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TAXONOMY AND BIOSTRATIGRAPHY OF THE LATE TRIASSIC ARCHOSAUROMORPH *TRILOPHOSAURUS*

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Abstract—*Trilophosaurus* is an aberrant archosauromorph from the Upper Triassic Chinle Group of the southwestern United States. We review the history of study of *Trilophosaurus*, revise the diagnosis of the genus and both species of *Trilophosaurus*, *T. buettneri* Case and *T. jacobsi* Murry, and summarize its biostratigraphic record. Reevaluation of *T. dornorum* Mueller and Parker reveals no diagnostic differences between it and *T. jacobsi*, rendering *T. dornorum* a junior subjective synonym of *T. jacobsi*. The two species of *Trilophosaurus* have well established temporal ranges, with *T. buettneri* extending from the middle Otischalkian to late Adamanian and *T. jacobsi* extending from early Adamanian into the Revueltian.

INTRODUCTION

Trilophosaurus is an aberrant archosauromorph reptile known from the Upper Triassic of the southwestern United States (Fig. 1). The two species of *Trilophosaurus*, *T. buettneri* and *T. jacobsi*, are known from microvertebrate remains, principally teeth and jaw fragments, and postcrania, a nearly complete articulated skeleton of *T. buettneri* and a composite skeleton of *T. jacobsi*. One of the diagnostic features of the genus is its transversely broadened, tricuspid teeth, which are distinct between the two species, thus allowing isolated teeth to be identified to species level. This has given *Trilophosaurus* biostratigraphic utility within the Upper Triassic Chinle Group.

Here we review previous studies focusing on *Trilophosaurus*, summarize the biostratigraphic record of the genus, and revise its genus- and species-level taxonomy. The current paper is part of a larger study being undertaken by the authors (Spielmann et al., in prep.) that will update the osteology of *T. buettneri*, provide the first postcranial osteology of *T. jacobsi* and discuss the growth, variation and functional morphology of *Trilophosaurus*.

Abbreviations: AMNH = American Museum of Natural History, New York; MNA = Museum of Northern Arizona; NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; MOTT, TTU = (Museum of) Texas Tech University; PEFO = Petrified Forest National Park, Arizona; TMM = Texas Memorial Museum, Austin; UMMP = University of Michigan Museum of Paleontology; USNM = U.S. National Museum (Smithsonian), Washington, D.C.; YPM = Yale Peabody Museum, New Haven.

PREVIOUS STUDIES

Trilophosaurus is one of the most completely known Late Triassic reptiles from the American Southwest, and has had over seven decades of intermittent research devoted to it. Here, we summarize the key studies examining *Trilophosaurus*, from the naming of *T. buettneri* in 1928 through the present.

In early 1928, Case originally named *Trilophosaurus buettneri* in a short note in the *Journal of the Washington Academy of Sciences* (Case, 1928a). This note was followed shortly thereafter by an article in the *Contributions of the Museum of Paleontology of the University of Michigan* that described the vertebrate fauna of beds in the Tecovas Formation near Walker's Tank, Crosby County, West Texas, of which *T. buettneri* was part (Case, 1928b). Numerous authors have cited this University of Michigan article (Case, 1928b) as the publication in which *T. buettneri* is named. However, it is clear from the presence of the "gen. and sp. nov." designation accompanying the line drawings in the Washington Academy of Sciences note (Case, 1928a) that Case was in fact erecting the genus and species in that publication, not in the later University of Michigan article (Case, 1928b). Both the original note (Case, 1928a) and the *Trilophosaurus* portion of the later faunal article (Case, 1928b) were based on a single maxillary fragment containing the transversely broadened teeth for which the genus is best known (Fig. 2A-F). The tricuspid nature of the teeth, with their symmetrically oriented central cusp, provided Case's impetus to name the taxon *Trilophosaurus*, or "three crested (lophed) reptile."

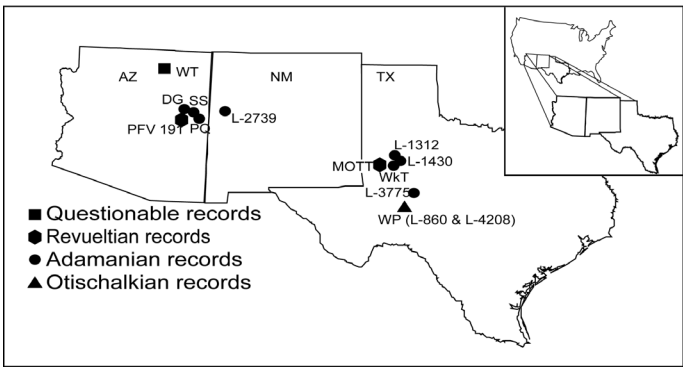

FIGURE 1. Index map showing the distribution of *Trilophosaurus* fossil localities in Arizona, New Mexico and Texas. Biostratigraphic subdivision after Lucas (1998). Locality numbers with an L prefix (i.e. L-4208) are NMMNH localities, and PFV indicates a Petrified Forest National Park locality. Abbreviations: DG – "Dying Grounds," MOTT – MOTT VLP 3624, 3869 and 3878; PFV – Petrified Forest National Park; PQ – *Placerias* quarry; SS – North Stinking Springs Mountain; WkT – Walker's Tank (*T. buettneri* type locality); WPA – Works Progress Administration sites (*Trilophosaurus* quarries); WT – Ward's Terrace. Modified from Heckert et al. (2006).

The first *Trilophosaurus* postcranial material was excavated between 1939 and 1941 by crews working for the U.S. Works Progress Administration (WPA) while excavating several localities in Howard County, West Texas. These localities contained predominantly *Trilophosaurus buettneri* remains, and so were designated *Trilophosaurus* quarries 1, 2, 3 and 3A. These quarries are located in the Colorado City Formation of the Chinle Group near Otis Chalk, Texas (Lucas et al., 1993). The collections made by the WPA are housed primarily at the Texas Memorial Museum, Vertebrate Paleontology Laboratory at the University of Texas at Austin. These WPA collections have served as the primary material for nearly all research regarding *Trilophosaurus buettneri*. TMM personnel authorized exchanges of these fossils with other institutions, thus, most of the WPA collections are in Austin, but other specimens, including composite skeletons, are present at AMNH, UMMP, and USNM, among others. Gregory appears to have brought a

minor collection, including at least two braincases, to YPM when he started his tenure there as well.

The extensive material present in the WPA collections allowed Gregory (1945) to publish an osteology of *Trilophosaurus buettneri*. Using material from all four quarries, he reconstructed the entire postcranial skeleton and produced a moderately detailed cranial reconstruction. The principal specimen that Gregory (1945) used to reconstruct *T. buettneri* is a nearly complete articulated skeleton (TTM 31025-140), missing only the skull anterior to the orbits, the left manus and portions of the tail. Also, Gregory (1945) reinterpreted *Trilophosaurus* as a protorosaur, whereas Case (1928a, b) had previously considered it a cotylosaur. This assignment of *Trilophosaurus* to the Protorosauria would not be challenged until the 1980s. Thus, for example, the information Kuhn (1969, p. 26, figs. 11-12) presented in his review of "Trilophosauria" (an ordinal term Romer, 1956, introduced for *Trilophosaurus* and allied genera) came directly from Gregory (1945).

