



The Late Triassic Archosauromorph Trilophosaurus as an Arboreal Climber

By: **Andrew Heckert**, Justin A. Spielmann & Spencer G. Lucas

Abstract

Two species of the unusual archosauromorph Trilophosaurus, *T. buettneri* Case and *T. jacobsi* Murry, are known from diverse localities in the Upper Triassic Chinle Group in the southwestern USA. Both species likely occupied similar ecological niches, based on morphological similarities in the postcrania, which are essentially identical. Trilophosaurus occurrences in the Chinle Group are relatively rare, but individual sites are exceptionally rich, suggesting that Trilophosaurus lived in a different paleoenvironment than more typical Chinle vertebrates, which lived in or near streams (phytosaurs, metoposaurs) or on floodplains (aetosaurs, rauisuchians, and dinosaurs). Two potential interpretations are that Trilophosaurus was either an arboreal climber or a fossorial digger. However, the gross skeletal features of Trilophosaurus are not compatible with a fossorial mode of life: the limbs are too long and gracile, proximal limb elements are longer than distal ones, and the claws are laterally compressed, not transversely broadened. The intermittent study of Trilophosaurus has caused the theory of it being arboreal, originally proposed by Gregory, to receive little mention in subsequent studies. We reexamined the functional morphology of Trilophosaurus using a qualitative functional morphological analysis of the skeleton, a quantitative examination of claw curvature, and a quantitative examination of manus/trunk and pes/trunk ratios. Claw morphology of Trilophosaurus shows similarities to the arboreal drepanosaurs *Drepanosaurus* and *Megalancosaurus*. Our analysis provides ample evidence to suggest that Trilophosaurus was arboreal.

THE LATE TRIASSIC ARCHOSAUFOMORPH *TRILOPHOSAUFURUS* AS AN ARBOREAL CLIMBER

JUSTIN A. SPIELMANN¹, ANDREW B. HECKERT² & SPENCER G. LUCAS²

Received: November 15, 2004; accepted: August 12, 2005

Key words: *Trilophosaurus*, Late Triassic, arboreal, claw curvature, functional morphology.

Abstract. Two species of the unusual archosauromorph *Trilophosaurus*, *T. buettneri* Case and *T. jacobsi* Murry, are known from diverse localities in the Upper Triassic Chinle Group in the southwestern USA. Both species likely occupied similar ecological niches, based on morphological similarities in the postcrania, which are essentially identical. *Trilophosaurus* occurrences in the Chinle Group are relatively rare, but individual sites are exceptionally rich, suggesting that *Trilophosaurus* lived in a different paleoenvironment than more typical Chinle vertebrates, which lived in or near streams (phytosauroids, metoposauroids) or on floodplains (aetosauroids, rauisuchians, and dinosaurs). Two potential interpretations are that *Trilophosaurus* was either an arboreal climber or a fossorial digger. However, the gross skeletal features of *Trilophosaurus* are not compatible with a fossorial mode of life: the limbs are too long and gracile, proximal limb elements are longer than distal ones, and the claws are laterally compressed, not transversely broadened. The intermittent study of *Trilophosaurus* has caused the theory of it being arboreal, originally proposed by Gregory, to receive little mention in subsequent studies. We reexamined the functional morphology of *Trilophosaurus* using a qualitative functional morphological analysis of the skeleton, a quantitative examination of claw curvature, and a quantitative examination of manus/trunk and pes/trunk ratios. Claw morphology of *Trilophosaurus* shows similarities to the arboreal drepanosauroids *Drepanosaurus* and *Megalancosaurus*. Our analysis provides ample evidence to suggest that *Trilophosaurus* was arboreal.

Riassunto. Nel Gruppo Chinle (Triassico Superiore) del Sudovest degli USA sono note due specie dell'insolito arcosauromorfo *Trilophosaurus*, *T. buettneri* Case e *T. jacobsi* Murry, provenienti da diverse località. Probabilmente entrambe le specie occupavano nicchie ecologiche simili, sulla base di affinità morfologiche nelle ossa postcraniche, che sono sostanzialmente identiche. I ritrovamenti di *Trilophosaurus* nel Gruppo Chinle sono relativamente rari, ma singole località possono essere significativamente ricche, suggerendo che *Trilophosaurus* visse in un ambiente diverso da quello dei tipici vertebrati della Chinle, che popolavano i fiumi o le loro vicinanze (fitosauroidi, metoposauroidi) o le

piane alluvionali (aetosauroidi, rauisuchii e dinosauri). Due interpretazioni etologiche sono possibili, e cioè che *Trilophosaurus* fosse un arboricolo, oppure uno scavatore. Tuttavia le caratteristiche scheletriche principali di *Trilophosaurus* non sono compatibili con lo stile di vita di un fossatore: le zampe sono troppo lunghe e gracili, gli elementi prossimali delle zampe sono più lunghi di quelli distali, e gli artigli sono compressi lateralmente e non allargati in senso trasversale. Essendo sporadici gli studi su *Trilophosaurus* l'interpretazione che fosse arboricolo, proposta inizialmente da Gregory, ricevette poca attenzione negli studi successivi. Noi abbiamo riesaminato la morfologia funzionale di *Trilophosaurus* utilizzando l'analisi qualitativa della morfologia funzionale dello scheletro, la valutazione quantitativa della curvatura degli artigli, e dei rapporti manus/tronco e pes/tronco. La morfologia degli artigli di *Trilophosaurus* mostra somiglianze con i drepanosauroidi arboricoli *Drepanosaurus* and *Megalancosaurus*. La nostra analisi fornisce ampie evidenze per sostenere che *Trilophosaurus* fosse arboricolo.

Introduction

Trilophosaurus is an unusual archosauromorph whose fossils are known principally from Upper Triassic strata of northwestern Texas, with fragmentary remains known from New Mexico and Arizona. The limited paleogeographical range and relative rarity of localities yielding *Trilophosaurus* fossils has resulted in only intermittent study of this animal since it was named by Case (1928). Further studies of *Trilophosaurus*, such as Gregory's (1945) osteology and Parks' (1969) thesis on its cranial anatomy and mastication, remain the most thorough examination of this unique animal and are the foundation upon which this study is built.

In Gregory's (1945) osteology of *Trilophosaurus buettneri* he asserted that *Trilophosaurus* was probably arboreal. This assertion has received little mention in

1 New Mexico Museum of Natural History and Science, 1801 Mountain Rd. NW, Albuquerque NM 87104-1375.
E-mail: Justin.Spielmann1@state.nm.us

2 Appalachian State University, 572 Rivers Street, Boone, NC 28608-2067.

subsequent studies of the animal. Hildebrand (1974) and Cartmill (1985), in their works on functional morphology, have outlined various morphological characters present in extant arboreal species. *Trilophosaurus* appears to have a considerable number of these characters, principally in the fore- and hind limbs. Additionally, the axial skeleton and limbs of *Trilophosaurus* are very similar to those of the extant arboreal green iguana (*Iguana iguana*). All of these features suggest *Trilophosaurus* was arboreal.

As noted by Hildebrand (1974), arboreal animals are not all specialized to the same degree. He states (p. 552) that in some arboreal animals "The feet and sometimes the tail, may be modified to grip the substrate, but the remainder of the body is not distinctive." We believe this is the case with *Trilophosaurus*, with key features of its skeleton suggesting it was arboreal. Accordingly, we restrict our analysis to pertinent osteological and functional features. Thus, in this article we report features of the pectoral girdle, humerus, manus, femur, pes, and unguals that indicate that *Trilophosaurus* was arboreal and compare them to the those present in extant terrestrial and arboreal reptiles. Also, we provide a mode of life reconstruction, principally describing the locomotion of *Trilophosaurus* and its utilization of its manus and pes in climbing.

Institutional abbreviations. In this article the following institutional abbreviations are used: New Mexico Museum of Natural History and Science (NMMNH); Michigan State University Museum (MSUM); Museum of Southwestern Biology (MSB/UNM).

Previous studies

Case (1928) described and named *Trilophosaurus buettneri* based on an anterior right dentary fragment, with the generic name describing its distinctive tricuspid teeth. *Trilophosaurus* was later studied extensively by Gregory (1945), who coined the term Trilophosauridae and described the osteology of *Trilophosaurus buettneri*, based on extensive collections made in the late 1930s and early 1940s. This remains the most in-depth description of the postcrania of *Trilophosaurus*.

