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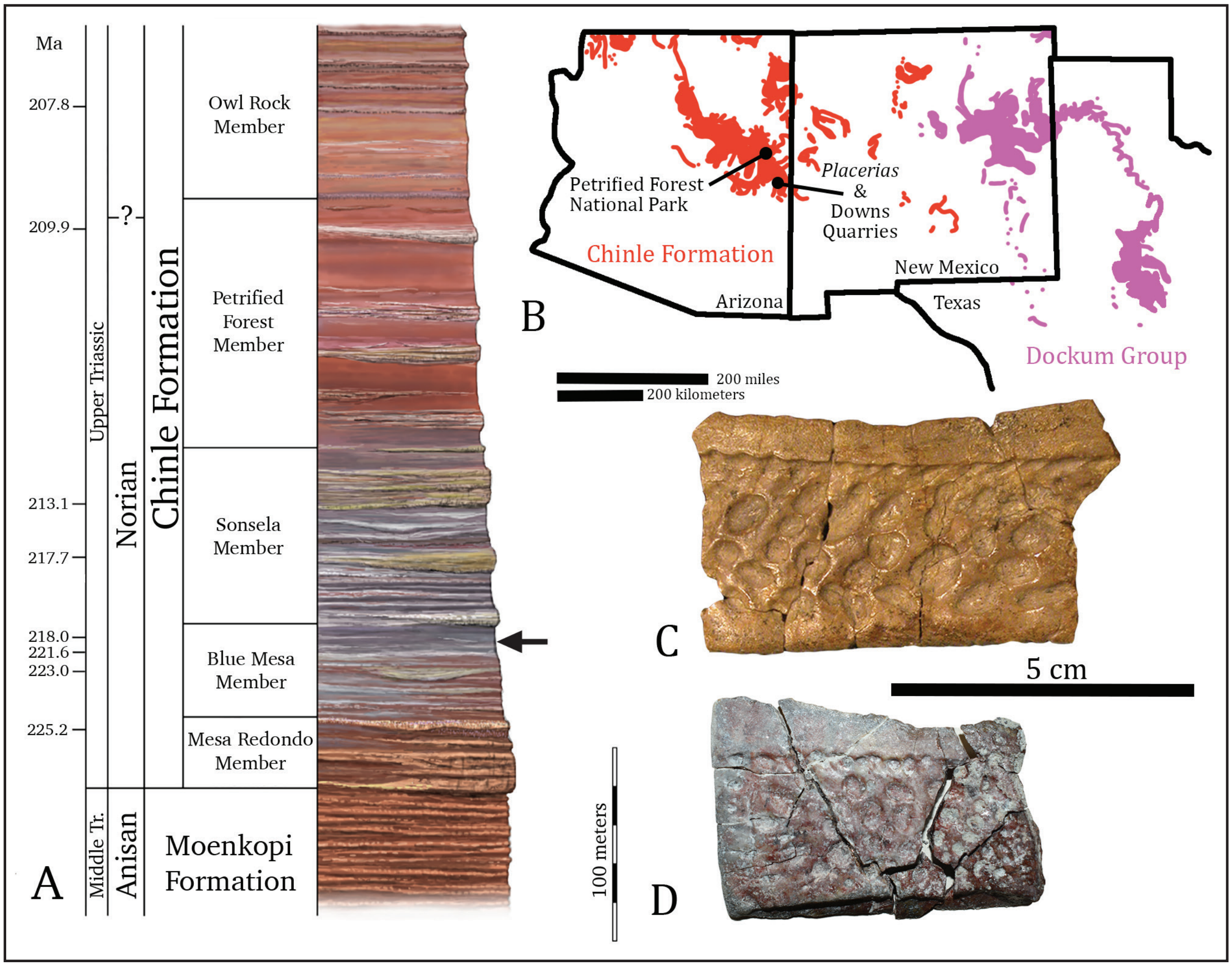

William A. REYES, William G. PARKER & Andrew B. HECKERT (2023). A new aetosaur (Archosauria: Pseudosuchia) from the upper Blue Mesa Member (Adamanian: Early–Mid Norian) of the Late Triassic Chinle Formation, northern Arizona, USA, and a review of the paratypothoracin *Tecovasuchus* across the southwestern USA.

Cover: Stratigraphic (**A**) and geographic occurrences (**B**) of the new typothoracine *Kryphioparma caerula* gen. et sp. nov. (**C**) and first unambiguous documentation of *Tecovosauchus chatterjeei* (**D**) within the Late Triassic Chinle Formation in northern Arizona.

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A new aetosaur (Archosauria: Pseudosuchia) from the upper Blue Mesa Member (Adamanian: Early–Mid Norian) of the Late Triassic Chinle Formation, northern Arizona, USA, and a review of the paratypothoracin *Tecovasuchus* across the southwestern USA

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The Late Triassic Chinle Formation in northern Arizona and Dockum Group in northwestern Texas preserve a high aetosaur biodiversity within the Adamanian teilzone, including *Desmatosuchus spurensis*, *Desmatosuchus smalli*, *Calyptosuchus wellesi*, *Adamanasuchus eisenhardtae*, *Typothorax coccinarum*, *Paratypothorax* sp., *Tecovasuchus chatterjeei*, and *Sierritasuchus macalpini*. Here, we present a new aetosaur *Kryphioparma caerula* gen. et sp. nov. from the upper Blue Mesa Member of the Chinle Formation, Adamanian teilzone, in northern Arizona. *Kryphioparma caerula* sp. nov. is documented based on several isolated osteoderms collected from the *Placerias* Quarry and Petrified Forest National Park. Although fragmentary, it is evident that the paramedian osteoderms of *Kr. caerula* exhibit a dorsal ornamentation composed of large, randomly oriented oblong pits; a low concentration of pits relative to available surface area; well-developed anterior bar; a probable high width-to-length ratio; dorsoventrally thickened; well-developed ventral strut; and grooves along the posterior margin. This suite of morphological characters indicates that *Kr. caerula* is a typothoracine similar to *Ty. coccinarum*, *Te. chatterjeei*, and *P. andressorum*; its stratigraphic occurrence within the upper Blue Mesa Member makes it the oldest documented typothoracine to date. The documentation of *Kr. caerula* within the *Placerias* Quarry brings to question the taxonomic affinities of paratypothoracin material identified as "*Tecovasuchus*" by previous authors, as well as the biostratigraphic utility of *Te. chatterjeei* across the southwestern United States. We present the first unambiguous material referable to *Te. chatterjeei* from the Downs Quarry and Petrified Forest National Park. The documentation of *Te. chatterjeei* in the Chinle Formation of northern Arizona and Tecovas Formation of northwestern Texas suggests that this taxon may be biostratigraphically informative as it is currently constrained to strata within the Adamanian teilzone similar to *Desmatosuchus* and *Ca. wellesi*.