Parks (1969), in an unpublished master's thesis, further refined Gregory's cranial reconstruction of *Trilophosaurus buettneri*. Parks reprepared much of the concreted cranial material that Gregory had examined, allowing him to better characterize the spatial relationships and sutures of the cranium. Another central aspect of Parks' (1969) thesis was a tooth replacement scheme in which the teeth were replaced in multiple waves with an Anlagen (tooth replacement spacing, see also z-spacing below) ranging from 7 to 9.

The first paleoecological study of the *Trilophosaurus* quarries was conducted by Elder in 1977 as part of her Ph.D. dissertation; this marked the first study of these quarries to focus on their paleoenvironment and fauna. Elder (1977, 1987) thus examined the taphonomy, paleoecology and paleocommunity of the four *Trilophosaurus* quarries. She noted a differentiation of size classes between quarries that had adult individuals (quarries 1, 3 and 3A) and quarries that consisted predominantly of juveniles (quarry 2). This separation of size classes prompted Elder (1977, 1987) to suggest herding behavior in *Trilophosaurus*.

Based on differences in preservation across the four *Trilophosaurus* quarries, Elder (1977, 1987) proposed two distinct taphonomic reconstructions. The relatively unworn nature of the bone and the occasional presence of articulated specimens in quarries 1 and 2 suggested to Elder (1977, 1987) that these quarries were catastrophic flood assemblages. Quarries 3 and 3A were interpreted as being the result of gradual deposition due to the invertebrate burrows present on some specimens. In her paleocommunity reconstruction, Elder (1977, 1987) placed *Trilophosaurus* as a primary consumer of terrestrial vegetation and as a food item for both the phytosaurs and poposaurs present in the fauna of the *Trilophosaurus* quarries.

DeMar and Bolt (1981) examined the tooth replacement of *Trilophosaurus buettneri* using the tooth replacement model of DeMar (1972, 1973), which was based on the *Zahnreihe* concept of Edmund (1960, 1969). *Zahnreihen* is a system used to represent the timing of tooth replacement events. The term "z-spacing" refers to the number of tooth positions between teeth that exhibit the same degree of replacement. Typically, DeMar and Bolt (1981) used empty alveoli, which they interpreted as recently erupted teeth that had yet to attach to the jaw, in order to determine z-spacing. Examining numerous *T. buettneri* partial skulls and lower jaws from WPA quarry 1, they concluded: (1) *Trilophosaurus* has a mean z-spacing of about 5-6 tooth positions, with an overall range between 2.5 and 8 tooth positions; (2) individual teeth were in usable condition for at least 70%-75% of their life span; (3) the high percentage of useful life in the teeth was achieved by changes in the replacement process itself and by decreasing the rate of tooth replacement; (4) there was an ontogenetic change in tooth morphology, suggesting that juveniles were carnivorous, whereas adults were herbivorous; (5) dental occlusion was not highly developed, with little tooth-on-tooth wear, and teeth did not wear into occlusion; (6) evolution of long z-spacing was made possible by the relatively long time the teeth remained in the tooth row; and (7) the reduction in tooth replacement rate may be related to maintaining the little occlusion that did exist. The conclusion of DeMar and Bolt (1981) that *T. buettneri* underwent ontogenetic change in tooth morphology was based on the interpretation that WPA quarry 1 individuals were adults, whereas WPA quarry 2 individuals were carnivorous juveniles. No subsequent workers, however, have considered the teeth of "juvenile *T. buettneri*" to be those of a carnivore.

Murry (1987) described and named *Trilophosaurus jacobsi* based on a right mandible fragment (Fig. 2G-J) from the *Placerias* quarry near Romero Springs, 10.4 km southwest of St. Johns, Arizona (Lucas et al., 1997). In addition, he referred three mandible fragments, two maxillary fragments and two isolated teeth to the taxon. According to Murry (1987), the principal feature distinguishing the teeth of *T. jacobsi* from those of *T. buettneri* is the asymmetrically oriented central cusp and the prominent medial and lateral cingula on each cusp. Murry (1987) also noted that *T. jacobsi* is considerably smaller than *T. buettneri*.

In a series of papers, Kirby (1989, 1991, 1993) examined the depositional paleoenvironments and vertebrate fauna of the Owl Rock Formation from Ward Terrace, northern Arizona. From this fauna Kirby reported a partial tooth, five posterior mandible fragments and two fragmentary quadrate condyles, all of which he assigned to *Trilophosaurus* cf. *T. buettneri*. This is a questionable record, as no other occurrence of *T. buettneri* is known that is younger than late Adamanian. Recently, Heckert et al. (2006) suggested that these tooth fragments either pertain to a procolophonid with similar tooth morphology, e.g. *Tricuspisaurus*, or are the result of screenwash contamination from earlier work completed by Tannenbaum (Kaye). Thus, this report, while included here for the sake of completeness, is not considered a substantiated record of *Trilophosaurus*.

Murry (1989), in a review of the microvertebrates from the Petrified Forest National Park, noted three teeth of *Trilophosaurus buettneri* from high in the Blue Mesa Member of the Petrified Forest Formation (strata Murry considered lower Petrified Forest Member of the Chinle Formation). He noted that none of the teeth possess prominent cingula, thus reinforcing his assignment of the teeth to *T. buettneri* and not to *T. jacobsi*.

Kaye and Padian (1994; also see Tannenbaum, 1983) included *Trilophosaurus* sp. in their review of the microvertebrate fauna of the *Placerias* quarry, thus acknowledging the work of Murry (1987). However, they considered the assignment of these teeth to *Trilophosaurus* as provisional because transversely expanded teeth of Late Triassic age can also pertain to procolophonids, sphenodontians and some other taxa, as noted by Fraser (1986) and Heckert et al. (2006).

Sues and Olsen (1993), in the course of reviewing procolophonids from the Upper Triassic of Virginia, noted that *Trilophosaurus jacobsi*, as described by Murry (1987), appeared more closely related to *Tricuspisaurus* and *Variodens*, both of which were considered procolophonids by Sues and Olsen (1993). Thus, Sues and Olsen (1993) proposed a new generic name for *T. jacobsi*, *Chinleogomphius*, and interpreted it as a procolophonid.

Lucas et al. (1993) reviewed the Late Triassic vertebrate fauna collected around Otis Chalk, Howard County, West Texas, designated the type fauna of the Otischalkian land-vertebrate faunachron (lvf) by Lucas and Hunt (1993). This includes the WPA *Trilophosaurus* quarries. Lucas et al. (1997) also reviewed the stratigraphic position of the *Placerias* quarry in eastern Arizona, assigning it to the Bluewater Creek Formation, of Adamanian age (also see Heckert et al., 2005).