Gregory's (1945) description of the morphology of the cranium of *Trilophosaurus buettneri* was relatively vague, in large part because the cranial material he studied was heavily concreted and concealed the majority of sutures. Parks (1969) reexamined the cranial anatomy of *Trilophosaurus buettneri* and fully described the morphology and spatial relationship of all the bones of the cranium and also revised the tooth replacement scheme proposed by Gregory (1945). This tooth replacement scheme was revised again by Demar & Bolt (1981). Merck (1995) published an abstract describing some of the features of the skull of *Trilophosaurus*, but

this study has not been published further. Although Parks' thesis remains a key work regarding *Trilophosaurus*, it is not germane to the primary focus of the current study, which is concerned with the postcranial anatomy of *Trilophosaurus*.

The samples utilized by Gregory (1945) in his monograph on *Trilophosaurus buettneri* were collected in 1939-1941 from three quarries in West Texas by members of the Works Projects Administration (WPA). These quarries, near Big Spring, in Howard County, Texas, were later termed simply quarry 1, quarry 2, and quarry 3 (Elder 1978; Long & Murry 1995; Lucas et al. 1993). While each possesses a distinctive fauna, all the quarries are fossil assemblages dominated by *Trilophosaurus* and were thus collectively referred to as the *Trilophosaurus* quarries. The collection that resulted from the WPA excavations is now housed at the Texas Memorial Museum (TMM) in Austin, Texas. A small sample of the extensive collection at TMM served as the primary material for Gregory's (1945) monograph, including an articulated skeleton (TMM 31025-140), lacking only the cranium anterior to the orbits, the left manus, and some caudal vertebrae. Additional *Trilophosaurus* material from quarry 2 was collected in 1947 by Gregory for the Yale Peabody Museum. The NMMNH also houses small collections from *Trilophosaurus* quarries 1 and 2 (NMMNH localities 860 and 4208, respectively).

Murry (1986, 1987) described and named a new species of *Trilophosaurus*, *Trilophosaurus jacobsi*, from the *Placerias* quarry in eastern Arizona, based on what he thought was a right dentary fragment (we have identified it as a left maxillary fragment). The distinguishing feature of *T. jacobsi*, as noted by Murry (1987), is that the central cusp of the unique tricuspid teeth of *Trilophosaurus* is offset labially. There has been some confusion as to the affinities of *Trilophosaurus jacobsi*, specifically whether it is a trilophosaur or a procolophonid (*Chinleogomphius* of Sues & Olsen 1993; Long & Murry 1995). This has recently been settled by the work of Heckert et al. (2003, in press), demonstrating that *Trilophosaurus jacobsi* is congeneric with *T. buettneri*.

Heckert et al. (2001) recorded a new site, the Kahle *Trilophosaurus* quarry (NMMNH locality 3775), from the Trujillo Formation in West Texas, and described the fauna from that site. Recent studies by Heckert et al. (2003, in press) have shown that the remains from Kahle's *Trilophosaurus* quarry belong to *Trilophosaurus jacobsi* and thus represent the only record of *T. jacobsi* other than isolated tooth and maxillary fragments (Murry 1987; Kaye & Padian 1994; Long & Murry 1995). Heckert (2004) has also described isolated tooth fragments of both species from microvertebrate faunas in Texas and documented fragmentary *T. jacobsi* teeth from New Mexico.

Prior to the discovery of the Kahle quarry there had been some speculation regarding the possibility of *Trilophosaurus* having two or more size classes. The WPA quarries 1 and 3 generally yielded larger individuals, whereas quarries 2 and 3A (Elder 1978) yielded smaller individuals. The type of *Trilophosaurus jacobsi* is especially small, indicating it was a juvenile, perhaps only a hatchling. These various size classes noted by some authors (Gregory 1945; Parks 1969; Murry 1987) are indicative of juvenile and adult morphs of each species. The Kahle *Trilophosaurus* quarry stands in contrast to previous sites with an abundance of both adult and juvenile specimens of *Trilophosaurus jacobsi*; previously studied quarries were homogenous in their assemblages, yielding only a single size class of *Trilophosaurus*.

Also of note is that all quarries containing significant *Trilophosaurus* remains are assemblages dominated by them. That is, in each of these quarries, fossils of *Trilophosaurus* account for at least 50% of all specimens preserved, and often exceed 80% of the identifiable bones. This contrasts with most Late Triassic quarries from the surrounding area, which have exceedingly diverse collections of tetrapods. An example of such a quarry is the Snyder quarry, which has a diverse assemblage that contains phytosaurs, aetosaurs, and theropods, in addition to fish, plant, and insect remains (Zeigler et al. 2003; Rinehart et al. 2003; Lucas et al. 2003). The only locality yielding multiple *Trilophosaurus* fossils but not dominated by *Trilophosaurus* is the Placerias quarry, the type locality of *Trilophosaurus jacobsi* Murry. The *Trilophosaurus jacobsi* material from this quarry consists of a few jaw fragments and approximately 20 isolated teeth, which stands in stark contrast to the thousands of elements of a few other tetrapod species from that quarry (e.g., Kaye & Padian 1994; Long & Murry 1995).

The idea that *Trilophosaurus* is arboreal is not a new interpretation, J. T. Gregory (1945) proposed it and noted (p. 324) "The well developed claws on both feet and the slender toes, suggest considerable ability to go up rough surfaces. The compressed claws are unlike those of fossorial animals and are not adapted to digging...it seems most probable that they served principally to secure the animal's feet in locomotion. The flexor muscles of the arm had strong origins on the humerus. The toes could have grasped branches or held rough surfaces in climbing." Although Gregory acknowledged that *Trilophosaurus*, at 1-2 m long, appears large for an arboreal animal, he stated, "[I]t is not impossible that they were [arboreal]. Large species of *Iguana* are arboreal in habit" (p. 325). This is the majority of evidence that Gregory presented to support his interpretation, and, while such evidence is compelling, it is far from conclusive. Due at least in part to the lack of conclusive support for his arboreal interpretation, subsequent authors have not investigated, or even men-

tioned, the potential of *Trilophosaurus* to occupy an arboreal niche. This study aims to rectify this lack of investigation by resurrecting Gregory's interpretation and expanding on it. The support for our interpretation of the arboreal nature of *Trilophosaurus* comes from a qualitative and quantitative comparative morphological analysis, qualitative functional morphological analysis, and a quantitative analysis of claw curvature.

Materials and methods. This study is based on a large collection of *Trilophosaurus* fossils from two localities: WPA quarry 2 (NMMNH locality 4208) and the Kahle *Trilophosaurus* quarry (NMMNH locality 3775). The majority of these fossils were collected by Robert Kahle and donated to the NMMNH. This donation augments collecting done by the NMMNH at locality 3775. In addition to the comparative and functional morphological studies of *Trilophosaurus*, we undertook a quantitative analysis of the claw curvature of the *Trilophosaurus* specimens from NMMNH locality 3775. We describe the methods of this study below.

The remains collected from NMMNH locality 3775 encompass numerous *Trilophosaurus* elements, including hundreds of limb bones, vertebrae, and at least two partial skulls. Following Feduccia (1993), we measured the claw curvature of numerous disarticulated specimens of *Trilophosaurus jacobsi* from this locality, to see if any general pattern could be elucidated. The richness of the site allowed us to measure 25 complete claws that range in size from what are considered adults to presumed juvenile claws.

In preparing the specimens for study we removed any matrix on the claw so as to have an unobstructed lateral (or medial) view of the claw. We then took the claws, some of which were still in matrix blocks and using clay attempted to level the claw. The claws were then photographed using a digital camera (Nikon Coolpix 995) from a constant height and with a constant lens setting (zoom) to maintain the proportions and angle of curvature of each claw. We then printed out the images of the claws and proceeded to make claw curvature measurements following Feduccia (1993).

In addition to the claw curvature analysis a comparative study was undertaken using specimens of extant arboreal or scansorial species borrowed from the Michigan State University Museum (MSUM) and the Museum of Southwestern Biology (MSB/UNM). The comparative specimens are summarized in Table 1.

