TAXONOMY AND BIOSTRATIGRAPHY OF THE LATE TRIASSIC ARCHOSAUROMORPH TRILOPHOSAURUS

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Abstract—Trilophosaurus is an aberrant archosauromorph reptile known 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 providing Case's impetus to name the taxon *T. buettneri* and discuss the growth, variation and functional morphology of *Trilophosaurus*.


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
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 protosaurus, whereas Case (1928a, b) had previously considered it a cottosaurus. This assignment of Trilophosaurus to the Protosaurus would not be challenged until the 1980s. Thus, for example, the information Kuhn (1969, p. 26, figs. 11-12) presented in his review of “Trilophosaurus” (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 re-prepared 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-sutures of the cranium). Another central aspect of Parks’ (1969) thesis, further refined by 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-1) from the Placerias quarry near Romoeno 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 quadratojugal 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, Chineleogaphius, 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 (Lv) 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 Chineleogaphius (=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
shows no characters other than size that distinguish it from other, established femora of *T. buettneri*.

Merek (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 (NMMNH 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 ostrichthians, vertebrae copepods and unionid bivalve shells. Heckert et al. (2001) also provided a summary of the biostatigraphic 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 archaosauriform reptiles.

Spiegelman 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, Spiegelman 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 illustrated 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, Sonsella 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 Sonsella Member of the Petrified Forest Formation are Revuelitian in age, so these records represent the only known records of *T. jacobsi* in the Revuelitian and are thus the youngest occurrences of the taxon.

Spiegelman et al. (2006b) reinterpreted the holotype of *Malerasaurus 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, Spiegelman et al. (2006b) noted that the other species of *Malerasaurus*, *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 Revuelitian, with *T. buettneri* extending from the middle Otischalkian to late Adamanian and *T. jacobsi* extending from the early Adamanian into the Revuelitian (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 bentonite 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-

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 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-34241, P-34307 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 *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-
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 actosaur *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.

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**FIGURE 4. Biostratigraphic distribution of *Trilophosaurus* occurrences in the southwestern USA.** See text for discussion. Modified from Heckert et al. (2006).
Mueller and Parker (2006) collected maxilla and danty 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. dororum*. However, we interpret *T. dororum* 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 3869 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 screenswashing 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 TRILOPHOSAURIIDAE 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. dororum* Mueller and Parker, 2006).

**Revised diagnosis:** An archosauromorph that can be distinguished from all other archosauromorphs by its transversely broad, tricuspid teeth and a furuncul 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 rhynechosauroid *Otischalkia elderae*.

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

**Discussion:** Long and Murray (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 Archosauromorpha 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, 168d, 189f.
1966 *Trilophosaurus buettneri*; Buettner, p. 122, figs. 181, 182.
1970 *Trilophosaurus buettneri*; Buettner, Kuhn, p. 24, pl. 11, fig. 1; pl. 12, figs. 6, 12.
1979 *Trilophosaurus buettneri*; Buettner, Kuhn, p. 24, pl. 12, figs. 1-4.
1981 *Trilophosaurus buettneri*; Buettner, DeMar and Bolt, p. 967, figs. 1, 4-5, 6s, 7-8.
1993 *Trilophosaurus buettneri*; Murry, p. 249, fig. 7h.
1993 *Trilophosaurus buettneri*; Lucas et al., p. 237, fig. 4a-i.
1997 *Trilophosaurus buettneri*; Benton, p. 144, fig. 6.5a-b.
2004 *Trilophosaurus buettneri*; Buettner, p. 1, figs. 37, 76.
2006 *Trilophosaurus buettneri*; Buettner et al., p. 1, figs. 3, 7f, H.
2006 *Trilophosaurus buettneri*; Buettner and Buettner, p. 119, fig. 5a.
2006 *Trilophosaurus buettneri*; Sues 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 subequall 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 postzygapophyses; 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; sacrail neural spines extend nearly the entire length of the centra; rectangular ectepicondyle; radial condyle of humerus larger than ulnar condyle; proximal femur is thombus-shaped; astragulus with pointed calcaneal articular surface; ridge developed on posterior astragulus; “neck” of astragulus gracile and elongate.

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

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**Reference:**

Case, p. 177, fig. 1.
Case, p. 1, pl. 1, figs. 1-5.
Gregory, p. 273, figs. 2-11, pls. 19-33, 8 unnumbered tables.
Romer, p. 165, figs. 88, 110c, 121i, 140t-u, 147b, 158b, 168d, 189f.
Buettner, p. 122, figs. 181, 182.
Mueller and Parker, p. 119, fig. 9.5G-G2, 9.13a.
Carroll, p. 264, figs. 13-2c, 13-3d, 13-6.
Murry, p. 249, fig. 7h.
Lucas et al., p. 237, fig. 4a-i.
Benton, p. 144, fig. 6.5a-b.
Buettner, p. 1, figs. 37, 76.
Buettner et al., p. 1, figs. 3, 7f, H.
Sues et al., p. 543, figs. 2, 3, 4i-t.
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

2001 *Trilophosaurus buettneri*: Heckert et al., p. 115, fig. 2a-e.
2004 *Trilophosaurus buettneri*: 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 ectepicondyle rounded; ulnar condyle of the humerus larger than radial spine of sacral vertebrae less than half the length of the centrum; 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; cingula forming deep grooves in large specimens, is also true of these large specimens from the Kahle quarry, as in 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*.

ACKNOWLEDGMENTS

Robert Sullivan and Jerry Harris provided helpful reviews that improved the manuscript. Michael Polcyn provided unpublished photographs of the North Stinking Springs *Trilophosaurus* specimen. Bill Parker provided photographs of the holotype of “*T. dornorum*.” Bob Kahle donated his collections to the NMMNH. SEM work was conducted at the Institute of Meteoritics at the University of New Mexico. Tim Rowe kindly provided loans of TMM material and assisted with our study of the collections at TMM.

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