Long and Murry (1995, p. 24-27), reviewed records of *Trilophosaurus* from the American Southwest and followed Sues and Olsen (1993) in removing *Chinleogomphius* (=*Trilophosaurus*) *jacobsi* from *Trilophosaurus*. Also, Long and Murry (1995) provided a discussion of morphologic differences that distinguish isolated humeri of *Trilophosaurus* from those of the rhynchosaur *Otischalkia*. They interpreted a large robust femur from *Trilophosaurus* quarry 1 as potentially indicative of a new species of *Trilophosaurus*. However, we consider this single femur to be from a large individual of *T. buettneri* because it

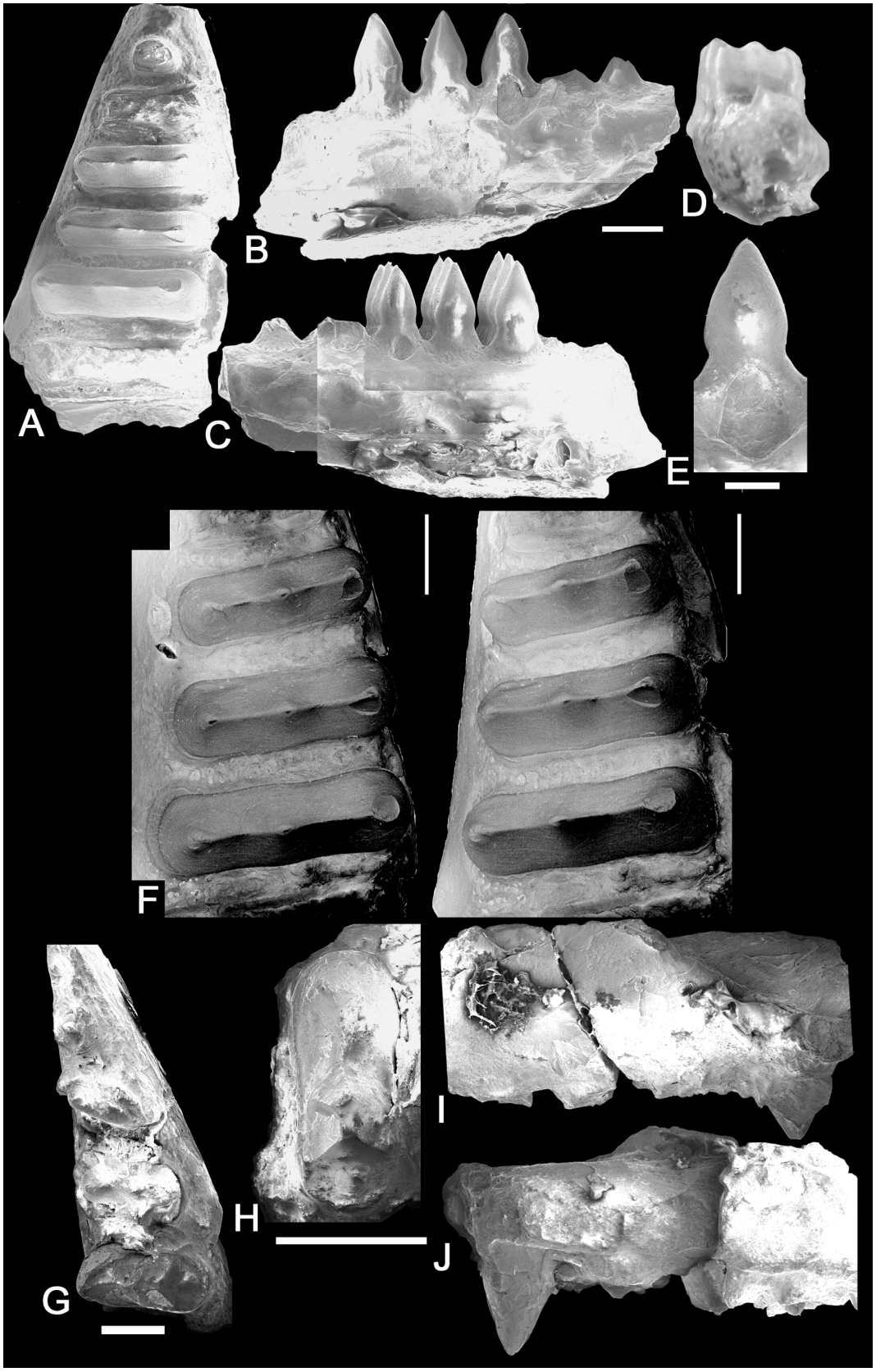

FIGURE 2. Holotypes of *Trilophosaurus buettneri* and *T. jacobsi*. **A-E**, Scanning electron micrographs of UMMP 2338, holotype right dentary of *Trilophosaurus buettneri* Case, UMMP 2338. **A**, occlusal, **B**, labial, **C**, lingual and **D**, anterior views. **E**, Close-up view of third tooth position of same in labial view. **F**, *Trilophosaurus buettneri*, UMMP 2338, holotype dentary in occlusal stereo view. **G-J**, Scanning electron micrographs of the holotype of *Trilophosaurus jacobsi*, MNA V3192. **G**, **I-J**, holotype left maxilla (?) in **G**, occlusal, **I**, labial and **J**, lingual views. **H**, occlusal view of penultimate preserved tooth. Scale bar represents 2 mm in **A-D** and 1 mm in **E-J**. Figure modified from Heckert (2004) and Heckert et al. (2006).

shows no characters other than size that distinguish it from other, established femora of *T. buettneri*.

Merck (1995) published an abstract with a preliminary redescription of the sutural relationships of the cranium of *T. buettneri*, again working with the WPA sample described previously by Gregory (1945) and Parks (1969). This study utilized high-resolution x-ray computed tomography ("CAT-scanning") to demonstrate that many of the cranial sutures that Gregory (1945) and Parks (1969) considered problematic, or disagreed upon, were in fact "sliding" sutures for which, the actual anteroposterior or dorsoventral position shifts depending on how deep into the bone the suture was pursued (Merck, 1995; pers. comm. to ABH). Unfortunately, this study remains unpublished in any more extensive format.

Heckert et al. (2001) reported a new *Trilophosaurus* locality, the Kahle *Trilophosaurus* quarry (NMNH L-3775), from Borden County, West Texas. *Trilophosaurus* fossils dominate this locality, much like the classic Otischalkian *Trilophosaurus* quarries. Heckert et al. (2001) summarized the fauna of the quarry, that in addition to *Trilophosaurus*, includes a single possible ornithischian tooth, vertebrae possessing extremely tall neural spines and thus potentially assignable to the problematic reptile *Spinosuchus caseanus* Huene, various indeterminate teeth of reptiles and osteichthyans, vertebrate coprolites and unionid bivalve shells. Heckert et al. (2001) also provided a summary of the biostratigraphic record of *Trilophosaurus*. It should be noted that Heckert et al. (2001) considered the genus *Trilophosaurus* to be monospecific (*T. buettneri*).

Polcyn et al. (2002) included *Trilophosaurus jacobsi* in their faunal list of taxa from North Stinking Springs Mountain, near St. Johns, Arizona. However, no discussion of the *T. jacobsi* specimens are included in the article. We identify the specimen in question as *T. buettneri* (see below). This site is high in the Blue Mesa Member of the Petrified Forest Formation and is of Adamanian age.