Michigan State Museum (MSUM)	
<i>Iguana iguana</i>	(MSUM SH. 3299)
<i>Varanus bengalensis</i>	(MSUM SH. 4255)
<i>Varanus salvator</i>	(MSUM SH. 3360)
Museum of Southwestern Biology (MSB/UNM)	
<i>Conolophus subcristatus</i>	(UNM 58668/>UNM 58667)
<i>Ctenosaura pectinata</i>	(UNM 38696)
<i>Dipsosaurus dorsalis</i>	(UNM 41524)
<i>Sauromalus varius</i>	(UNM 38694)
<i>Varanus indicus</i>	(MSB 44397)
<i>Varanus timorensis</i>	(UNM 38695)

Tab. 1 - Comparative reptile specimens used in this study.

Comparative and functional morphology

The initial interpretation of almost any fossil tetrapod found in fluvial sediments is that it is terrestrial, or semi-aquatic. The exceptions to this are animals with

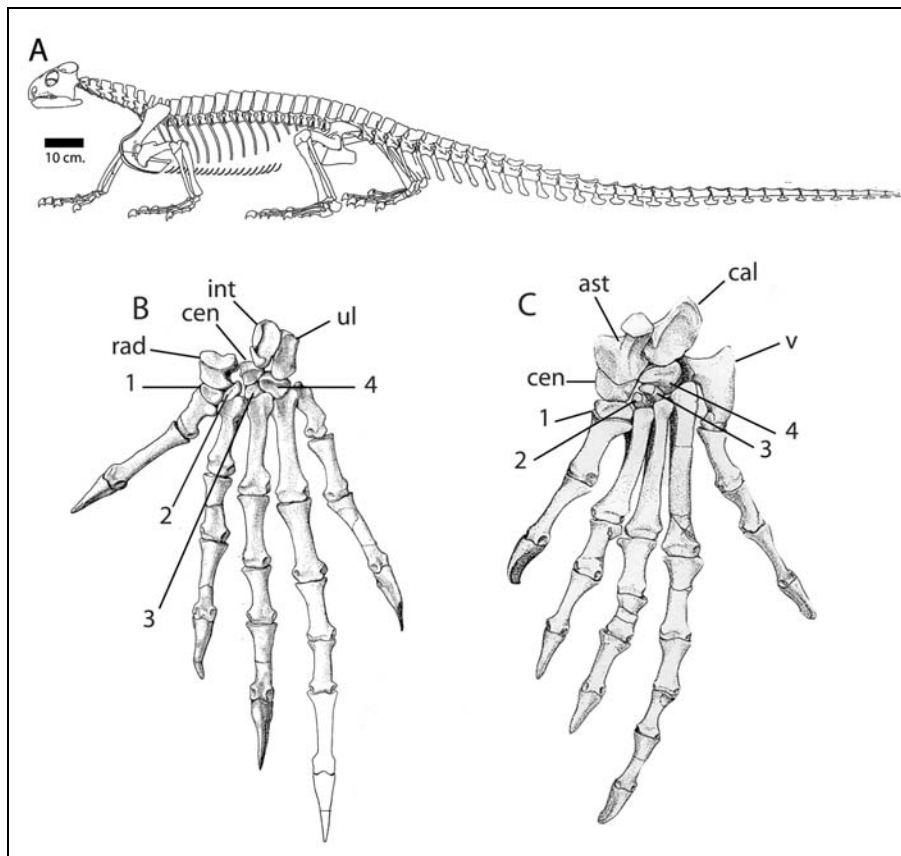


Fig. 1 - A, *Trilophosaurus buettneri* restoration in a walking pose (from Gregory 1945). B, left manus of *Trilophosaurus buettneri* (from Gregory 1945). C, left pes of *Trilophosaurus buettneri* (from Gregory 1945). Note the orientation of the digits, especially the medially projecting first digit of the manus and the laterally diverging fifth digit of the pes. Also note the increase in length from the proximal to the penultimate phalanges in most of the digits. **Abbreviations:** ast - astragalus, cal - calcaneum, cen - centrale, int - intermedium, rad - radiale, ul - ulnare, 1-4 - distal carpals/tarsals, v - fifth metatarsal.

Genus	Manus/Trunk Ratio	Pes/Trunk Ratio
<i>Proterosuchus</i>	0.1200	0.1920
<i>Vjushkovia</i>	0.1080	0.1960
<i>Rutiodon</i>	0.0976	0.1301
<i>Stagonolepis</i>	0.0813	0.1707
<i>Saurosuchus</i>	0.0758	0.2154
<i>Postosuchus</i>	0.0854	0.2520
<i>Pseudhesperosuchus</i>	0.1667	0.3333
<i>Euparkeria</i>	0.1440	0.2640
<i>Riojasuchus</i>	0.0800	0.2480
<i>Trilophosaurus</i>	0.2400	0.3125

Tab. 2 - Proportion ratios among Late Triassic Archosauromorphs.

skeletal specializations specifically adapted to a particular mode of life, e.g. extended digits supporting a patagium in pterosaurs. Therefore, we compare the skeletal structure of *Trilophosaurus* to that of other archosauromorphs to construct a null hypothesis, namely that *Trilophosaurus* is a typical archosauromorph and shows morphological characters that are comparable to other terrestrial Triassic archosauromorphs. To test this hypothesis *Trilophosaurus* was compared to a variety of approximately contemporaneous archosauromorphs that also bracket *Trilophosaurus* phylogenetically.

The archosauromorphs used for comparison, based on published figures, are: the rhynchosaurs *Otischalkia elderae* (Elder 1978; Hunt & Lucas 1991; Long & Murry 1995), *Hyperodapedon gordonii* (Benton 1983), and *Rhynchosaurus articeps* (Benton 1990); the erythrosuchid *Erythrosuchus africanus* (Gower 1996, 2003); the archosauriform *Euparkeria capensis* (Ewer 1965); the archosaur *Erpetosuchus granti* (Benton & Walker 2002); the aetosaurs *Longosuchus meadei* and *Desmatosuchus haplocerus* (Long and Murry 1995); the poposaurid *Postosuchus kirkpatricki* (Chatterjee 1985; Long & Murry 1995); the crocodylomorph *Dromicosuchus grillator* (Sues et al. 2003); and the sphenosuchid *Terristrisuchus gracilis* (Crush 1984). Casts and specimens of the poposaurid *Postosuchus kirkpatricki*, the aetosaur *Desmatosuchus haplocerus*, and the phytosaur *Pseudopalatus buceros* were also examined for comparative purposes. The reconstructions in Parrish (1986), especially of *Pseudhesperosuchus*, were used in the manus and pes proportion analysis.

Body proportions. The most striking feature of the appendicular skeleton of *Trilophosaurus* is the size of its manus and pes, especially compared to the trunk (Fig. 1A). Using the anatomical reconstructions of terrestrial and semi-aquatic archosauromorphs in Parrish (1986, figs. 3-11), trunk, manus and pes lengths were measured to obtain a sense of their proportions in a

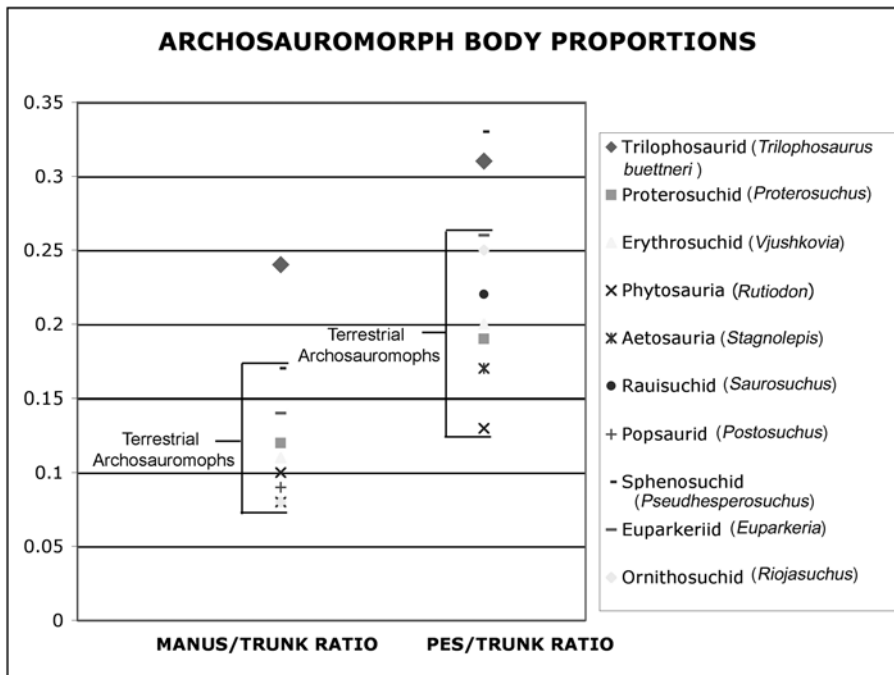


Fig. 2 - Plot showing the body proportions of *Trilophosaurus* and known terrestrial archosauromorphs. Manus/pes length was determined as the distance from the longest digit to where the carpometacarpus/tarsometatarsus meets the ulna and radius/tibia and fibula, respectively. The trunk was the distance from the anterior portion of the skull to the acetabulum. All data drawn from published figures in Parrish (1986) and Gregory (1945). The aberrant position of the *Pseudhesperosuchus* data point in the pes/trunk ratio column is due to the measuring protocols used, and does not reflect the amount of the pes actually interacting with the ground. This is apparent when considering that *Trilophosaurus* has plantigrade manus and pes whereas *Pseudhesperosuchus* has a digitigrade manus and pes. See Table 2 for raw data.