Keywords: Aetosauria, Chinle Formation, Triassic, *Placerias* Quarry

INTRODUCTION

The Aetosauria Marsh (1884) is a clade of heavily armored pseudosuchian tetrapods that is currently constrained to strata of Late Triassic age (Carnian-Rheatian, ~237–201 Ma; Heckert and Lucas 2000, Desojo et al. 2013, Parker 2016a). Aetosaurs have been reported from continental strata across the globe including Europe, India, Africa, and North and South America (Desojo et al. 2013). Historically, our evolutionary understanding of the Aetosauria was predominantly based on their osteoderms (e.g., Long and Ballew 1985, Long and Murry 1995, Heckert and Lucas 1999, Parker 2007). This is partially a result of their osteoderms being some of the most commonly collected fossilized elements recovered from Late Triassic strata. Osteoderms are integumental ossifications that are independent of the main skeletal system, allowing them to become easily dispersed during the taphonomic process, particularly in fluvial systems

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(Desojo et al. 2013, Scheyer et al. 2014). However, in the last two decades, the discovery of relatively complete skeletons and skulls for a variety of aetosaurian taxa provided a means of more holistically assessing interspecific variation within the clade (e.g., Heckert and Lucas 1999, Heckert et al. 2010, Taborda et al. 2015, Parker 2016a, Schoch and Desojo 2016, Reyes et al. 2020, Paes-Neto et al. 2021a). Currently, the Aetosauria includes 28 taxa, with 21 genera being monospecific (Parker 2016a); however, recent studies (Parker and Martz 2011, Taborda et al. 2015, Schoch and Desojo, 2016; Hoffman et al. 2019, Paes-Neto et al. 2021b) have brought to question the taxonomic status of taxa documented from skeletally immature individuals (e.g., *Typothorax antiquum* Lucas et al., 2002; *Aetosaurus ferratus* Fraas, 1877; *Polesinesuchus aurelioi* Roberto-Da-Silva et al., 2014), suggesting that they may be skeletally immature individuals of other recognized species. Of these, 18 recognized species (~65%) are known exclusively from the Late Triassic strata of the United States (US) particularly from the Late Triassic Chinle Formation and Dockum Group in the southwest (Desojo et al. 2013); these two stratigraphic units are widely accepted to have been deposited during the Norian and Rhaetian epochs; however, the base of the Dockum Group might be Carnian in age (Lucas 1998, Stocker 2013).

The upper Blue Mesa–lower Sonsela Members of the Chinle Formation (Parker and Martz 2011, Martz et al. 2012), and the Tecovas–Trujillo Formations (=lower and middle Cooper Canyon Formation; Lehman et al. 1992, Martz 2008, Martz et al. 2013) of the Dockum Group, preserve the highest aetosaur diversity (Desojo et al. 2013). The *Placerias* Quarry and adjacent Downs Quarry (Camp and Welles 1956, Jacobs and Murry 1980, Kaye and Padian 1994, Long and Murry 1995, Lucas et al. 1997, Parker 2018, Heckert et al. 2021), have long been considered one the most taxonomically diverse localities of the Chinle Formation; the four documented aetosaur taxa from the quarry complex are *Desmatosuchus spurensis* Case (1920), *Desmatosuchus smalli* Small (2002), *Calyptosuchus wellesi* Long and Ballew (1985), and an ambiguous paratypothoracin that was tentatively referred to the genus "*Tecovasuchus*" Martz and Small (2006) (Long and Murry 1995, Parker 2005, Heckert et al. 2007, Parker 2018, von Baczko et al. 2021). Recent paleontological fieldwork at Petrified Forest National Park (PEFO) in Arizona led to the discovery of the Thunderstorm Ridge locality (PFV 456), a site that preserves a taxonomic diversity on par with that of the *Placerias*-Downs quarry complex (Kligman et al. 2018, 2020, 2023, Jenkins et al. 2020, Marsh and Parker 2020, Marsh et al. 2020). The Thunderstorm Ridge locality preserves osteoderms referrable to *Desmatosuchus*, *Ca. wellesi*, *Tecovasuchus chatterjeei*, and *Kryphioparma caerula* gen et sp. nov, a new taxon with typothoracine taxonomic affinities. In this contribution we describe osteoderms referrable to *Kr. caerula* from both the *Placerias* Quarry and Thunderstorm Ridge locality, including a reassessment of the ambiguous paratypothoracin material referred to "*Tecovasuchus*" and how this impacts the proposed biostratigraphical utility of *Te. chatterjeei* in the southwestern US (Heckert et al. 2007).

MATERIALS AND METHODS

Geological setting

The Thunderstorm Ridge locality (PFV 456) is located within the upper Blue Mesa Member of the Chinle Formation in PEFO, Arizona, USA (Fig. 1). The upper Blue Mesa Member was deposited ~223–218 Ma (Ramezani et al. 2014, Kent et al. 2019, Rasmussen et al. 2020) by a northwest-flowing fluviolacustrine system on the western margin of sub-equatorial central Pangea at a paleolatitude of 5°–15°N in a humid monsoonal climate (Dubiel et al. 1991, Dubiel and Hasiotis 2011, Martz et al. 2012, Atchley et al. 2013, Trendell et al. 2013). The temporal bounds of the upper Blue Mesa Member place the Thunderstorm Ridge locality within the Adamanian estimated holochronozone (Martz and Parker 2017; Fig. 1). The fossiliferous horizon is a 15 cm-thick, poorly-sorted siltstone, with a dense concentration of coprolites, carbonate nodules, angular intraformational clasts, both micro- and macrovertebrate fossilized remains, as well as invertebrate *steinkerns* and impressions (Kligman et al. 2023). The vertebrate remains are three-dimensionally preserved with external surfaces lacking evidence of abrasion, indicating that these elements were initially deposited in a low-energy setting. The well-mixed and disarticulated nature of the bones are a result of an avulsion event that also introduced the angular intraformational clasts and carbonate nodules into the layer. The sedimentology and fauna preserved within the fossiliferous horizon indicate deposition along a marginal lacustrine paleoenvironment (Kligman et al. 2018, 2020, 2023, Jenkins et al. 2020).

The *Placerias* Quarry (loc. nos. UCMP A269 and MNA 207-1) is located within the Late Triassic strata of the Chinle Formation southwest of the city of St. Johns in northern Arizona (Camp and Welles 1956). The outcrops in this area are poorly exposed which limits lithostratigraphic correlation to the better exposed strata of the