Heckert (2001, 2004) reviewed the microvertebrate fauna of seven localities of Otischalkian and Adamanian age from Arizona, New Mexico and West Texas. These include *Trilophosaurus* quarry 1 (NMMNH L-860), lower Kalgary site (NMMNH L-1312, upper Kalgary site (NMMNH L-1430) and Sixmile Spring locality (NMMNH L-2739), all of which yielded new microvertebrate records of either *Trilophosaurus buettneri* (L-860; L-1312), *T. jacobsi* (L-2739) or both taxa (L-1430). This is especially useful in regard to the two species of *Trilophosaurus* because they can be differentiated based on tooth morphology, which is rare among Late Triassic archosauromorph reptiles.

Spielmann et al. (2005) examined the functional morphology of *Trilophosaurus* and concluded that it was arboreal, an interpretation initially proposed by Gregory (1945) but ignored by subsequent workers. Based on claw curvature, manus and pes proportions, fore and hind limb morphology and comparisons to extant arboreal and terrestrial iguanids and varanids, Spielmann et al. (2005, 2006a) reconstructed *Trilophosaurus* as climbing in a fashion similar to an iguana.

After further preparation of material from the Kahle *Trilophosaurus* quarry, it became evident that an incomplete skull recovered from the site was referable to *Trilophosaurus jacobsi* based on its dentition. Thus, in a subsequent description of the skull, Heckert et al. (2006) resurrected *Trilophosaurus jacobsi* as a valid species of *Trilophosaurus* and synonymized the generic name *Chinleogomphius* with *Trilophosaurus*. In addition, Heckert et al. (2006) revised both species of *Trilophosaurus* based on tooth morphology, discussed the stratigraphic placement of the Kahle quarry and reillustrated the holotypes of both species of *Trilophosaurus*.

Mueller and Parker (2006) described and named a new species of *Trilophosaurus*, *T. dornorum*, based on a partial left maxilla and partial left dentary (Fig. 3A-D) from the Jim Camp Wash Bed, Sonsela Member of the Petrified Forest Formation in the Petrified Forest National Park, Arizona. They also referred to this taxon an isolated tooth, incomplete left and right maxillae, left and right dentary fragments and a partial maxilla from various localities around the Post quarry collecting area in West Texas, which is in the Bull Canyon Formation. We do not consider *T. dornorum* to be distinct from *T. jacobsi*, for reasons discussed below. The importance of these specimens is that both the Bull Canyon Formation and the Sonsela Member of the Petrified Forest Formation are Revueltian in age, so these records represent the only known records of *T. jacobsi* in the Revueltian and are thus the youngest occurrences of the taxon.

Spielmann et al. (2006b) reinterpreted the holotype of *Malerisaurus langstoni* (from *Trilophosaurus* quarry 2), originally described by Chatterjee (1986) as a protorosaur, as a chimera consisting principally of *Trilophosaurus buettneri* material. They restricted the holotype of *M. langstoni* to the skull fragments, which they synonymized with *T. buettneri*. Interestingly, Spielmann et al. (2006b) noted that the other species of *Malerisaurus*, *M. robinsonae*, from the Maleri Formation of India, appears to have a femur with a large and extensive internal trochanter, a feature that is known elsewhere in the Late Triassic solely in *Trilophosaurus*. Thus, they concluded that the holotype of *M. robinsonae*, also named and described by Chatterjee (1980), may also include *Trilophosaurus* material. If portions of *M. robinsonae* indeed pertain to *Trilophosaurus* it would change the paleogeographic distribution of the genus from a taxon endemic to the southwestern United States to one that potentially lived across a broad portion of Pangea.

BIOSTRATIGRAPHIC RECORD OF THE GENUS *TRILOPHOSAURUS*

The biostratigraphic record of *Trilophosaurus* extends from the middle Otischalkian into the Revueltian, with *T. buettneri* extending from the middle Otischalkian to late Adamanian and *T. jacobsi* extending from the early Adamanian into the Revueltian (Fig. 4). Each species is known from relatively few sites with abundant body fossils, the WPA quarries (NMMNH L-860 and L-4208) for *T. buettneri* and the Kahle quarry (NMMNH L-3775) for *T. jacobsi*, while the rest of the record consists of microvertebrate specimens, primarily teeth. Currently, the genus *Trilophosaurus* is known from Arizona, New Mexico and West Texas (Fig. 1).

NMMNH locality 860 (*Trilophosaurus* quarry 1)

In and around Big Spring, Texas, the Chinle Group consists of, in ascending order, the Camp Springs and Colorado City formations (Lucas and Anderson, 1993; Lucas et al., 1994). Locally, in and around the Otis Chalk collecting area, including *Trilophosaurus* quarry 1, the Colorado City Formation is truncated by overlying Cretaceous strata. The Colorado City Formation consists of interbedded bentonitic mudstone and sandstone. Five laterally extensive sandstones were numbered and used by Grover (1984) as marker beds. The *Trilophosaurus* quarry is stratigraphically low in the Colorado City Formation, approximately 30 m above the Camp Springs/Colorado City contact and slightly above Grover's (1984) sandstone #3. The tetrapod assemblage from the Otis Chalk collecting area is the type assemblage of the Otischalkian lvf (Lucas and Hunt, 1993a, b; Lucas, 1998). As noted elsewhere, including Heckert (2004), the Otischalkian index taxon *Parasuchus* (=*Paleorhinus*) occurs in marine strata and thus indicates that part or all of the Otischalkian lvf is late Carnian (Tuvalian) (Hunt and Lucas, 1991; Lucas, 1997, 1998).

The fossil record of *Trilophosaurus buettneri* from this quarry is considerable and provided the majority of the specimens that were used by Gregory (1945) in his monograph. However, in his review of the microvertebrate material from this locality, Heckert (2004) noted that very few isolated teeth of *T. buettneri* have been collected, with only one specimen, NMMNH P-34010, being definitively identifiable as *T. buettneri*. Heckert (2004, p. 29) postulated three possible interpretations for the lack of isolated teeth: "(1) *Trilophosaurus* did not actually live in the vicinity of the locality, but individuals were transported and buried with their dentitions relatively intact shortly after death; (2) iso-