wide variety of archosauromorphs. For these measurements the lengths of the manus and pes were determined by the length, in lateral view, from the longest digit to where the metacarpus/metatarsus meets the radius and ulna/tibia and fibula, respectively. The trunk lengths were determined by measuring from the anterior premaxilla to the last sacral vertebrae as reconstructed in the various illustrations. Using the full body reconstruction of *Trilophosaurus* in Gregory's (1945, pl. 33) osteology, a table (Tab. 2) and corresponding graph (Fig. 2) was generated comparing the manus/trunk length ratio and the pes/trunk length ratio. This ratio is more meaningful than either the manus/total length or pes/total length ratios because the long tail of *Trilophosaurus* offsets the lengths of the large manus and pes (Fig. 1A). Also, full body lengths were not included because of the subjective nature of most archosauromorph tail lengths due to incomplete caudal series.

Trilophosaurus has manus and pes proportions that are exceedingly large for its trunk size (Fig. 2). The manus/trunk ratio of *Trilophosaurus* is double that of most archosauromorphs measured, the archosauriform *Euparkeria* and the sphenosuchid *Pseudhesperosuchus* being exceptions, but even these two taxa yield ratios substantially lower than *Trilophosaurus*. *Trilophosaurus* has the second largest pes/trunk ratio, behind *Pseudhesperosuchus*. The ratios for both *Pseudhesperosuchus* and *Trilophosaurus* are considerably higher than those of the other archosauromorphs. It should be noted that while *Pseudhesperosuchus* has a large manus/trunk and pes/trunk ratio, this is because of its

elongated metacarpus and metatarsus, which skew the manus/trunk and pes/trunk ratios. The results for *Pseudhesperosuchus* should not be considered indicative of the size of the manus and pes, which actually interacted with the ground, especially considering that *Pseudhesperosuchus* has a digitigrade manus and pes, whereas *Trilophosaurus* has a plantigrade manus and pes (Gregory 1945; Parrish 1986).

These major differences in body proportions refute the null hypothesis previously put forward. Specifically, it is obvious that *Trilophosaurus* has completely different appendicular proportions than any contemporaneous, or even closely related, terrestrial or semi-aquatic archosauromorph.

The large manus and pes of *Trilophosaurus* was likely used to help bridge gaps while maneuvering in trees, as in various arboreal iguanids like *Iguana iguana*. Such gap bridging is often associated with a rigid trunk (S. Renesto, pers. comm.), which Gregory (1945) noted in *Trilophosaurus*, in addition to elongated limb proportions (Hildebrand 1974; Cartmill 1985). *Trilophosaurus* differs from most arboreal animals in that its elongated limb proportions are due to elongation of the manus and pes, specifically the phalanges. This is atypical because an arboreal animal whose manus and pes is elongated usually has elongated metacarpals and metatarsals. A majority of limb ratio studies (i.e., Middleton & Gatesy 2000) use ratios excluding phalangeal proportions. Thus, when incorporating *Trilophosaurus* data into such studies inevitably it groups with terrestrial, not arboreal, animals. Such measurement regimes are

ignoring valuable data, especially in light of recent studies interpreting certain theropods, such as *Microraptor zhaoianus* (Xu et al. 2000) and *Epidendrosaurus ningchenensis* (Zhang et al. 2002), as arboreal based purely on phalangeal and ungual proportions.

Axial skeleton. The vertebral column of *Trilophosaurus* has features that distinguish it among archosauromorphs. There are even considerable differences between it and the closely related rhynchosaurs. This is apparent not only in the number of vertebrae but also in their morphology.

The relatively short neck and exceedingly long tail are the most distinguishing features of the axial skeleton of *Trilophosaurus*. *Trilophosaurus* has 7 cervical, 17 dorsal, 2 sacral and approximately 40 caudal vertebrae (Gregory 1945) (Fig. 1A). Generally archosauromorphs have 10 or more amphicoelous cervical vertebrae, whereas *Trilophosaurus* has only 7 opisthocoelous cervical vertebrae. The distinctiveness of *Trilophosaurus* is evident even when compared to closely related clades such as rhynchosaurs, the only other archosauromorphs with similar cervical counts. The rhynchosaurs *Hyperodapedon* (Benton 1983) and *Paradapedon* (Chatterjee 1974) both have 8 cervicals, 16 dorsals (although *Hyperdapedon* may have 17), and 2 sacral vertebrae. The major difference in vertebral structure and number is that the rhynchosaurs have between 25 and 30 caudals, whereas *Trilophosaurus* has approximately 40 caudals, resulting in a extremely long tapered tail. Indeed, the tail is so long that it accounts for more than half the length of the animal. However, the length of the tail of *Trilophosaurus* is somewhat open for interpretation as Gregory (1945) reconstructed the tail using 20 vertebrae found either articulated or associated with the articulated skeleton he used as the primary material for his osteology. This tail reconstruction contains 33 vertebrae and due to the elongation of the most posterior caudal vertebrae he postulated the tail contained approximately 40 vertebrae. *Trilophosaurus* has tail proportions that are comparable to those of the scansorial *Iguana iguana* in overall proportions and likely used it in a similar manner, for balance. Using a long tail for balancing is a common feature among arboreal animals and contrasts with the relatively short and massive tails of fossorial diggers (Coombs 1983).

The morphology of the caudal vertebrae also differs considerably between the rhynchosaurs and *Trilophosaurus*. The caudals of *Hyperdapedon* have centra that are rhomboid in lateral view, with large chevrons that are twice the height of the vertebrae from which they originate (Benton 1983). *Paradapedon huxleyi* has caudals with centra that are highly compressed antero-posteriorly, so much so that the neural spines extend further anteriorly and posteriorly than do the centra

(Chatterjee 1974). *Trilophosaurus* has caudal vertebrae that differ considerably from those of rhynchosaurs. The caudal centra are cylindrical and become more elongated both relatively and absolutely posteriorly along the caudal series.

Trilophosaurus also possesses distinctive chevrons. At the anterior end of the caudal series, *Trilophosaurus*' chevrons are approximately as tall as the vertebrae they originate from. There is a morphological change of the chevrons from the anterior to posterior end of the caudal series. The chevrons range from typical V-shaped, posteroventrally directed chevrons anteriorly to chevrons that have an uncommon hatchet shape in lateral view and ventral expansions that parallel the cylindrical caudal series posteriorly.

Numerous extant arboreal species have tails that are prehensile and are used to aid in climbing. The caudal vertebrae and chevrons of *Trilophosaurus* indicate that its tail was not prehensile, although it could have been used to aid in balancing and bracing itself against the substrate. Although cylindrical and elongate centra are often seen in the prehensile tails of extant animals, the elongate zygapophyses of *Trilophosaurus* preclude its tail from being prehensile. Thus, the caudal vertebrae have pre- and post-zygapophyses that interlock tightly with one another along the caudal series. Such a rigid structure of the tail would have limited its movement both dorsally and laterally. Also, the chevrons of *Trilophosaurus* have wedge-shaped dorsal facets that insert between the centra, limiting flexure of the tail ventrally. Similar hatchet-shaped chevrons are also present in pachypleurosaurs (Sanders 1998) and the phytosaur *Mystriosuchus* (Gozzi & Renesto 2003); in these aquatic animals the chevrons increase the stiffness of the tail to allow for a stronger swimming stroke. Thus, the tail was stiff and unable to move very far in any direction. Such restriction of tail movement would not allow for any grasping or curling. With no grasping or curling, the tail could not offer any type of prehensile movement. However, the unique hatchet-shaped chevrons on the posterior half of the caudal series of vertebrae could have conceivably been used to increase the friction of the tail against the substrate and added further rigidity, which would have aided in bracing *Trilophosaurus* while climbing. Extant arboreal reptiles use the bulk of their elongated tails to maintain their balance while climbing, *Trilophosaurus* likely used its tail in a similar manner.