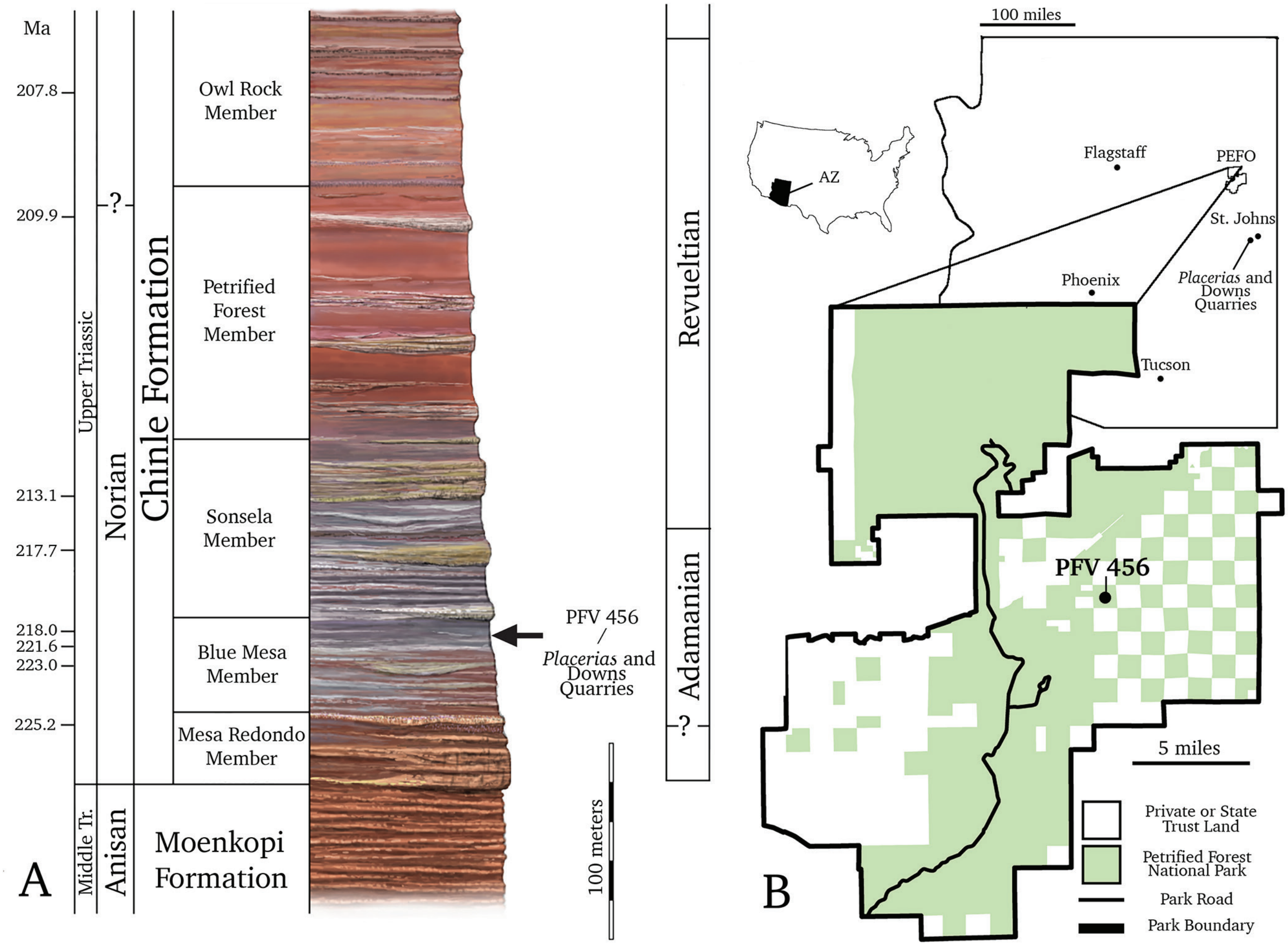

Figure 1. Stratigraphic position in the Chinle Formation (**A**) of PFV 456 and the Placerias and Downs Quarries in Arizona (modified from Reyes et al. 2020 and Kligman et al. 2023), and their geographic occurrence (**B**). U-Pb ages based on Ramezani et al. (2014) and Rasmussen et al. (2020). **Abbreviations**: **AZ**=Arizona; **PEFO**=Petrified Forest National Park; **Tr.**=Triassic.

Chinle Formation within PEFO (Lucas et al. 1997, Fiorillo et al. 2000, Heckert et al. 2021). However, U-Pb detrital zircon geochronology indicates an early-Norian maximum depositional age of 219.39±0.16 Ma for the *Placerias* Quarry within the Adamanian estimated holochronozone (Ramezani et al. 2014, Martz and Parker 2017). Previous studies correlated the *Placerias* Quarry to the lower Sonsela Member (Martz et al. 2012, Atchley et al. 2013, Marsh et al. 2019), however the new temporal constraints of the Chinle Formation at PEFO (Rasmussen et al. 2020) indicate that the *Placerias* Quarry is age-equivalent (or chronostratigraphically correlative) to the upper Blue Mesa Member similar to the Thunderstorm Ridge locality (Kligman et al. 2023; Fig. 1). This is supported by lithostratigraphic correlations with the nearby Salado Site (Ramezani et al. 2014, Parker 2018) which has good exposures of the Mesa Redondo, Blue Mesa, and lower Sonsela Members in clear superposition (Parker 2018). The Salado Site lies in the upper Blue Mesa Member strata and includes a vertebrate assemblage and lithology similar to the *Placerias* Quarry and proximity allows for good correlation between the two sites (Ramezani et al. 2014, Parker unpublished data). Strata above the *Placerias*/Downs quarries at the site are a sequence of sandstones with petrified wood and extrabasinal chert clasts very similar to the lower Sonsela at PEFO further supporting this correlation (Parker unpublished data).

The Downs Quarry itself is characterized by two distinct fossiliferous intervals, and the deeper of the two produced most of the specimens collected from the *Placerias* Quarry (Camp and Welles 1956, Jacobs and

Murry 1980). The Downs Quarry (loc. MNA 207-2) is located ~30 m east of the *Placerias* Quarry and in a slightly higher stratigraphic position, but also preserves a similar faunal assemblage (Jacobs and Murry 1980, Kaye and Padian 1994, Long and Murry 1995, Lucas et al. 1997, Parker 2005, Heckert et al. 2005, 2021). The *Placerias*/Downs quarries are both situated in a claystone lens with abundant carbonate nodules that are consistent with pedogenically modified fluvial sediments associated to seasonal variations in the water table during periods of aridity (Fiorillo et al. 2000).

Collection and preparation

Specimens UCMP 165173 (Fig. 2A–F) and UCMP 126847 (Fig. 2G–L) were both collected from the *Placerias* Quarry (UCMP A269). However, we are unable to ascertain if both specimens were collected from the same quadrant in the grid system presented by Camp and Welles (1956) because only UCMP 165173 has a field number (no. C63M) associated with it; we speculate that these elements were both collected from the deeper of the two fossiliferous horizons because that level is characterized by a high abundance of isolated osteoderms (Camp and Welles 1956, Jacobs and Murry 1980). Specimens PEFO 51662 (Fig. 2M–R) and PEFO 46468 (Fig. 2S–X) were collected from the Thunderstorm Ridge locality. Those elements were preserved within the fossiliferous coprolite facies (described above). Butvar B-72 was used to stabilize and consolidate the elements in the field prior to collecting them in sediment blocks using a variety of hand tools. The osteoderm fragments were removed from the sediment block using a combination of air scribes, pin vices, acetone, and water under microscopic magnification. The remainder of the sediment blocks were later screen washed for microvertebrates. The fragmentary osteoderms of *Kryphioparma caerula* (Fig. 2) housed at the UCMP and PEFO were photographed using a Nikon D3500 DSR camera with a 20–70mm wide angle lens.

Institutional abbreviations

MNA, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **PEFO**, Petrified Forest National Park, Arizona, U.S.A. (**PFV** refers to a locality number from PEFO); **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TTU-P**, Museum of Texas Tech University of Paleontology, Lubbock, Texas, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869,
sensu Gauthier & Padian, 1985
PSEUDOSUCHIA Zittel, 1887–1890,
sensu Gauthier & Padian, 1985
AETOSAURIA Marsh, 1884, *sensu* Parker, 2007
STAGONOLEPIDIDEA Lydekker, 1887, *sensu* Parker, 2007
AETOSAURINAE Marsh, 1884,
sensu Heckert & Lucas, 2000
TYPOTHORACINAE von Huene, 1915, *sensu* Parker, 2016a
KRYPHIOPARMA gen. nov.
Figs. 2–4

ZooBank LSID—urn:lsid:zoobank.org:act:51CE8FC2-F613-4306-B4BD-1CECFE2D2570.

Diagnosis—Paramedian osteoderms exhibit dorsal ornamentation composed of large, randomly oriented oblong pits; low concentration of pits relative to available surface area (unlike *Typothorax* and *Redondasuchus*); well-developed anterior bar (shared with *Tecovasuchus*, *Calyptosuchus*, but unlike *Desmatosuchus*); dorsoventrally thickened (shared with *Tecovasuchus*, but unlike *Paratypothorax*); well-developed ventral strut (shared with typothoracines, but not stagonolepidoids); grooves along the posterior margin (shared with *Tecovasuchus* and *Paratypothorax*); a probable high width-to-length ratio (shared with typothoracines, and *Coahomasuchus*, but not stagonolepidoids).

Etymology—*Kryphioparma*, Greek for “kryphoides”, meaning mysterious, and “parma”, for small, round shield. The genus name highlights both the limited information known for the taxon and the carapace that characterizes the Aetosauria.

KRYPHIOPARMA CAERULA sp. nov.
Figs. 2–4

Zoobank LSID—urn:lsid:zoobank.org:act:DD0FED1D-C878-47DE-AC90-F5897B8305C9.

Diagnosis—Same as for genus.

Etymology—*caerula*, Latin for “cearulus”, meaning blue, after the Blue Mesa Member of the Chinle Formation. The stratigraphic member in which the type specimens were collected from.