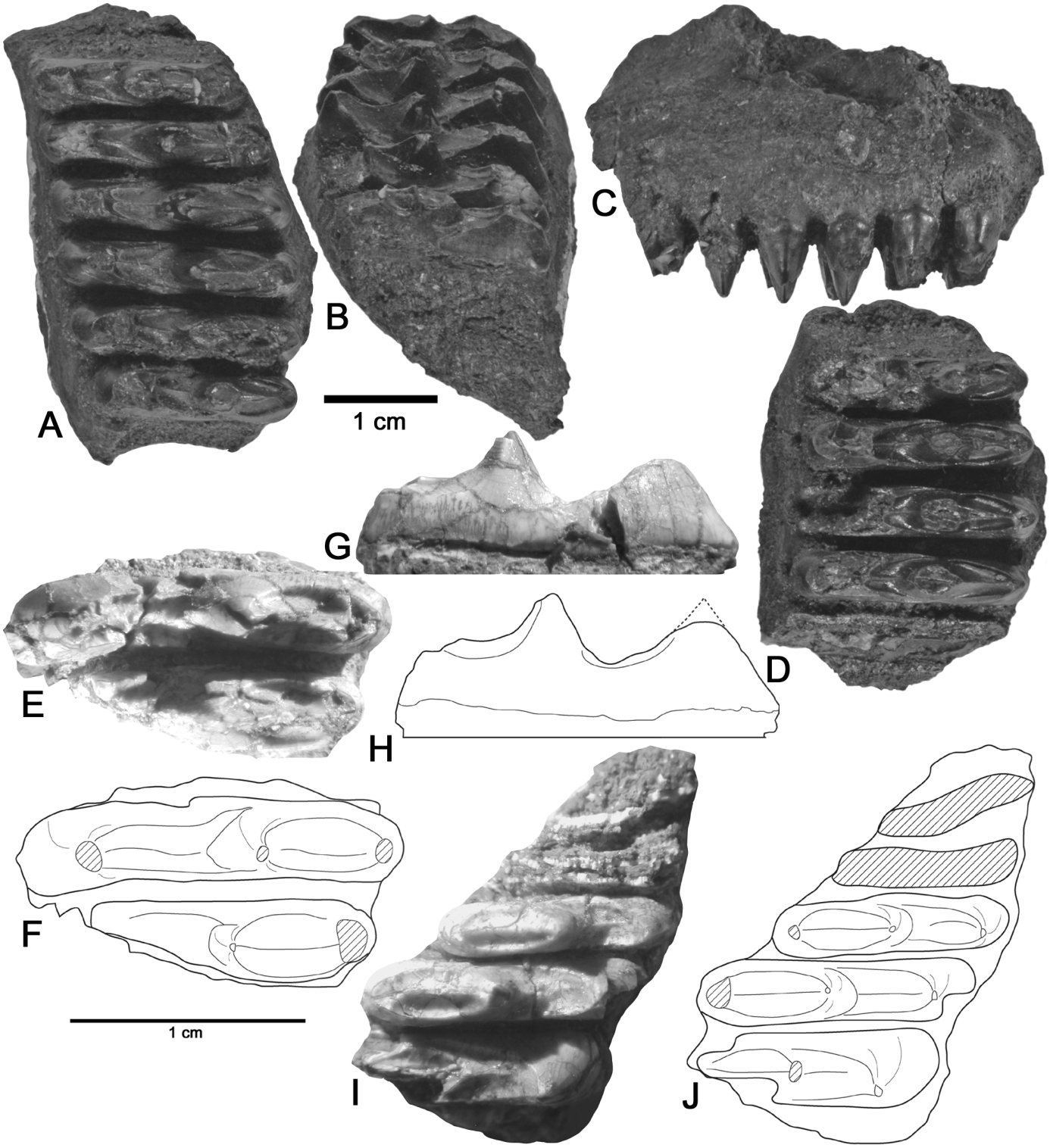

FIGURE 3. Comparison of the holotype of *Trilophosaurus dornorum* to large *T. jacobsi* teeth from the Kahle *Trilophosaurus* quarry (NMMNH locality 3775). **A-D**, Partial maxilla and dentary of the holotype of *Trilophosaurus* "*dornorum*" (= *T. jacobsi*), PEFO 31165. **A-C**, Partial maxilla in **A**, occlusal, **B**, oblique and **C**, lateral views. **D**, Partial dentary in occlusal view. **E-J**, Photographs and line drawings of large isolated jaw fragments (NMMNH P-54151) of *Trilophosaurus jacobsi* from the Kahle *Trilophosaurus* quarry (NMMNH L-3775). **E-H**, One maxillary/dentary fragment in **E-F**, occlusal and **G-H**, posterior? views. **I-J**, Another maxillary/dentary fragment in occlusal view. Dotted lines are inferred cusp height based on cusp base. **A-D**, after Mueller and Parker (2006).

lated *Trilophosaurus* teeth are highly distinct and may have been collected by crew members preferentially relative to other taxa; and (3) *Trilophosaurus* teeth may have been sufficiently worn by the time they were shed that they are generally unrecognizable." Of these three conclusions, Heckert (2004) suggested that the "interplay of (2) and (3) is the most likely."

However, the interpretation of *Trilophosaurus* as an arboreal climber, as concluded by Spielmann et al. (2005), along with the general

absence of plant material in the quarry, seem to validate option (1) by way of negative evidence. Two of us (JAS and ABH) thoroughly examined the original collections made from quarry 1, housed at the Texas Memorial Museum, and found no large cache of isolated *T. buettneri* teeth in the collection, so unless crew members were collecting the distinctive teeth for themselves, interpretation (2) appears unlikely. Both Heckert (2004) and Elder (1978, 1989) agree that body fossils present in the quarry were not carried far prior to deposition.

NMMNH locality 4208 (*Trilophosaurus* quarry 2)

Trilophosaurus quarry 2 occurs within the same stratigraphic interval as quarry 1. However, quarry 2 is not as rich as quarry 1, yielding far fewer specimens overall and thus fewer *T. buettneri* specimens. Although *Trilophosaurus* fossils dominate the assemblage at quarry 1, the fauna of quarry 2 is more diverse, with metoposaur fossils, including nearly complete skulls, representing approximately half of the recovered specimens. Most of the *Trilophosaurus* material from quarry 2 is postcrania with little or no association. The only exception to this is portions of the holotype of "*Malerisaurus langstoni"* (Spielmann et al., 2006b).

NMMNH locality 1312 (Lower Kalgary site)

The Lower Kalgary site is low in the Tecovas Formation, just above the Camp Springs Formation and approximately 4 m above the base of the Chinle Group (Lucas and Luo, 1993). The presence of the phytosaur *Rutiodon* and the aetosaur *Stagonolepis* indicate an Adamanian age for the Tecovas Formation. However, as noted by Heckert (2004), the lower part of the Tecovas may be equivalent to the Colorado City Formation, and one of the scutes identified as a paramedian of the Adamanian index fossil *Stagonolepis* may be misidentified and actually belong to the Otischalkian *Longosuchus*.

Heckert (2004) noted that at this site teeth of *T. buettneri* are common; the best preserved is NMMNH P-34291. Less complete, but similar teeth, were cataloged as NMMNH P-34292. Other *Trilophosaurus*? sp. records are incomplete crowns that were mass-cataloged as NMMNH P-34293, though some of these incomplete specimens may pertain to procolophonids (e.g., NMMNH P-30817).

NMMNH locality 1430 (Upper Kalgary site)

The Upper Kalgary site is approximately 400 m south of the Lower Kalgary site. It is 10.5 m higher in the section than the lower site and is Adamanian in age (Lucas and Luo, 1993; Heckert, 2004).

This is the only known site to contain both *T. buettneri* and *T. jacobsi* material together. According to Heckert (2004), teeth of both species are relatively common, with the *T. buettneri* teeth from the site cataloged as NMMNH P-34373 to P-34375 and the *T. jacobsi* teeth cataloged as NMMNH P-26421, P-34073 and P-34372. Heckert (2004) also noted that there are a variety of both enamel-less and fragmentary teeth of both species collected from the site.

