodus sp.* | Right Palatal | 6 | 20.078 | 10.078 |
| E | LF 5724 | Homestead | *Arganodus* sp. | Left Palatal | 7 | 16.712 | 7.591 |
| F | LF 5725 | Homestead | *Arganodus sp.* | Right Palatal | 7 | 23.081 | 13.390 |
| G | LF 5726 | Homestead | *Arganodus sp.* | Right Palatal | 8 | 17.321 | 11.116 |
| H | LF 6272 | Homestead | *Arganodus* sp. | Right Splenial | 7 | 14.000 | 8.609 |
| I | LF 5727 | Homestead | cf. *Ptychoceratodus*? | Left Splenial? | 5? | 12.519 | 9.022 |
| J | LF 5728 | Homestead | cf. *Ptychoceratodus*? | Left Palatal? | 6 | 6.064 | 3.490 |
| K | LF 5729 | Homestead | cf. *Ptychoceratodus*? | Left Palatal? | 6 | 5.395 | 2.952 |
| L | LF 5730 | Homestead | cf. *Ptychoceratodus* | Left Splenial | 4 | 2.407 | 1.790 |
| M | LF 5731 | Homestead | cf. *Ptychoceratodus* | Left Palatal | 5 | 3.613 | 2.613 |
| N | LF 5732 | Homestead | cf. *Ptychoceratodus* | Left Palatal | 5 | 3.026 | 1.932 |
| O | LF 5733 | Homestead | cf. *Ptychoceratodus* | Left Palatal | 5 | 2.826 | 2.132 |
| P | LF 5734 | Homestead | cf. *Ptychoceratodus* | Right Splenial? | 5 | 2.224 | 1.814 |
| Q | LF 5735 | Homestead | cf. *Ptychoceratodus* | Left Palatal? | 5? | 5.374 | 3.490 |
| R | LF 6273 | Homestead | cf. *Ptychoceratodus?* | Right Splenial | 6 | 11.109 | 6.932 |
| S | NMMNH P-90530 | NMMNH L-3380 | *Arganodus* sp. | Right Palatal | 7 | 16.361 | 9.490 |

APPENDIX 1. (*continued*)

| Fig. 4 | Catalog Number | Locality | Proposed Identification | Position | Ridge Count | Length (mm) | Width (mm) |
|---|---|---|---|---|---|---|---|
| T | NMMNH P-90531 | NMMNH L-3380 | *Arganodus* sp. | Right Splenial | 6 | 16.674 | 10.204 |
| U | NMMNH P-90532 | NMMNH L-6818 | *Arganodus* sp. | Left Splenial | 7 | 12.928 | 7.026 |
| V | NMMNH P-90533 | NMMNH L-6818 | *Arganodus* sp. | Right Palatal | 6 | 13.472 | 6.349 |
| W | NMMNH P-90534 | NMMNH L-6818 | *Arganodus* sp. | Left Splenial | 6 | 12.790 | 8.125 |
| X | UCM-76502-A | UCM-97074 | *Arganodus* sp. | Left Splenial | 6 | 15.601 | 9.249 |
| Y | UCM-76502-B | UCM-97074 | *Arganodus* sp. | Left Splenial | 7 | 13.308 | 9.307 |
| Z | UCM-76502-C | UCM-97074 | *Arganodus* sp. | Left Splenial | 6 | 16.319 | 9.234 |

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