Holotype—UCMP 165173 (Fig. 2A–F), incomplete right paramedian osteoderm.

Paratype—UCMP 126847 (Fig. 2G–L), medial fragment of left paramedian osteoderm.

Referred specimens—PEFO 51662 (Fig. 2M–R) and

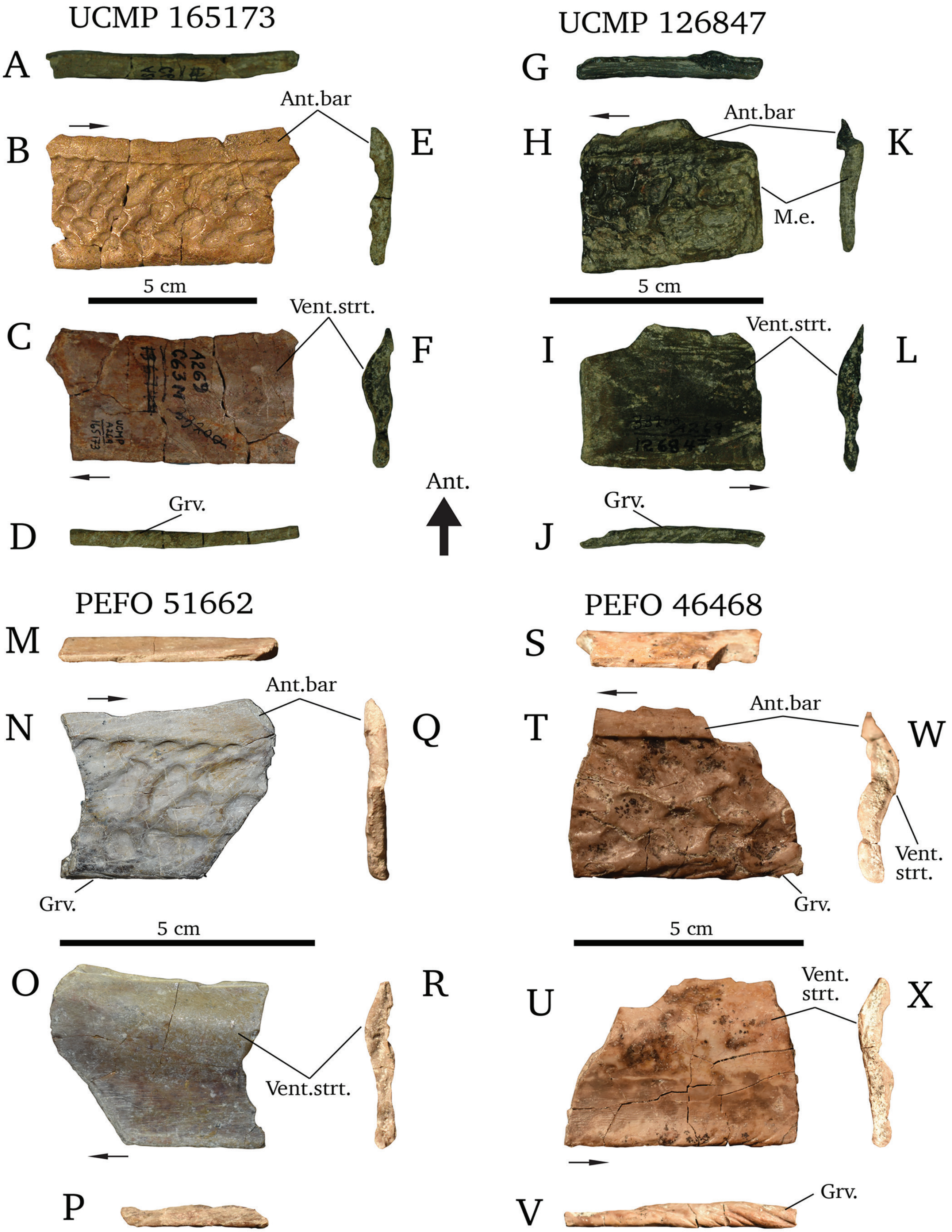

Figure 2. Caption on page 6.

Figure 2. Paramedian osteoderm fragments of *Kryphioparma caerula* gen. et sp. nov. Holotype and paratype specimens collected from the *Placerias* Quarry, UCMP 165173 (**A–F**) and UCMP 126847 (**G–L**), respectively. Referred specimens collected from PFV 456, PEFO 51662 (**M–R**) and PEFO 46468 (**S–X**). Orientations: anterior (**A, G, M, S**), dorsal (**B, H, N, T**), ventral (**C, I, O, U**), posterior (**D, J, P, V**), medial cross-section (**F, K, R, W**), and lateral cross-section (**E, L, Q, X**) views. **Abbreviations: Ant**.=Anterior, **Ant. bar**=Anterior bar, **Grv.**=Grooves, **M.e.**=Medial edge, **Vent. strt.**=Ventral strut. Small, unlabeled arrows indicate lateral direction.

PEFO 46468 (Fig. 2S–X) fragmentary paramedian osteoderms.

Type locality—UCMP A269, *Placerias* Quarry (Camp and Welles 1956; Fig. 1).

Referred locality—PFV 456, Thunderstorm Ridge locality (Kligman et al. 2023; Fig. 1).

Age—Late Triassic, early-mid Norian, U-Pb detrital zircon maximum depositional age constraint ~223-218 Ma for the upper Blue Mesa Member, Chinle Formation (Ramezani et al. 2014, Rasmussen et al. 2020; Fig. 1); Adamanian estimated holochronozone (Martz and Parker 2017).

Stratigraphic Occurrence—Chinle Formation, upper Blue Mesa Member (Martz et al. 2012, Ramezani et al. 2014, Kligman et al. 2023; Fig. 1).

Description and remarks—The osteoderm fragments presented here for *Kryphioparma caerula* sp. nov. (Fig. 2) lack the flexure associated with lateral osteoderms (Parker 2007, 2016a). They are also not reminiscent of ventral osteoderms because they are not square-shaped like those observed in the trunk region of *Coahomasuchus chathamensis* Heckert et al. (2017) and *Typothorax coccinarum* Cope (1875) (Martz 2002, Heckert et al. 2010) nor are they elongate and flexed like those observed in the caudal region of *Coahomasuchus kahleorum* Heckert and Lucas (1999) and *Calyptosuchus wellesi* Case (1932) (Long and Ballew 1985, Long and Murry 1995). Thus, their quadrangular appearance indicates that they are fragments of dorsal paramedian osteoderms (Fig. 2B, C, H, I, N, O, T, U).