NMMNH locality 858 (*Placerias* quarry)

Murry (1987) collected and named *T. jacobsi* based on a single maxilla fragment (MNA V3192) from the *Placerias* quarry in east-central Arizona. The quarry is located low in the Bluewater Creek Formation (Chinle Group) and is of early Adamanian age (Lucas et al., 1997; Heckert et al., 2005). From this locality, only maxillae (MNA V3194 and V3197), dentaries (MNA V3193, 3198 and 3199) and tooth fragments (MNA V3195 and V3200) of *T. jacobsi* were reported by Murry (1987). Long and Murry (1995) referred sacral vertebrae, incomplete fore- and hind limb elements and pelvic girdle material from the *Placerias* in the UCMP and MNA collections to *Trilophosaurus* sp., noting that the MNA material may all represent a single individual. We interpret this material as pertaining to *T. jacobsi* because no material from *T. buettneri* has been recovered from the quarry (see list of referred specimens in Appendices 1 and 2 for additional information).

NMMNH locality 2739 (Sixmile Spring locality)

Heckert (2004) collected a microvertebrate fauna from the Sixmile Spring locality in west-central New Mexico, which is low in the Chinle Group, approximately 9.5 m above the base of the Bluewater Creek Formation (Heckert and Lucas; 2002a). This locality is at approximately the same stratigraphic level as the *Placerias* quarry in Arizona. As noted by Heckert (2004), the presence of the aetosaur *Stagonolepis* in the Bluewater Creek Formation indicates an Adamanian (latest Carnian, late Tuvalian) age for this locality.

Heckert (2004) reported three incomplete tooth fragments (NMMNH P-34447, P-34448 and P-34472) that were derived from polycuspate teeth. He thus assigned these three tooth fragments to aff. *T. jacobsi*. We include these teeth in our discussion, regardless of the tentative nature of the assignment, for the sake of completeness.

Walker's Tank (*T. buettneri* type locality)

Case collected the holotype of *T. buettneri* in the 1920s (Case, 1928a, b) from a locality near Walker's Tank in Crosby County, West Texas. This locality is stratigraphically low in the Tecovas Formation. The holotype is the only known *Trilophosaurus* specimen from this locality.

PFV 122 (Dying Grounds)

Heckert (2004) sampled three horizons in the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, Arizona. The collecting area these samples came from has traditionally been referred to as the "Dying Grounds" (see Heckert, 2004, p. 130, and Parker, 2002, for a history of the term Dying Grounds). The Dying Grounds are stratigraphically high in the Blue Mesa Member, approximately 47 m above its base and 30 m below the overlying Sonsela Member (Heckert and Lucas, 2002b; Heckert, 2004; Parker, 2006; Woody, 2006). The fauna of the Dying Grounds is part of the type assemblage of the Adamanian lvf and is latest Carnian in age (Lucas and Hunt, 1993a; Lucas, 1997, 1998).

Murry (1989a, b, fig. 7H) first illustrated a single *Trilophosaurus buettneri* tooth from this site. This locality represents the stratigraphically highest unambiguous occurrence of *T. buettneri* teeth. However, Heckert (2004) did not recover any *Trilophosaurus* teeth from the site, even after extensive screenwashing. Thus, we conclude that *Trilophosaurus* teeth are extremely rare at this locality.

North Stinking Springs

Polcyn et al. (2002) included *T. jacobsi* in the faunal list of their North Stinking Springs site, near North Stinking Springs Mountain in Arizona. Unfortunately, the specimen was neither discussed nor illustrated. Based on photographs of the specimen, provided by Polcyn, we conclude that it is actually a *T. buettneri* tooth, not a *T. jacobsi* tooth. This site is in the Blue Mesa Member of the Petrified Forest Formation (Heckert et al., 2005).

NMMNH locality 3775 (Kahle *Trilophosaurus* quarry)

The Kahle *Trilophosaurus* quarry is the most productive *Trilophosaurus* locality of the last half-century. Robert Kahle discovered it in the early 1990s while working in West Texas near Big Spring. After its initial discovery, Kahle made extensive collections from the site. He later contacted the NMMNH and has since worked with the NMMNH in collecting and documenting this important locality (Lucas et al., 1993; Heckert et al., 2001, 2006).

The Kahle quarry is located in a moderate brown, clast-supported conglomerate of rounded, flattened, intraformational mud pebbles up to 2 cm in diameter with a matrix that is a rounded, moderately poorly-

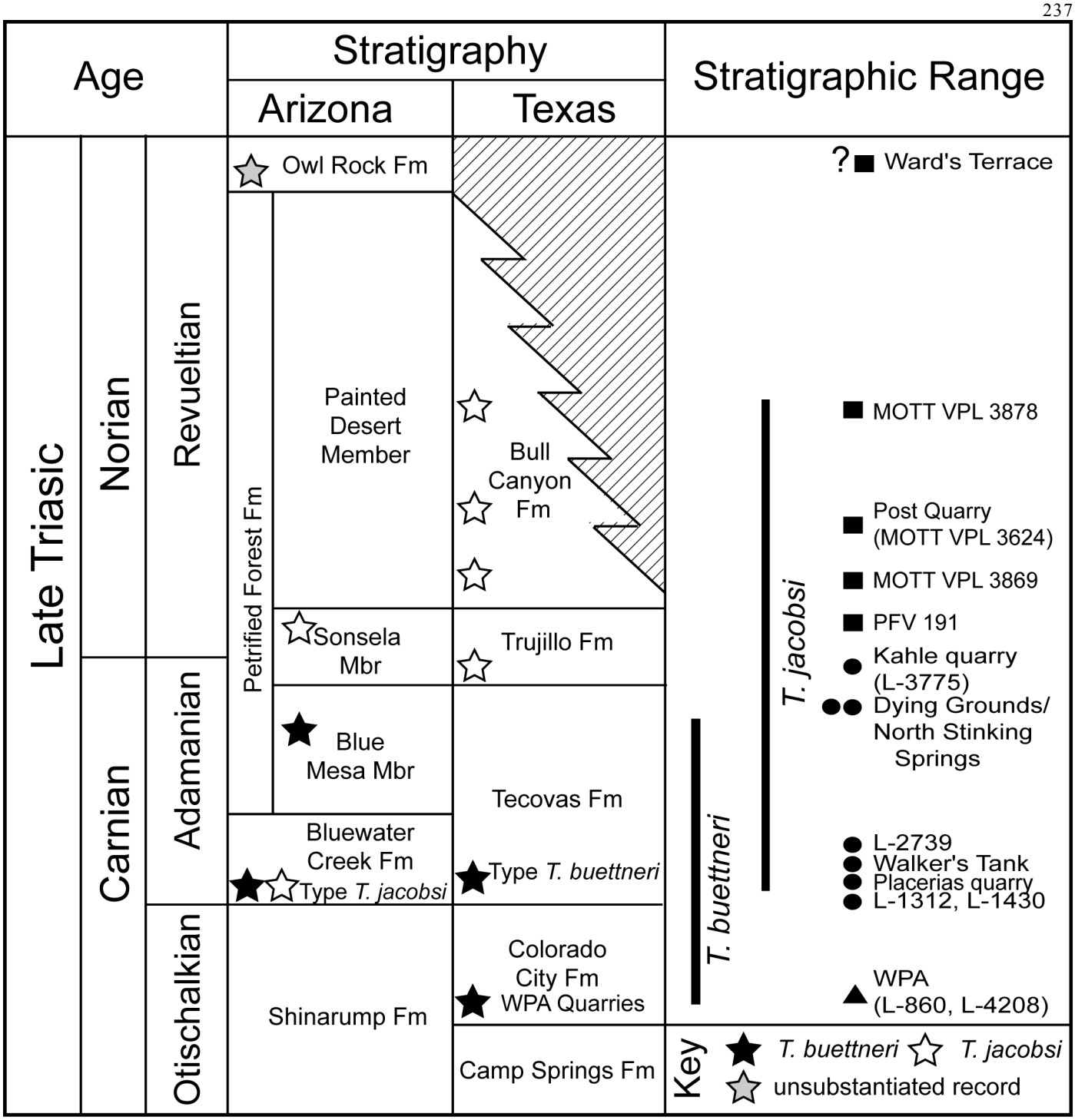

FIGURE 4. Biostratigraphic distribution of *Trilophosaurus* occurrences in the southwestern USA. See text for discussion. Modified from Heckert et al. (2006).