Pectoral girdle. The pectoral girdle of *Trilophosaurus* shows some modification from that of most archosauromorphs, as would be expected of an arboreal animal.

The scapulae of *Trilophosaurus* are considerably broader dorsally compared to other archosauromorphs (Romer 1956). Further cartilaginous expansion of the

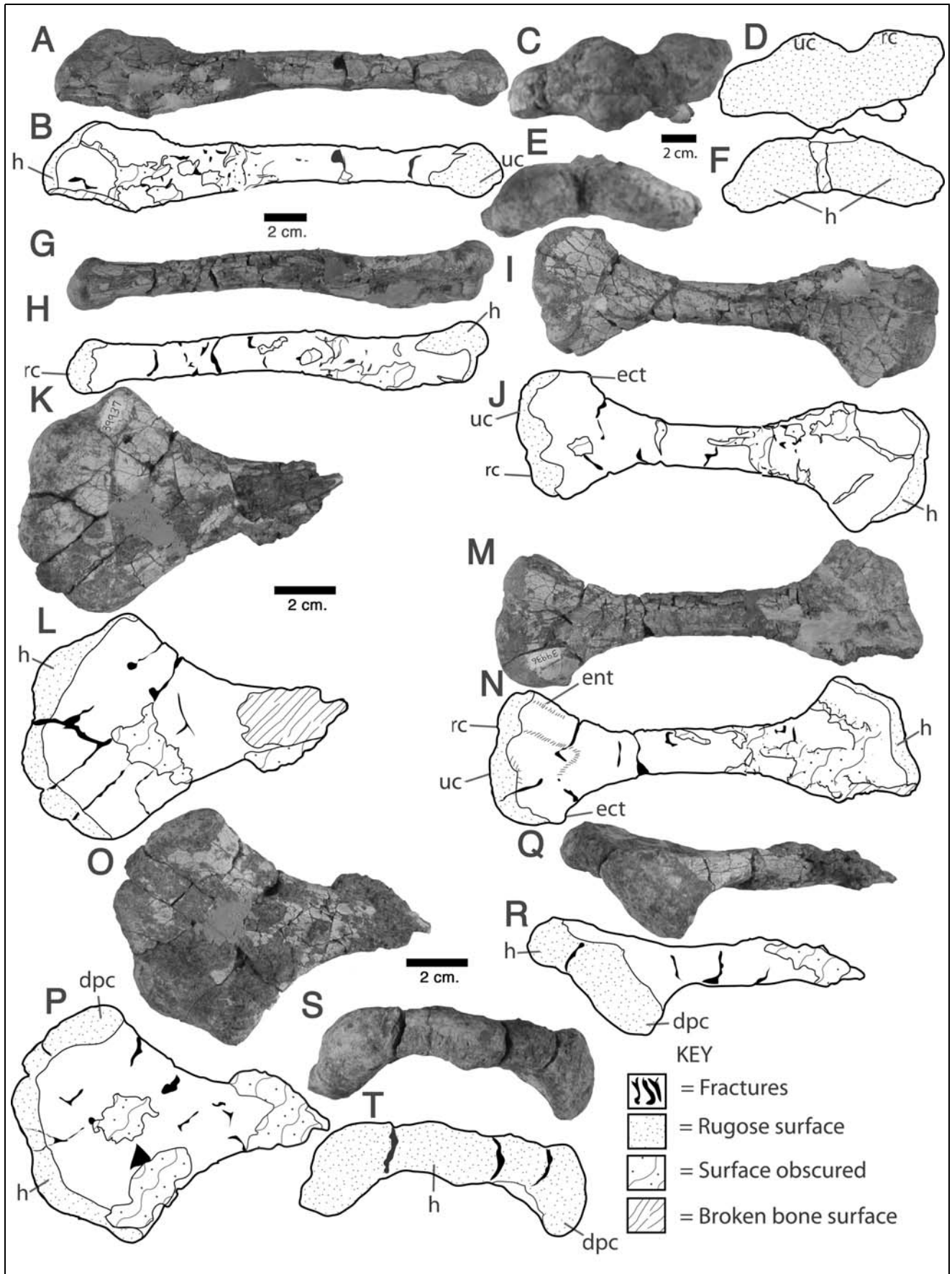


Fig. 3 - Left humerus of *Trilophosaurus jacobsi* (NMMNH P-39936) lacking the deltopectoral crest (A-J, M-N) in A and B, anterior view; C and D, distal view; E and F, proximal view; G and H, posterior view; I and J, dorsal view; M and N, ventral view. A left humeral head of *T. jacobsi* (NMMNH P-39937) in K and L, dorsal view; O and P, ventral view; Q and R, anterior view; S and T, proximal view. Note the size of the deltopectoral crest and length of the entepicondyle. Abbreviations: dpc - deltopectoral crest, ect - ectepicondyle, ent - entepicondyle, h - head, rc - radial condyle, uc - ulnar condyle.

scapular blade is indicated by the irregular shape of the blades' dorsal surface (Gregory 1945), giving *Trilophosaurus* even larger and more robust scapulae than suggested by the preserved bone. Such scapular expansions would have allowed for a larger area for the origin of the scapular deltoid, which inserts into the highly modified proximal humerus, discussed below. The dorsal margin of the coracoid is shelf-like and extends farther posteriorly than the tip of the dorsal scapular blade. No other archosauromorphs exhibit this condition. The glenoid fossa articulates with the humerus on three sides (anteriorly, posteriorly, and ventrally), suggesting a very strong connection between these two elements. In contrast, other archosauromorphs have a glenoid fossa that bounds their humeri on only two sides (anteriorly and ventrally).

The pectoral girdle of *Trilophosaurus* has numerous large areas for the origins of much of the forelimb musculature. The large coracoid has a significant area for the origin of the pectoralis, which, coupled with a large insertion area on the deltopectoral crest, discussed below, would have given *Trilophosaurus* a very strong forelimb musculature, useful in maintaining balance and footing while climbing. A prominent tubercle anterior to the glenoid indicates a large area for the origin of the triceps (Gregory 1945), which would attach distally to the large olecranon of the ulna and serve to extend the forearm (Romer 1949). A muscular forearm would have helped *Trilophosaurus* to exert a large amount of force in order to move along and grasp substrates.

Humerus. The humerus of *Trilophosaurus* (Fig. 3) is highly specialized and has proximal and distal heads with several characteristics that are unique among archosauromorphs. These include features of both the proximal and distal ends of the humerus.

The proximal head of the humerus (Fig. 3 C-D, K-L, O-P) of *Trilophosaurus* is one of the most unique aspects of its anatomy. It features an anterior expansion that is matched only in the rhynchosaur *Ostichalkia elderae* and the aetosaur *Desmotosuchus haplocerus*, causing occasional confusion as to the taxonomic assignment of isolated humeri (Long & Murry 1995). In contrast, most archosauromorph humeri have an anteriorly linear proximal head with a medio-ventrally deflected deltopectoral crest, giving the proximal head an almost teardrop shape in dorso-lateral view. *Trilophosaurus* has a distinctive proximal head that anteriorly comes to a point, more so than *Desmotosuchus*, giving it a tetradial head in dorsoventral view (Fig. 3 I-L). Both anterior and posterior ends of the humeral head are expanded ventrally, giving the head a symmetrical, inverted U-shape in proximal view (Fig. 3 S-T). This also contrasts with most archosauromorphs, which have asymmetrical humeral heads in proximal view.