Because of the relatively complete preservation of the dorsal carapace for various aetosaurian taxa including *Co. chathamensis*, *Co. kahleorum*, *Ty. coccinarum*, *Desmatosuchus spurensis*, *Desmatosuchus smalli*, *Ca. wellesi*, *Aetosauroides scagliai* Casamiquela (1960), *Aetosaurus ferratus*, and *Paratypothorax andressorum* Long and Ballew (1985), we can deduce the regional position (i.e., cervical, trunk, sacral, caudal) from which these paramedian fragments are most likely derived (following discussion in Parker 2007, Parker and Martz 2010). The general morphology of the osteoderm fragments of *Kr. caerula* indicate that the paramedian osteoderms were flat and rectangular. Thus, they lack the dorsal anterolateral curvature characteristic of paramedian osteoderms from the cervical and anterior-most trunk region (Parker 2007) seen in other typothoracines, differing from the un-curved anterior paramedians of *Co. kahleorum* (NMMNH P-18496, Heckert and Lucas 1999) and *Aetosaurus ferratus* (SMNS 5770, Schoch 2007). The fragments lack evidence of mediolateral flexure (Fig. 2D, J, P, V), such flexure is a characteristic morphology of paramedian osteoderms from the cervical and most of the caudal region in aetosaurs (e.g., *Ca. wellesi*, UMMP 13950, Parker 2018), so we can reject their referral to these regions of the dorsal carapace. We hypothesize that the paramedian osteoderm fragments of *Kr. caerula* are most likely derived from the trunk region due to the large portion of the carapace the trunk composes; alternatively, these fragments may also be derived from the sacral and / or anterior-most caudal regions. The dorsal paramedian osteoderms across these regions are subject to morphological variation in their flexure, orientation of the dorsal process, presence of beveling along the posterior edge, and development of the dorsal eminence; that variation is best observed in aetosaurs that preserve a well-articulated carapace such as *Ty. coccinarum* (NMMNH P-56299, Martz 2002, Heckert et al. 2010), *Ca. wellesi* (Case 1932, Long and Ballew 1985, Parker 2018), and *Co. kahleorum* (Heckert and Lucas 1999). Some features stay consistent, most notably the dorsal ornamentation (Parker 2016a, Reyes personal observation). However, recent studies focused on the intraspecific variation of paramedian osteoderms indicate that the dorsal ornamentation can vary in its complexity (i.e., radial, anastomosing, random) between the various regions of the carapace within some taxa (e.g., *Ae. scagliai*, Taborda et al. 2015; *Co. chathamensis*, Hoffman et al. 2019) and is likely related to ontogeny and / or sexual dimorphism; this area of research is incipient and requires further sampling across the clade to determine the extent of intraspecific variation within the aetosaurian carapace. With this in mind, we compare the dorsal paramedian osteoderms of *Kr. caerula* with homologous osteoderms of other aetosaurs documented from the Late Triassic strata in the southwestern US (e.g., Long and Murry 1995, Heckert and Lucas 1999, 2000, Parker 2007, 2008, 2016a; Parker et al. 2008; Parker and Martz, 2010); this includes *De. spurensis* (Fig. 3B), *De. smalli* (Fig. 3B), *Ca. wellesi* (Fig. 3C), *Paratypothorax* sp. (Fig. 4J), *Ty. coccinarum* (Fig. 4N), *Te. chatterjeei* Martz

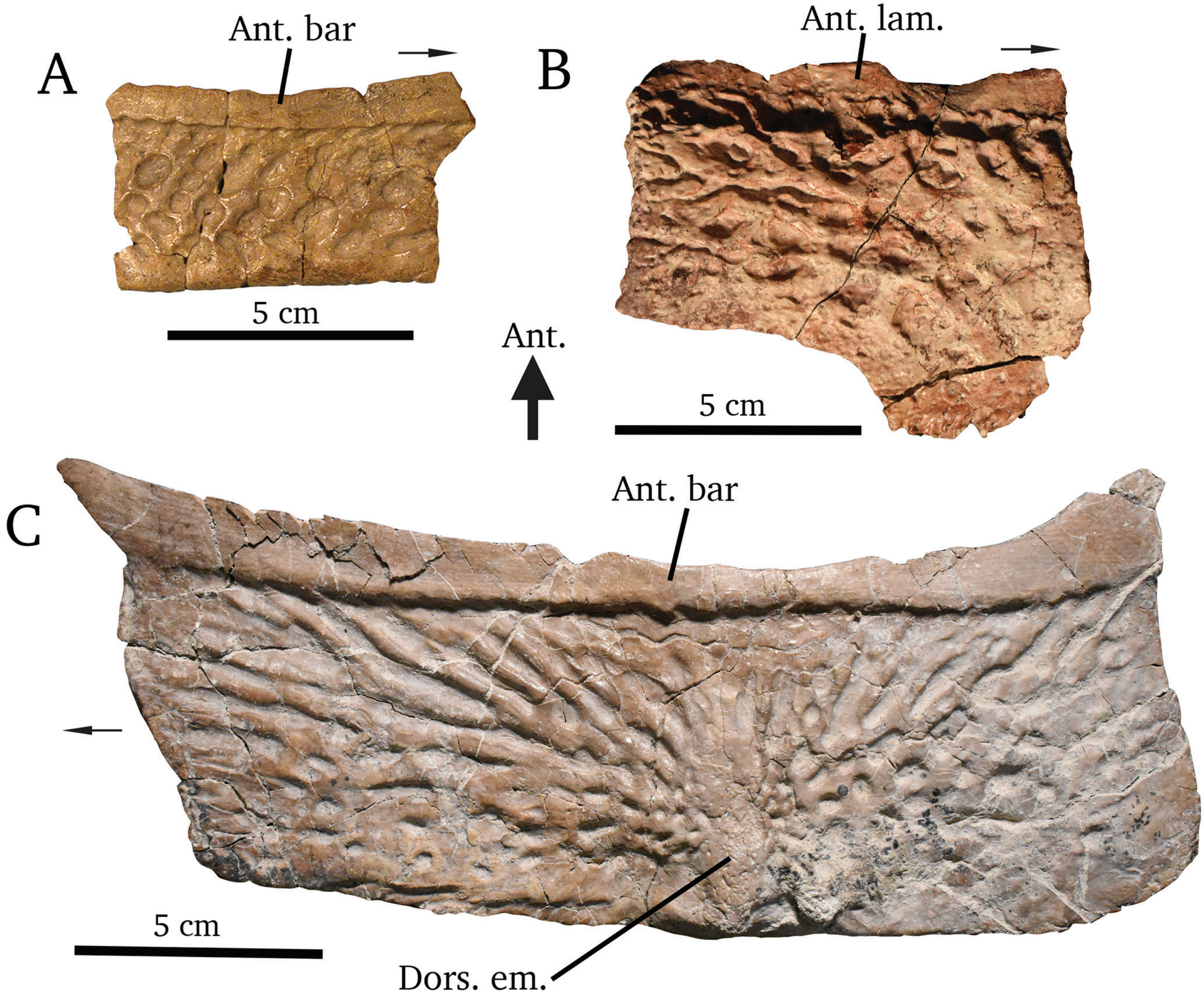

Figure 3. **A.** Holotype paramedian osteoderm of *Kryphioparma caerula* gen. et sp. nov. in comparison to that of other stagonolepidoid taxa documented within the *Placerias* Quarry and PFV 456, UCMP 165173. **B.** *Desmatosuchus*, PEFO 49568. **C.** *Calypotosuchus wellesi*, PEFO 46222. Orientation: All in dorsal view. **Abbreviations**: **Ant.**=Anterior, **Ant. bar**=Anterior bar, **Ant. lam.**=Anterior lamina, **Dors. em.**=Dorsal eminence. Small, unlabeled arrows indicate lateral direction.

and Small (2006) (Fig. 4C–J), *Scutarx deltatylus* Parker (2016b), *Sierritasuchus macalpini* (Parker et al. 2008) and *Adamanasuchus eisenhardtae* Lucas et al. (2007).