sorted sublitharenite (Heckert et al., 2001). It has been difficult to determine exactly where the Kahle quarry occurs stratigraphically, because it lies close to the contact between the Tecovas and Trujillo formations (Heckert et al., 2001). However, the latest interpretation of the site, by Heckert et al. (2006) concludes that it is stratigraphically low in the Trujillo Formation.

The Kahle *Trilophosaurus* quarry has produced a copious amount of material, nearly all of it (over 90%) assigned to *T. jacobsi*. The predominance of *Trilophosaurus* material at the site is reminiscent of *Trilophosaurus* quarry 1. While nearly all of the *T. jacobsi* material recovered constitute postcrania, a few exceptional skulls have been collected, one of which enable Heckert et al. (2006) to reestablish *T. jacobsi* as a trilophosaurid and not a procolophonid. This site also contains the only identified postcrania of *T. jacobsi*.

PFV 191 (*T. "dornorum"* type locality)

PFV 191 is located approximately 20 m above the top of the Blue Mesa Member of the Petrified Forest Formation (Mueller and Parker, 2006). The presence of the aetosaur *Paratypothorax* and the phytosaur *Pseudopalatus* in lower horizons of nearby sites (Crystal Forest, PFV 173 and Mountain Lion Mesa, PFV 295) suggest a Revueltian age for the site.

Mueller and Parker (2006) collected maxilla and dentary fragments as "float on small mudstone mounds at the base of an escarpment" from PFV 191. Based on these fragments they named a new species of *Trilophosaurus*, *T. dornorum*. However, we interpret *T. dornorum* as a synonym of *T. jacobsi* (see below). No description of the specimen's condition is available in Mueller and Parker (2006), but from their published photographs (Fig. 3A-D) it appears that none of the teeth in their holotype are complete, many having chipped or rounded cusps.

MOTT VLP 3624, 3869 and 3878

The various MOTT localities are all located south of Post in Garza County, Texas, in the Bull Canyon Formation, referred to as the "Cooper Canyon Formation" by Mueller and Parker (2006). At MOTT VPL 3869, the fossils come from a mudstone less than 1 m thick above a carbonate granule conglomerate that is approximately 8 m above the base of the Bull Canyon Formation (Mueller and Parker, 2006). MOTT VPL 3624, also known as the Post Quarry, has produced a number of temnospondyl amphibians and large archosauromorphs (Chatterjee, 1985; Long and Murry, 1995). MOTT VPL 3878 occurs in the upper part of the Bull Canyon Formation, approximately 50 m above the level of the Post Quarry; at this locality fossils are sparse, and the fauna is dominated by phytosaurs and aetosaurs. This occurrence of *T. jacobsi* is the youngest occurrence of the taxon.

VPL 3869 has produced the greatest number of *T. jacobsi* remains among the MOTT localities, with two partial right maxillae (TTU-P10413 and TTU-P10582), a partial left maxilla (TTU-P10583) and right and left dentary fragments (TTU-P10586) having been recovered thus far. An isolated tooth of *T. jacobsi* (TTU-P09497) is the only *Trilophosaurus* fossil recovered from VPL 3624. *Trilophosaurus* remains from VPL 3878, like those from VPL 3624, consist of a single specimen, a partial maxilla of *T. jacobsi* (TTU-P10447).

Ward's Terrace

Kirby (1989, 1991, 1993) reported isolated teeth and fragmentary skull bones of *T. buettneri* from the Owl Rock Formation near Ward's Terrace in north-central Arizona, which is late Revueltian in age. This would considerably expand the biostratigraphic range of *T. buettneri*. However, as noted by Heckert et al. (2006), the teeth Kirby reported appear similar to *Tricuspisaurus*, a procolophonid found in similar age strata in Britain (Robinson, 1956; Fraser, 1986). Also, Heckert et al. (2006) postulated that the fossils could represent *Trilophosaurus*, but be due to contamination from screenwashing a stratigraphically older site. In any case, we follow Heckert et al. (2006) in considering this record of *T. buettneri* questionable.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768
Subclass DIAPSIDA Osborn, 1903
Superorder ARCHOSAUROMORPHA Huene, 1946
Family TRILOPHOSAURIDAE Gregory, 1945

Genus *Trilophosaurus* Case 1928a

1928a *Trilophosaurus* Case, p. 177
1993 *Chinleogomphius* Sues and Olsen, p. 285

Type species: *Trilophosaurus buettneri* Case, 1928a.

Included species: The type species and *T. jacobsi* Murry, 1987 (= *T. dornorum* Mueller and Parker, 2006).

Revised diagnosis: An archosauromorph that can be distinguished from all other archosauromorphs by its transversely broad, tricuspid teeth and a femur with a prominent internal trochanter that extends one-third of the way down the shaft. A tetralobate humerus also distinguishes *Trilophosaurus* from all other archosauromorphs, except aetosaurs and the rhynchosaur *Otischalkia elderae*.

Distribution: Upper Triassic of the American Southwest (Texas, New Mexico and Arizona) (Figs. 1, 4).

Discussion: Long and Murry (1995) noted three records of *Trilophosaurus* sp., in the UCMP collection, from the lower Petrified Forest Formation in the Petrified Forest National Park. These records consisted of caudal vertebrae from Agate Bridge N (UCMP locality V82239, PFV 161) and Saurian Valley (UCMP locality V82251, PFV 97) and an uncataloged ilium from the Saurian Valley locality. Irmis and Parker (2005) interpreted the caudal vertebrae as being Archosauria indet. and were not able to relocate the ilium. Given the tentative nature of the identification of the ilium and the reidentification of the vertebrae by Irmis and Parker, we do not include any of these three records in our referred material (Appendices 1-2).