The unique anterior expansion of the proximal humeral head in *Trilophosaurus* is not seen to the same extent in other archosauromorphs or extant arboreal reptiles, but appears closest in morphology to that of the iguanid *Iguana iguana*. However, it provided *Trilophosaurus* with an area for the attachment of musculature that would aid in climbing. Such expansions created a large area for the insertion of the supracoracoideus muscle. This muscle is used to prevent the trunk from sagging (Romer 1949). A large supracoracoideus muscle would have allowed *Trilophosaurus* to be able to control the dorso-ventral position of its trunk relative to its limbs. This level of control would have allowed *Trilophosaurus* to keep its body close to any surface it chose to climb, which is necessary to prevent toppling while climbing (Cartmill 1985).

The deltopectoral crest of *Trilophosaurus* (Fig. 3 K-L, O-T) is very large for a non-dinosaurian archosauromorph. It appears triangular in anterior view and is very similar to the deltopectoral crest of *Iguana iguana*. Such a prominent deltopectoral crest suggests a large insertion for the pectoralis muscle. Indications of a large pectoralis suggest *Trilophosaurus* could pull its arm backward and downward with great force during locomotion (Romer 1949).

The distal head of the humerus of *Trilophosaurus* is also highly distinctive (Fig. 3 C-D, I-J, M-N), with the large entepicondyle being the key feature. The entepicondyle of *Trilophosaurus* is shelf-like and has no entepicondylar foramen penetrating it, in contrast to *Pseudopalatus*, *Desmotosuchus*, and *Postosuchus*, all of which have prominent foramina. While proportionately smaller, the entepicondyle of *Iguana iguana* is also prominent and lacks a foramen. *Trilophosaurus* has a prominent triangular ectepicondyle (Fig. 3 I, J), whereas no prominent ectepicondyle is discernable on any of the archosauromorphs examined. However, a comparable ectepicondyle is found on the humerus of *Iguana iguana*. An expansion of the distal humerus, posteroventral to the radial condyle (Fig. 3 C, D), is unique to *Trilophosaurus* and increases the size of the distal humerus considerably, covering a third of the distal humeral area.

This expansion of the distal humerus also has significance for the extensor muscles of the forearm. The expansion, anterior to the ulnar condyle, shows a large amount of rugosity, which is more pronounced ventrally than dorsally (Fig. 3 C-D). This rugosity indicates that the distal humeral expansions served as a large area for the origin of the extensor muscles of the forearm and manus. The anconeus, extensor carpi radialis, extensor digitorum communis, and extensor carpi ulnaris all originate from this prominent expansion (Romer 1949).

In *Trilophosaurus*, the flexor muscles, as well as the extensor muscles, had strong attachments on the humerus, specifically on the entepicondyle. Function-

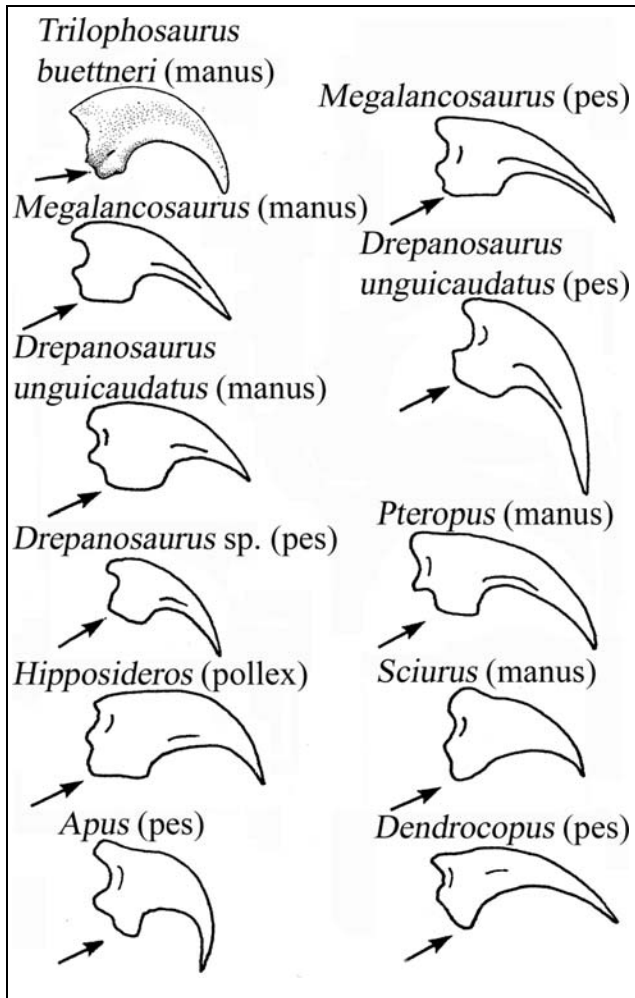


Fig. 4 - Comparison between the claws of *Trilophosaurus*, drepanosaurs, and other climbing mammals and birds. The black arrow indicates the process for the insertion of the flexor muscles. *Trilophosaurus buettneri* claw modified from Gregory (1945), all other claws from Renesto & Paganoni (1995).

ally, the entepicondyle serves as one of the primary attachment sites for the muscles of the forearm. The shelf-like entepicondyle indicates a large surface area for the origin of the flexor muscles of the forearm, the epitrochleoanconeus, flexors, and pronator profundus. The length of the entepicondyle is up to 20% of the length of the humerus in *Trilophosaurus*; in comparison, *Desmotosuchus*, *Postosuchus*, and *Pseudopalatus* have entepicondyles that are 13%, 16%, and 16% of their overall humeral length. The larger entepicondyle, compared to other archosauromorphs, indicates that the muscles of the forearm of *Trilophosaurus* are very large for an animal its size, resulting in a powerful forearm. A large entepicondyle is characteristic of many arboreal animals (Coombs 1983). Such flexors would have increased the power with which the manus could contract its digits, thus influencing the grip of the manus.

Manus. One of the primary grasping tools of any arboreal animal is its manus. *Trilophosaurus* has a manus structure that is completely different from that of any other archosauromorph (Fig. 1B), especially in regard to the orientation of the digits. Such an aberrant digit structure is only seen in certain gliding, lacertid reptiles (Colbert 1970; Evans & Haubold 1987). Skeletal features associated with the musculature supporting these digits indicate that *Trilophosaurus* in life would have been able to exert a strong grasp on a substrate.

The orientation of the digits in the manus of archosauromorphs is extremely consistent, *Trilophosaurus* being one of the few exceptions. The standard archosauromorph manus has its first through fourth digits subparallel and has a divergent, laterally projecting, fifth digit. The orientation of the digits of *Trilophosaurus* is in direct opposition to this standard model – its first digit projects medially, and the second through fifth digits are subparallel (Fig. 1B).

In Archosauromorpha, there is no manus structure analogous to that of *Trilophosaurus*; only the gliding lacertid reptiles *Coelurosauravus* and *Icarosaurus* share a similar orientation of digits (Colbert 1970; Evans & Haubold 1987). These gliding lacertids are thought to have used their manus and pes to climb trees in order to gain launching points from which to glide (Colbert 1970; Evans & Haubold 1987), which is behavior seen in all gliding species (Hildebrand 1974). *Icarosaurus* and *Trilophosaurus* both possess a divergent, medially directed, first digit of the manus. While the complete manus of *Icarosaurus* is not preserved, Colbert (1970) based his interpretation of a divergent first digit of the manus of *Icarosaurus* on an offset first metacarpal. The manus and pes of *Coelurosauravus* have long, slender, cylindrical digits capped with laterally compressed claws with prominent flexor insertions (Evans & Haubold 1987), as does *Trilophosaurus* (Fig. 1B).

Reconstructing the musculature of the manus and pes is difficult. This is due to the palmar aponeurosis and plantar aponeurosis, which leave no indications of the origin of the flexor muscles of the manus and pes. What can be inferred is the presence of large flexors due to the large subungual process present on the claws of both the manus and pes of *Trilophosaurus* (Fig. 4). Together with large flexor muscles come sizable extensor muscles inserting into the digits. Large extensors, specifically the extensor digitorum communis and the extensor carpi ulnaris, are suggested by a large origination site of these muscles on the anterior expansion of the distal humerus, discussed above.

The unique orientation of the digits of *Trilophosaurus*, together with the strong extensors and flexors of the manus of *Trilophosaurus*, would allow for a solid grip directed toward the area beneath the body, due to the medially directed first digit.