Although our morphological understanding of *Kr. caerula* is limited to a few osteoderm fragments (Fig. 2), those fragments provide sufficient morphological information to differentiate them from those of other aetosaurs, including all other known Adamanian taxa. The dorsal ornamentation of the paramedian osteoderms of *Kr. caerula* is composed of large, randomly oriented, well-incised oblong pits (Fig. 2B, H, N, T). The density of those pits relative to the available dorsal surface area is low approximately 20 pits per 5 cm transverse width; the opposite condition is observed in *Ty. coccinarum* (Long and Murry 1995, Martz 2002; Fig. 4N) where pits are also randomly oriented but have a higher concentration relative to available surface area. The dorsal ornamentation in *Kr. caerula* (Fig. 3A) is unlike the ornamentation composed of pits and grooves radiating from the center of ossification observed in *Ca. wellesi* (Long and Ballew 1985, Parker 2018; Fig. 3C), *Ad. eisenhardtae* (PEFO 34638, Lucas et al. 2007), *Co. kahleorum* (Heckert and Lucas 1999), *Sc. deltatylus* (PEFO 34045, Parker 2016b), or *Rioarribasuchus chamaensis* Zeigler et al. (2003). These

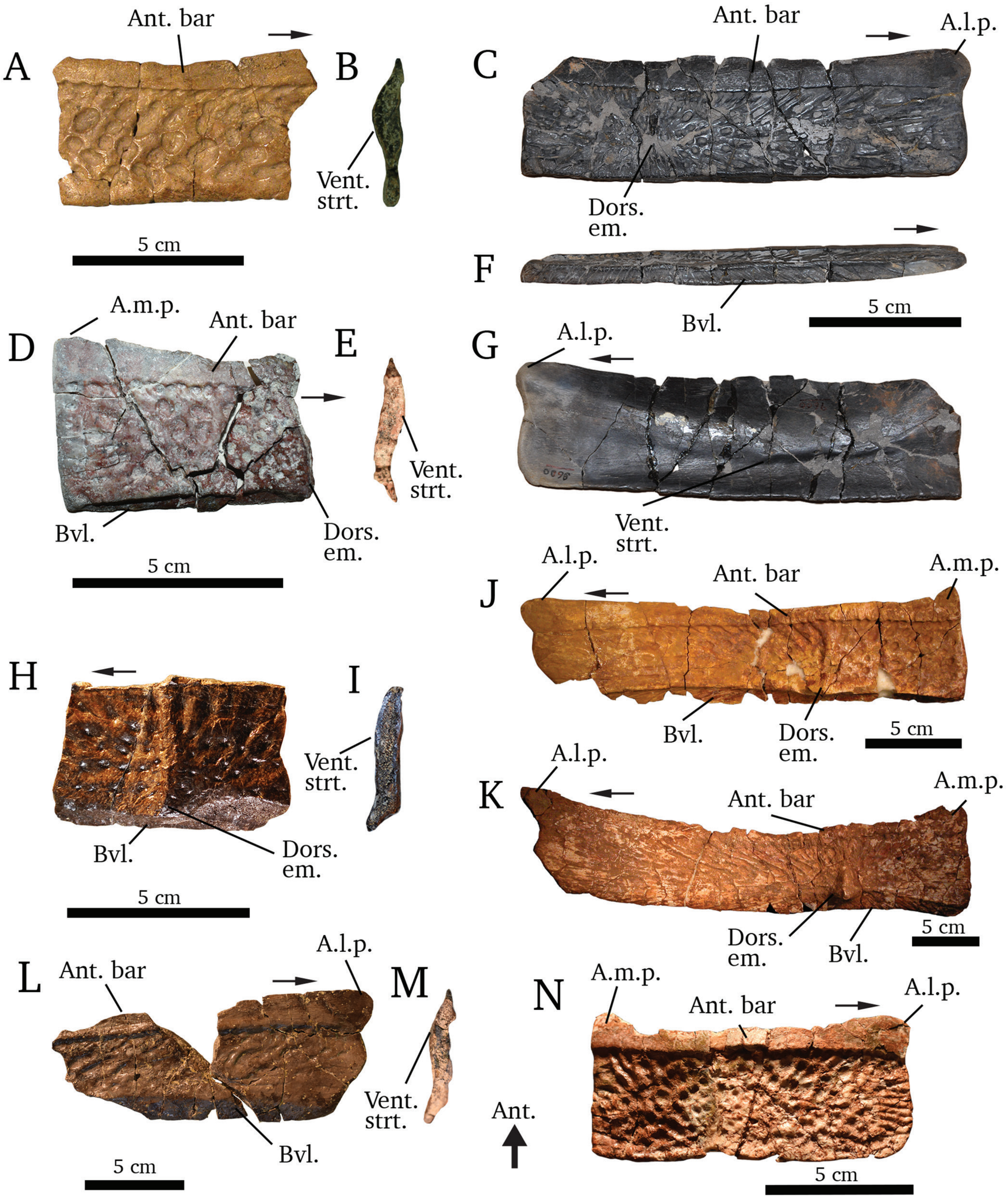

Figure 4. Cation on page 9.

Figure 4. Paramedian osteoderms of Adamanian typothoracines documented within the Chinle Formation (**A, B, D, E, H, I, L, M**) and Dockum Group (**C, F, G, J, K, N**). *Kryphioparma caerula* gen. et sp. nov., UCMP 165173 (**A, B**). *Tecovasuchus chatterjeei*, PEFO 49404 (**D, E**), NCSM 35011 (**H, I**), UMMP 9600 (**C, F, G**), and TTU-P 9222 (**J**). Ambiguous paratypothoracin, MNA V3202 (**L-M**). *Paratypothorax* sp., TTU-P 9169 (**K**). *Typothorax coccinarum*, TTU-P 9214 (**N**). Orientations: Dorsal (**A, C, D, H, J, K, L, N**), Ventral (**G**), posterior (**F**), medial cross-section (**B, M**), lateral cross-section (**E, I**) views. **Abbreviations: Ant.**=Anterior, **Ant. bar**=Anterior bar, **A.l.p.**=Anterolateral process, **A.m.p.**=Anteromedial process, **Bvl.**=Beveled edge, **Dors. em.**=Dorsal eminence, **Vent. strt.**=Ventral strut. Small, unlabeled arrows indicate lateral direction.

osteoderms instead exhibit the anastomosing to intermediate ornamentation pattern as defined by Taborda et al. (2015). Anteriorly, the osteoderms of *Kr. caerula* exhibit a well-developed anterior bar on the dorsal surface (Fig. 3A), a condition shared with most aetosaurs except *De. smalli* and *De. spurensis*, which exhibit a depressed lamina (Long and Ballew 1985, MNA V9300, Parker 2008; Fig. 3B). These features differentiate *Kr. caerula* from *Desmatosuchus* and *Ca. wellesi*, which are also documented in the *Placerias* Quarry (Camp and Welles 1956, Parker 2018; Fig. 3) and Thunderstorm Ridge locality.

We interpret UCMP 165173 as representing the lateral portion of a fragmentary trunk paramedian osteoderm. This fragment indicates that the paramedian osteoderms of *Kr. caerula* exhibit an apparent high width-to-length ratio, being much transversely wider than anteroposteriorly long (Fig. 4A); a condition shared with the typothoracines (Parker 2007; Fig. 4), *Ty. coccinarum* (Martz 2002, Heckert et al. 2010; Fig. 4N), *Ri. chamaensis* (NMMNH P-33820, Zeigler et al. 2003, Parker 2007), *Paratypothorax* sp. (PEFO 3004, Hunt and Lucas 1992, Long and Murry 1995, Martz et al. 2013; Fig. 4K), and *Te. chatterjeei* (TTU-P 545, Martz and Small 2006; Fig. 4C, 4J). This differs strongly from stagonolepidoids such as *Ca. wellesi* (Long and Ballew 1985), *De. spurensis* (Parker 2008), and *Si. macalpini* (UMMP V60817, Parker et al. 2008). Like typothoracines, *Kr. caerula* also exhibits a well-developed ventral strut on the ventral surface (Figs. 2F, L, O, W-X; 4H), where the strut thickens in the direction of the center of ossification. That differs from the condition observed in *Ca. wellesi* (Parker 2018), *Ad. eisenhardtae* (Lucas et al. 2007), and *Sc. deltatylus* (Parker 2016b) which exhibit a weakly developed ventral strut, or *Desmatosuchus* (Parker 2008) and *Si. macalpini* (Parker et al. 2008), which lack it completely. Thus, these morphological features of *Kr. caerula* align with typothoracines (Martz 2002, Martz and Small 2006, Parker 2016a; Fig. 4), but as noted above the dorsal ornamentation of *Kr. caerula* does not align with that observed in *Ty. coccinarum* (Fig. 4N). A notable feature of the fragmentary paramedian osteoderms of *Kr. caerula* is that the posterior margin is dorsoventrally thickened like the condition observed in *Te. chatterjeei* (Martz and Small 2006, Heckert et al. 2007; Figs. 2D, J, P, V, 4F), but unlike the condition exhibited by *Paratypothorax* sp. (PEFO 3004) in which the paramedian osteoderms are thinner in comparison (Reyes personal observation).