Trilophosaurus buettneri Case, 1928a
Fig. 2A-F

1928a *Trilophosaurus buettneri* Case, p. 177, fig. 1.
1928b *Trilophosaurus buettneri*: Case, p. 1, pl. 1, figs. 1-5.
1945 *Trilophosaurus buettneri*: Gregory, p. 273, figs. 2-11, pls. 19-33, 8 unnumbered tables.
1956 *Trilophosaurus buettneri*: Romer, p. 165, figs. 88, 110c, 121i, 140t-u, 147b, 158b, 186d, 189f.
1966 *Trilophosaurus buettneri*: Romer, p. 122, figs. 181, 182.
1969 *Trilophosaurus buettneri*: Parks, p. 1, figs. 1-22, 24-39.
1969 *Trilophosaurus buettneri*: Kuhn, p. 24, pl. 11, fig. 1; pl. 12, figs. 6, 12.
1969 *Trilophosaurus buettneri*: Kuhn, p. 24, pl. 12, figs. 1-4.
1981 *Trilophosaurus buettneri*: DeMar and Bolt, p. 967, figs. 1, 4-5, 6?, 7-8.
1986 *Trilophosaurus buettneri*: Murry, p. 116, fig. 9.5G-G2, 9.13a.
1988 *Trilophosaurus buettneri*: Carroll, p. 264, figs. 13-2c, 13-3d, 13-6.
1989 *Trilophosaurus buettneri*: Murry, p. 249, fig. 7h.
1993 *Trilophosaurus buettneri*: Lucas et al., p. 237, fig. 4a-i.
1997 *Trilophosaurus*: Benton, p. 144, fig. 6.5a-b.
2004 *Trilophosaurus buettneri*: Heckert, p.1, figs. 37, 76.
2006 *Trilophosaurus buettneri*: Heckert et al., p. 1, figs. 3, 7F, H.
2006 *Trilophosaurus buettneri*: Mueller and Parker, p. 119, fig. 5a.
2006 *Trilophosaurus buettneri*: Spielmann et al., p. 543, figs. 2, 3, 4i-t.

Holotype: UMMP 2338, an incomplete right dentary fragment bearing parts of five teeth from the Tecovas Formation near Walker's Tank, Texas, USA (Fig. 3-E).

Referred material: A complete list of referred material will be presented in Spielmann et al., in prep.

Revised diagnosis: A species of *Trilophosaurus* distinguished from *T. jacobsi* by the lack of prominent cingula linking the cusps both labiolingually across the center of the tooth and also along the mesial and distal margins of the tooth; central cusp subequal in height to the labial and lingual cusps; central cusp not displaced labially or lingually, so tooth crown is labiolingually symmetrical in occlusal view; cervical vertebrae with bifurcated postzygapophses; procoelous cervical centra; double keeled sacral centra; a lack of prominent ridges on the sacral vertebrae extending from the posterior margin of the pre- and postzygapophyses to the base of the neural spine; sacral neural spines extend nearly the entire length of the centra; rectangular ectepicondyle; radial condyle of humerus larger than ulnar condyle; proximal femur is rhombus-shaped; astragalus with pointed calcaneal articular surface; ridge developed on posterior astragalus; "neck" of astragalus gracile and elongate.

Description: Case (1928a, b) and Gregory (1945) have provided descriptions of specimens of *Trilophosaurus buettneri*.

Discussion: There has been no disagreement as to what constitutes *Trilophosaurus buettneri*, other than that some authors have considered *T. buettneri* and *T. jacobsi* a single species.

Trilophosaurus jacobsi Murry, 1987
Figs. 2G-J, 3A-J

1987 *Trilophosaurus jacobsi* Murry, p. 773, figs. 1-3.
1993 *Chinleogomphius jacobsi*: Sues and Olsen, p. 285.
2001 *Trilophosaurus buettneri*: Heckert et al., p. 115, fig. 2a-e.
2004 *Trilophosaurus jacobsi*: Heckert, p. 1, figs. 77, 100.
2005 *Trilophosaurus jacobsi*: Spielmann et al., p. 395, figs. 3, 5, 7.
2006 *Trilophosaurus dornorum* Mueller and Parker, p. 119, figs. 3, 5b.

Holotype: MNA V3192, a tooth-bearing left maxilla fragment from the *Placerias* quarry, Upper Triassic Bluewater Creek Formation, Arizona, USA (Fig. 2G-J).

Referred material: A complete list of referred material will be presented in Spielmann et al., in prep.

Diagnosis: A species of *Trilophosaurus* distinguished from *Trilophosaurus buettneri* by the presence of prominent cingula linking the cusps both labiolingually across the center of the tooth and also along the mesial and distal margins of the tooth; the tooth is asymmetric in occlusal view, with the central cusp offset labially; the central cusp is asymmetric in occlusal view with a rounded, convex lingual margin and a more complex, steeper-sided, doubly concave labial margin; lingual cusp is low, transversely expanded and mesiodistally compressed; cervical vertebrae have no bifurcation of the postzygapophyses; cervical centra amphicoelous; single keeled sacral centra; prominent ridges on the sacral vertebrae extending from the posterior margin of the pre- and postzygapophyses to the base of the neural spine; length of the neural spine of sacral vertebrae less than half the length of the centrum; ectepicondyle rounded; ulnar condyle of the humerus larger than radial condyle; proximal femur is elliptical with a central depression; astragalus with rounded calcaneal articular surface; "neck" of astragalus thicker and taller than that of *T. buettneri*.

Discussion: The distinct tooth morphology of each species of *Trilophosaurus* is documented in Heckert et al. (2006). The osteology of *Trilophosaurus jacobsi* that we will report elsewhere (Spielmann et al., in prep.) allows for the first comparison of postcranial characters between the two species of *Trilophosaurus*, indeed, differences in the postcrania are evident within both the vertebral column and limbs. The pectoral and pelvic girdles of both species appear similar.

***Trilophosaurus* "*dornorum*:"** As noted above, Mueller and Parker (2006) named a new species of *Trilophosaurus*, *T. dornorum*, based on maxilla and dentary fragments from the Petrified Forest National Park, Arizona and the Post Quarry collecting area, West Texas. Muller and Parker (2006, p. 121) provided the following diagnosis of *T. dornorum*: "medial and lingual cusps are similar in size and the medial cusp is offset labially. Cingula form deep grooves on larger specimens. Anterior and posterior cingula connecting both labial and lingual cusps to medial cusp, three to three and one-half maxillary teeth posterior to lateral process of maxilla. Maxilla and dentaries are more robust in structure than *T. buettneri* and *T. jacobsi*."

Nevertheless, this diagnosis reveals no tangible reason why *T. dornorum* is distinct from *T. jacobsi*. The claim that medial and lingual cusps being similar in size distinguishes it from *T. jacobsi* is demonstrably incorrect: large, isolated maxilla and dentary fragments of *T. jacobsi* collected from the Kahle quarry show that the cusps become subequal in size in large individuals. Thus, we interpret the holotype of *T. dornorum* as belonging to a large individual of *T. jacobsi*. "Cingula forming deep grooves in large specimens," is also true of these large specimens from the Kahle quarry, as is the cingula connecting both labial and lingual cusps to the medial cusp. The number of teeth posterior to the lateral flange (lateral process of Mueller and Parker [2006]) should not be used as a diagnostic character, given the documented variation in the number of teeth in a tooth row (DeMar and Bolt, 1981). Finally, the robustness of the specimen "is not sufficient for taxonomic differentiation" of *T. dornorum*, as readily admitted by Mueller and Parker (2006, p. 122). Thus, all the features claimed by Muller and Parker (2006) as diagnostic of *T. dornorum* are also present in large individuals of *T. jacobsi*, so we synonymize *T. dornorum* with *T. jacobsi*, and consider the holotype and referred material of *T. dornorum* to be large individuals of *T. jacobsi*.

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