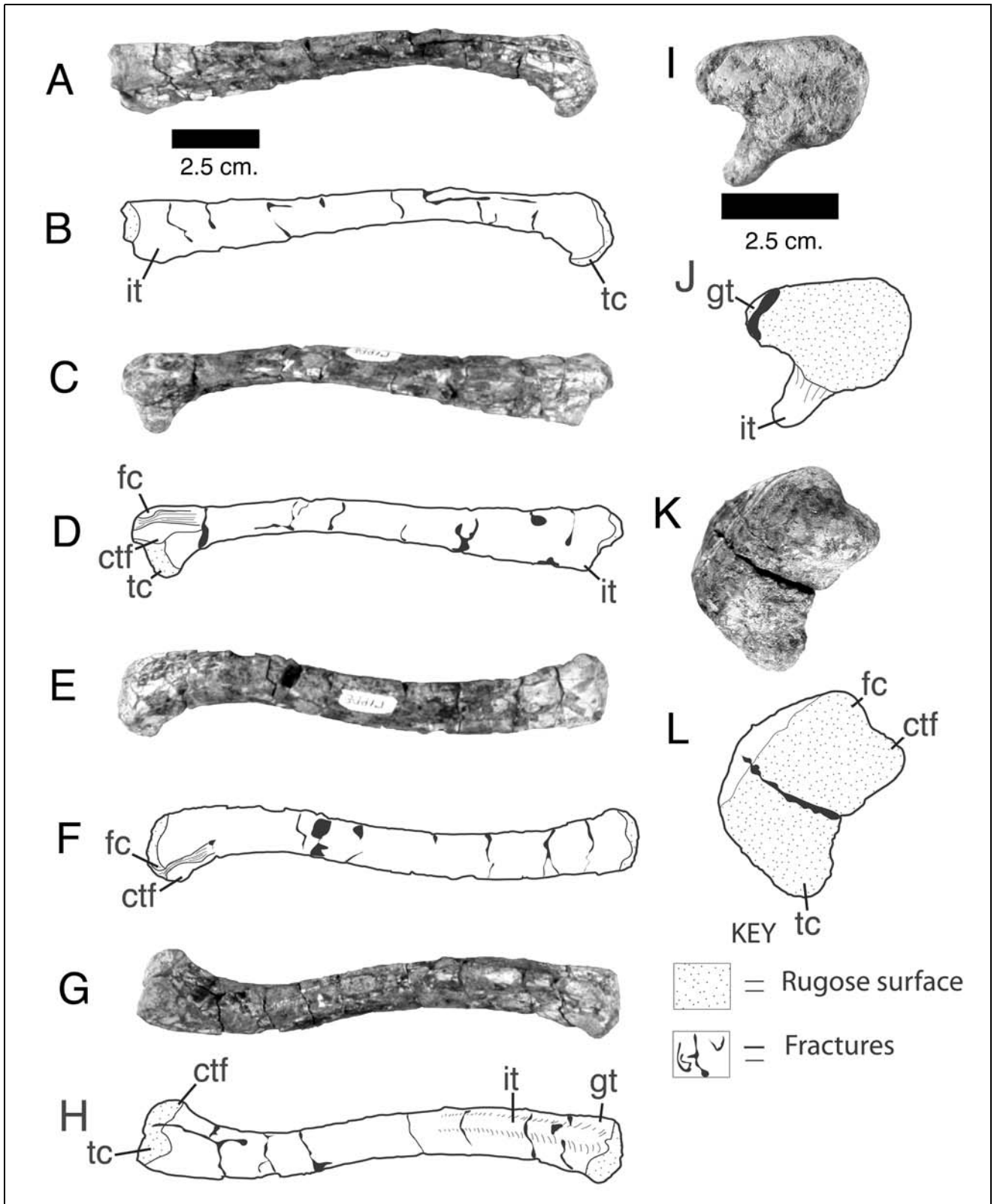


Fig. 5 - Right femur (photos reversed) of *Trilophosaurus jacobsi* (NMMNH P-39917) in A and B, anterior view; C and D, posterior view; E and F, dorsal view; G and H, ventral view; I and J proximal view; K and L, distal view. Note the extension of the internal trochanter down the femoral shaft and the small distance between the proximal internal trochanter and the proximal femoral head. **Abbreviations:** ctf - cristotibiofibularis, fc - fibular condyle, gt - greater trochanter, it - internal trochanter, tc - tibial condyle.

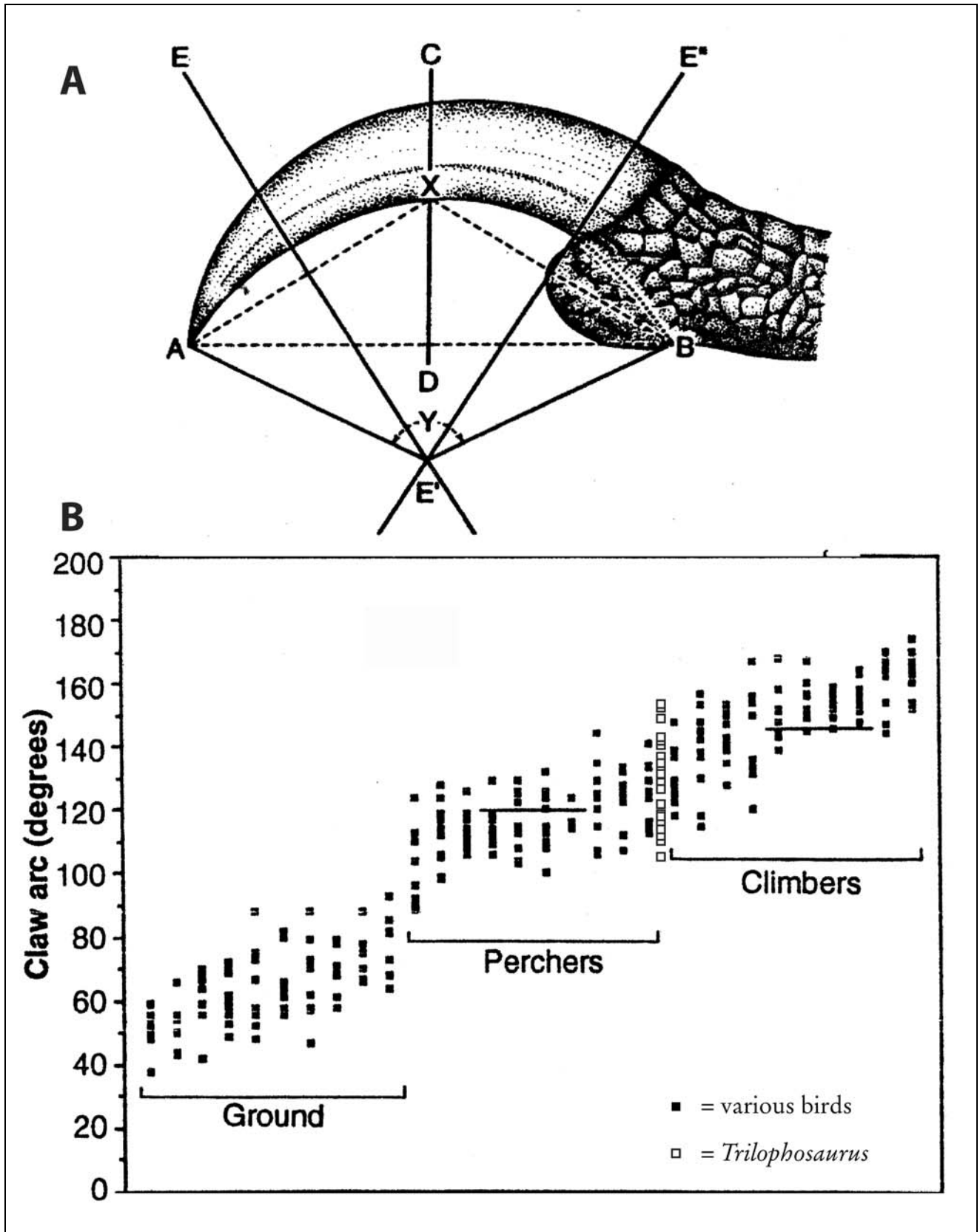


Fig. 6 - A, Diagram of geometric measurements of claw curvature. A perpendicular (CD) is drawn to bisect the chord (AB) of the inner arc, which is itself bisected at the point X. Perpendiculars are drawn (EE' and E'E') to bisect the chords AX and XB. These perpendiculars, when extended, meet at the center (E) of the circle of which the arc is a part. The radii are then drawn to each end of the arc (EA and EB). The angle (Y) between these radii (read directly from protractor) is a measure of the degrees of the arc (after Feduccia 1993). B, Chart showing the claw curvatures of diverse birds with three distinct claw types. Each column is a single species. *Trilophosaurus* clearly falls outside of the interval containing ground dwelling birds (modified from Feduccia 1993).