Unlike the condition observed in *Te. chatterjeei* (Fig. 4G, I) and *Paratypothorax* sp. (Fig. 4J), the osteoderms of *Kr. caerula* do not exhibit a beveled posterior margin (Parker 2016a; Fig. 4A). However, this morphological feature is not consistent across the dorsal carapace as exemplified by *Paratypothorax* sp. (Hunt and Lucas 1992) and *Te. chatterjeei* (Martz and Small 2006, Heckert et al. 2007; Fig. 4F, H, J). Beveling along the posterior margin of the paramedian osteoderms is absent in the caudal region of *Paratypothorax* sp. (PEFO 3004, Lucas et al. 2006) and not fully exposed in dorsal view in the anterior trunk region of *Te. chatterjeei* (UMMP 9600, TTU-P 545, Martz and Small 2006, Heckert et al. 2007; Fig. 4C, F). However, the dorsal ornamentation in those paramedian osteoderms is clearly different from that of *Kr. caerula* (Fig. 4A); *Te. chatterjeei* exhibits small, spaced-out circular pits with long grooves near the posterolateral dorsal surface (Martz and Small 2006; Fig. 4J), while in *Paratypothorax* sp. dorsolateral surface is dominated by long parallel grooves (Lucas et al. 2006; Fig. 4K).

One paramedian osteoderm fragment of *Kr. caerula* (UCMP 126847) (Fig. 2G–L) preserves an anteroposteriorly straight medial edge indicating that it is from the left side. This medial edge lacks the strong articulation composed of interlocking grooves and ridges (Fig. 2K) that are observed in *Desmatosuchus* (Case 1922, Long and Ballew 1985, Parker 2007, 2008). Lastly, the paramedian osteoderms of *Kr. caerula* exhibit inclined grooves on their posterior margin (Fig. 2D, J, N, T, V). These grooves have also been documented in paratypothoracin taxa (Fig. 4F, J, K), where they incline towards the dorsal eminence / center of ossification (Martz and Small 2006, Reyes personal observation); this appears to also be case *Kr. caerula* (Fig. 2) where the grooves on the posterior margin incline towards the center of ossification. Unfortunately, due to the fragmentary nature of the preserved paramedian osteoderms of *Kr. caerula*, we are unable to confirm the presence of a dorsal eminence.

DISCUSSION

The fragmentary nature of the paramedian osteoderms of *Kryphioparma caerula* (Fig. 2) inhibit us from quantitatively assessing its topological position within the Aetosauria. However, through qualitative analysis we can narrow its topological positioning to a more inclusive clade. Based on the paramedian osteoderms (Fig. 2) exhibiting an apparent high width-to-length ratio, a well-developed ventral strut, and well-developed anterior bar, we hypothesize that *Kr. caerula* is most likely a typothoracine (Parker 2016a) similar to *Typothorax coccinarum*, *Tecovasuchus chatterjeei*, and *Paratypothorax* sp. *Kryphioparma caerula* is further differentiated from *Ty. coccinarum* (Fig. 4N) based on the low concentration of large, randomly oriented, oblong pits on the dorsal surface (Long and Ballew 1985, Martz 2002). It is differentiated from *Paratypothorax* sp. (Fig. 4K) based on the difference in the robustness of the paramedian osteoderms, lack of a beveled posterior margin, the absence of long radiating grooves on the dorsal surface, and the presence of a well-developed anterior bar (Hunt and Lucas 1992, Lucas et al. 2006). It is further differentiated from *Te. chatterjeei* (Fig. 4C, J) in that the dorsal ornamentation consists only of large, oblong pits, lacks long transverse grooves, and beveling is absent along the posterior margin (Martz and Small 2006).

Ambiguous paratypothoracin material from the *Placerias* and Downs quarries

The *Placerias* (loc. nos. UCMP A269 and MNA 207-1) and Downs (loc. no. MNA 207-2) quarries preserve an array of disarticulated micro- and macrovertebrate fauna (Camp and Welles 1956, Jacobs and Murry 1980, Kaye and Padian 1994). Among the macro fauna, aetosaur remains are some of the more abundant elements at these two localities (Long and Murry 1995, Parker 2018). Currently three named taxa, *Desmatosuchus spurensis*, *Desmatosuchus smalli*, and *Calyptosuchus wellesi*, are formally recognized (Long and Murry 1995, Heckert et al. 2005, Parker 2018, von Baczko et al. 2021). However, several cranial and post-cranial elements cannot be assigned unambiguously to these taxa due to the loss of original association (Fiorillo et al. 2000, Parker 2018). Long and Murry (1995) referred some ambiguous lateral osteoderms (MNA V3202) from the Downs Quarry to the cervical region of *Ca. wellesi* based on the morphological variation from the lateral osteoderms observed in the holotype specimen of *Ca. wellesi* (UMMP 13950) (Case 1932) and *De. spurensis* (Case 1922, 1929). However, further studies demonstrated that these lateral osteoderms as well as other fragmentary paramedian osteoderms (MNA V3202) belonged to a previously unrecognized paratypothoracin aetosaur which these authors tentatively referred to "*Tecovasuchus*" (Parker 2005, 2007, Heckert et al. 2007). Their referral was based on the lateral osteoderms exhibiting a posteriorly oriented, dorsoventrally compressed, horn-shaped eminence with a triangular outline in dorsoventral view that is keeled anteriorly and embayed posteriorly. The lateral osteoderms also exhibit a small, sigmoidal dorsal flange with a curved posteromedial corner, a large lateral flange with an ornamentation composed of long radiating grooves, and a strongly acute flexure between the dorsal and lateral flanges. Additionally, an associated paramedian osteoderm (Fig. 4L, M) exhibits a high width-to-length ratio, well-developed anterior bar, dorsoventrally thick with well-developed ventral strut, and sigmoidal lateral edge with a short, curved anterolateral process and incised posterolateral corner. Most notable was the presence of a beveled posterior margin which is shared with *Te. chatterjeei* but lacking in known paramedian osteoderms of *Kr. caerula*.

The documentation of "*Tecovasuchus*" in the *Placerias* and Downs quarries brought to question the biostratigraphic utility of this taxon in correlating the Dockum Group and Chinle Formation across Texas, New Mexico, and Arizona (Heckert et al. 2007). Although the paramedian and lateral osteoderms of MNA V3202 (Parker 2005, 2007) are similar to those of *Te. chatterjeei* (Martz and Small 2006), the dorsal ornamentation shows significant variation across the paramedian osteoderm (Fig. 4L, M). In *Te. chatterjeei* the ornamentation on the lateral half of the paramedian osteoderm is characterized by small, spaced-out, predominantly circular pits with transversely oriented grooves near the lateral edge (UMMP 9600, TTU-P 9222) (Martz and Small 2006, Heckert et al. 2007; Fig. 4C, F, G, J); in comparison the ornamentation of MNA V3202 is characterized by larger oblong pits that cover most of the dorsal surface with no evidence of transversely oriented grooves (Fig. 4L) (Parker 2005) similar to the ornamentation described here for *Kryphioparma caerula* (Fig. 4A). It is possible that MNA V3202 is referrable to *Kr. caerula* and the presence of the beveled posterior margin on the paramedian osteoderm is a result of regional variation in the dorsal carapace as observed in *Paratypothorax* sp. (Hunt and Lucas 1992, Lucas et al. 2006) and *Te. chatterjeei* (Martz and Small 2006, Heckert et al. 2007). However, due to the limited material associated with *Kr. caerula* we are unable to unambiguously refer MNA V3202 to this new taxon, which may very well be a paratypothoracin, nor can we confirm that it is indeed "*Tecovasuchus*" as hypothesized by previous authors (i.e., Parker 2005, 2007, Heckert et al. 2007). Alternatively, this variation may be intraspecific, possibly related to ontogeny; recent studies suggest that lateral osteoderms undergo drastic flexural change (Schoch and Desojo 2016) and that the dorsal ornamentation of paramedian osteoderms is subject to variability through skeletal maturity (Heckert 2015, Hoffman et al. 2019). However, this is an area of research only recently being explored, and further study is required to assess the influence of ontogeny on the aetosaurian carapace (Taborda et al. 2015).

Biostratigraphic utility of *Tecovasuchus chatterjeei*

Because of the ambiguity surrounding the taxonomic affinities of MNA V3202 and the documentation of *Kryphioparma caerula*, we cannot refer MNA V3202 to *Tecovasuchus chatterjeei*. This brings to question the biostratigraphic utility of *Te. chatterjeei* across the Dockum Group and Chinle Formation that was originally proposed by Heckert et al. (2007). The Thunderstorm Ridge locality within PEFO preserves osteoderms from a high diversity of aetosaurs, including *Desmatosuchus* (Fig. 3B), *Calyptosuchus wellesi* (Fig. 3C), *Kr. caerula* (Fig. 2M–X), and the first unambiguous material referrable to *Te. chatterjeei* (Martz and Small 2006) (PEFO 49404, Fig. 4D, E) from the upper Blue Mesa Member of the Chinle Formation in PEFO. Our documentation of *Te. chatterjeei* is based on a partial right trunk paramedian osteoderm (Fig. 4D, E) that exhibits a unique combination of characters including being dorsoventrally thick with a high width-to-length ratio, well-developed anterior bar, well-developed ventral strut, a beveled posterior margin, anteroposteriorly elongate keeled eminence that is more medially situated on the dorsal surface and projects posteriorly over the beveled margin, grooves on the beveled surface that incline towards the dorsal eminence, and dorsal surface between the medial edge and dorsal eminence that is covered with small, spaced out, predominantly circular pits. Additionally, recent field excavations at the Downs Quarry have produced new unambiguous material referrable to *Te. chatterjeei* (NCSM 35011) (Fig. 4H, I). This fragmentary paramedian osteoderm does not preserve the anterior bar but is referrable to *Te. chatterjeei* based on the same characters mentioned above for PEFO 49404.

Specimens PEFO 49404 (Fig. 4D) and UCMP 165173 (Figs. 2B, 4A) exemplify the morphological disparity in the dorsal ornamentation (described above) between *Te. chatterjeei* and *Kr. caerula*. Our documentation of *Te. chatterjeei* in PEFO and the Downs Quarry supports the biostratigraphic utility of that taxon originally proposed by Heckert et al. (2007). However, the osteoderms originally referred to "*Tecovasuchus*" (NMMNH P-25641, P-18305, P-18422) from the Late Triassic strata of New Mexico by Heckert et al. (2007) remain ambiguous because they are too fragmentary and poorly preserved. Additionally, it is plausible that, like MNA V3202, the lateral osteoderm MNA V2898 (Heckert et al. 2007) from the *Placerias* Quarry is referrable to *Kr. caerula* instead of *Te. chatterjeei*, which has only been unambiguously

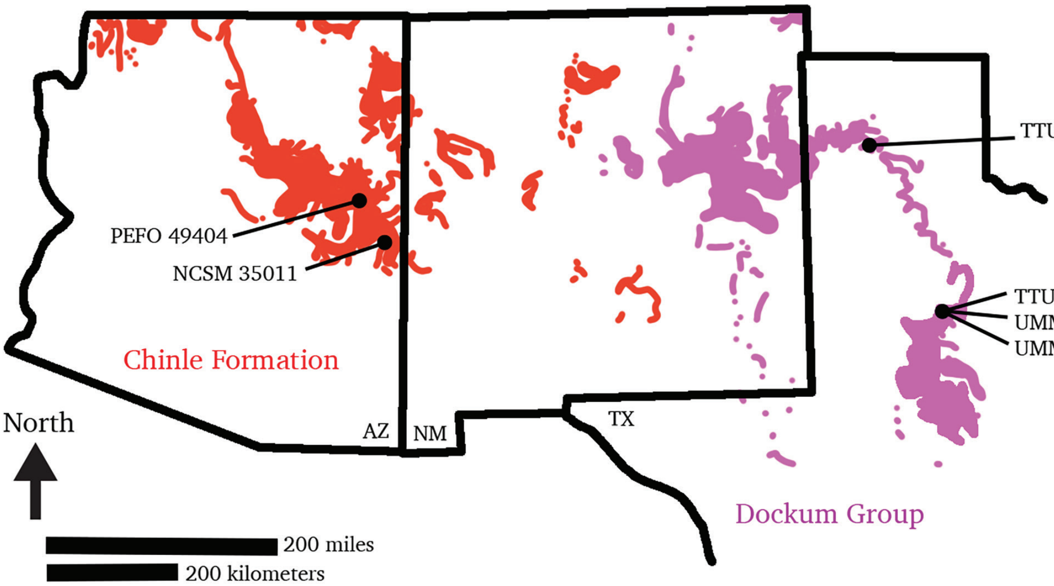

Figure 5. Revised regional occurrences of *Tecovasuchus chatterjeei* across the Chinle Formation and Dockum Group of the southwestern United States (modified from Martz 2008 and Heckert et al. 2007). **Abbreviations: AZ**=Arizona, **NM**=New Mexico, **TX**=Texas.

documented at the Thunderstorm Ridge locality and the Downs Quarry (this study) (Figs. 4D, E, H, I, 5). Based on the reported material, we can only confirm the occurrence of *Te. chatterjeei* in the Tecovas Formation, Dockum Group, Texas (Martz and Small 2006, Heckert et al. 2007) (Fig. 5), and upper Blue Mesa Member, Chinle Formation, Arizona (Fig. 5). Thus, like *De. spurensis* and *Ca. wellesi* (Parker 2016a, Parker and Martz 2011; Fig. 3)*, Te. chatterjeei* is currently restricted to the early-Norian age strata within the Adamanian estimate holochronozone (Martz and Parker 2017).

CONCLUSIONS

In this contribution we document the presence of *Kryphioparma caerula* gen. et sp. nov., a new aetosaur with typothoracine taxonomic affinities from the *Placerias* Quarry, St. Johns, and the Thunderstorm Ridge locality (PFV 456), PEFO, within the Chinle Formation of northern Arizona, early-Norian aged Adamanian estimated holochronozone. The stratigraphic occurrence of *Kr. caerula* within the upper Blue Mesa member in PEFO makes it the oldest documented typothoracine within the Chinle Formation of Arizona. The identification of *Kr. caerula* within the *Placerias* Quarry brings to question the taxonomic affinities of the ambiguous paratypothoracin material that was previously identified as "*Tecovasuchus*" (MNA V2898, V3202). Our comparative analysis of MNA V3202 with other unambiguous specimens of *Tecovasuchus chatterjeei* highlights the disparity in their dorsal ornamentations, thus rejecting the referral of MNA V3202 to *Te. chatterjeei* made by previous authors. Additionally, the documentation of *Kr. caerula* presents an alternative taxon to which that material could be referred. However, the disarticulated nature of the specimens collected from the *Placerias* and Downs quarries complicates the referral of this material to *Kr. caerula*. Lastly, the first unambiguous occurrences of *Tecovasuchus chatterjeei* (PEFO 49404, NCSM 35011) in the upper Blue Mesa Member of the Chinle Formation, suggests that this taxon may be biostratigraphically informative because it is currently restricted to the Adamanian estimated holochronozone.

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