Femur. Like the humerus, the femur of *Trilophosaurus* (Fig. 5) is unique among archosauromorphs. The defining character of the femur of *Trilophosaurus* is the extensive internal trochanter. Such trochanter dimensions, together with the overall shape of the femur, bear a striking resemblance to the femur of *Araeoscelis*.

The femur of *Trilophosaurus* has a proximal head that is teardrop-shaped in proximal view (Fig. 5 I-J), while other archosauromorphs have proximal heads that are laterally expanded in proximal view. The slight sigmoidal flexure at the proximal and distal ends of the femur of *Trilophosaurus* (Fig. 5 E-H) contrasts with the much more exaggerated flexure in *Pseudopalatus*, in which the entire shaft of the femur is sigmoidal, whereas the femora of *Postosuchus*, *Erythrosuchus*, *Dromicosuchus* are much more linear.

The prominent internal trochanter (Fig. 5 A-D, G-J) extends from near the proximal head and runs nearly a third of the length of the entire femur. Except for size this trochanter strongly resembles that of the basal reptile *Araeoscelis* (Williston 1914; Gregory 1945) and that of *Iguana iguana*. We compare the internal trochanter of *Trilophosaurus* to the archosaurian fourth trochanter based on Gregory & Camp (1918) [but see Parrish (1983) for an alternative interpretation of femoral homology]. In general, archosauromorph femora on the whole have proportionately much smaller internal trochanters (also called fourth trochanters) that are little more than small triangular projections, generally a fourth of the way down the femur.

The femur of *Trilophosaurus* shows characteristics indicating it was used for quick and powerful movement. The internal trochanter is the insertion of the caudifemoralis, an important femoral retractor. Such a large and extensive process would indicate a very large caudifemoralis, giving *Trilophosaurus* powerful hind limb movement as mentioned above. The internal trochanter is located more proximally in *Trilophosaurus* than in nearly all other archosauromorphs, except for *Araeoscelis*. Functionally, the internal trochanter, being close to the proximal femoral head, allows for the rapid retraction of the femur, via the caudifemoralis (Parrish 1986), thus allowing for rapid movement of the femur, and thus the entire hind limb.

Pes. The pes of *Trilophosaurus* (Fig. 1C), like the manus, is distinct from that of other archosauromorphs. As discussed earlier, the pes is relatively large, representing an enormous percentage of the trunk length of *Trilophosaurus* (Fig. 1A). While retaining the phalangeal formula of primitive archosauromorphs, *Trilophosaurus* has a pes with a distinct orientation of digits. The typical archosauromorph condition is to have digits directed anteriorly, including a fifth digit that is offset due to the L-shaped fifth metatarsal. In contrast, the first four di-

gits of the pes of *Trilophosaurus* have a strong medial curvature, whereas the fifth digit is strongly curved laterally (Fig. 1C). Also, unique among the archosauromorphs, the manus and pes of *Trilophosaurus* may have penultimate phalanges that are longer than proximal phalanges. This character is found only in arboreal birds (Hopson 2001) and pterosaurs (Unwin 1996a,b). The orientation of the digits and relative digital lengths are all similar to the arboreal *Iguana iguana*.

Among archosauromorphs, *Trilophosaurus* has a unique ankle. The astragalus and calcaneum contact each other obliquely with no interlocking contact as in other archosauromorphs (Parrish 1986; Sereno 1991). The large perforating foramen and the lack of an interlocking astragalus and calcaneum is reminiscent of the eosuchian *Youngina*, the nothosaur *Tangasaurus*, and to a lesser extent the protosaur *Protorosaurus* (Romer 1956). The laterally-projecting calcaneal tuber found in phytosaurs and proterosuchids is also present in *Trilophosaurus*, although in *Trilophosaurus* the tuber is expanded both laterally and dorsally, giving it a much more blade-like appearance than in either phytosaurs or proterosuchids. The combination of the perforating foramen and laterally projecting calcaneal tuber places *Trilophosaurus* in the primitive tarsal group among archosauromorphs (Parrish 1986).

A difficulty faced by any arboreal animal is a controlled head first descent. Arboreal reptiles have a primitive locomotor posture that allows supination of the hind limb, enabling the foot to grip and the animal to achieve a controlled head first descent (Cartmill, 1985). Not only did the primitive posture of *Trilophosaurus* allow it to supinate its foot, but it appears to have had a very cartilaginous, and therefore flexible, ankle. This flexibility was enhanced by the lack of a fibular facet, so there was little to no fibular-calcaneal contact (Gregory 1945).

Unguals. The orientation of the unguals, or claws, on the digits of *Trilophosaurus* does not appear to resemble that of other primitive archosauromorphs. Most primitive archosauromorphs have claws that are broad and that project straight out of the phalanges without any significant curvature. The claws of *Trilophosaurus* (Fig. 6A) are, as Gregory (1945, p. 312) described them, "large strongly compressed laterally, long, recurved, [and] sharp pointed." The claws of the pes of *Trilophosaurus* also do not project straight out of the phalanges; they are instead directed slightly medially or laterally (Fig. 1 C). The first and fourth phalanges of the pes have claws that are oriented inwards, the first phalanx oriented laterally and the fourth phalanx medially, towards the second and third phalanges, indicating that they would allow for better grasping of a central point. Such an arrangement of the phalanges is not seen

in other primitive archosauromorphs and would seemingly be of little value among ground-dwelling animals.

NMMNH Specimen Number	Claw Curvature (degree)
P-40117	111.5
P-40118	106.5
P-40119	155.5
P-40120	120.5
P-40121	124.5
P-40122	141.5
P-40123	114.5
P-40124	117.0
P-40125	119.0
P-40126	114.0
P-40127	132.0
P-40128	146.75
P-40129	148.5
P-40130	116.5
P-40131	124.5
P-40132	137.5
P-40133	141.0
P-40134	131.5
P-40135	136.0
P-40136	118.5
P-40137	150.75
P-40138	128.0
P-40139	156.5
P-40140	142.0
P-40141	134.5

Tab. 3 - Claw curvature of selected NMMNH *Trilophosaurus* specimens.

The claws of the manus and pes of *Trilophosaurus* resemble the claws of *Megalancosaurus* (Calzavara et al. 1980; Renesto 1994, 2000; Renesto & Paganoni 1995) (Fig. 6). The claws of *Trilophosaurus* are hooked to a significant degree, sharp, and as narrow as those of climbing animals and *Megalancosaurus* (Renesto 1994, 2000) (Fig. 6; Table 3). *Trilophosaurus* also shares with *Megalancosaurus*, birds, and climbing mammals a similar insertion point along the ventral process of the claw for the flexor muscle (Renesto & Paganoni 1995) (Fig. 6). As Renesto & Paganoni (1995 p. 96) pointed out "long, sharp, and narrow hooked claws, provided with ventral process for the insertion of flexor muscles, are characters that can be found in climbing animals." Such a subungual process is a characteristic found throughout arboreal animals (Coombs 1983).

Claws like those of *Trilophosaurus* are key features used to generate a vertical force to climb. To generate such a force *Trilophosaurus* would have needed to

be able to interlock with its supporting surface to generate a nonvertical contact surface (Cartmill 1985); interlocking would also increase the amount of friction, another key component in climbing (Hildebrand 1974). Such interlocking could easily be accomplished by the sharp claws of *Trilophosaurus*, drepanosaurs, and other arboreal animals. The strong flexors inserting to the ventral process of the claws would allow arboreal animals to use their own body weight to prevent slipping in any direction (Hildebrand 1974).

A large manus and pes with specialized claws is not only indicative of arboreal animals but also of fossorial, digging animals. While some might postulate a fossorial mode of living for *Trilophosaurus* based on these factors, the morphology of the claws does not support such an interpretation. *Trilophosaurus* does not possess any specialized claws like *Drepanosaurus*, which, prior to the work of Renesto (2000), was interpreted as fossorial (Pinna 1980, 1984, 1986). This interpretation had *Drepanosaurus* using the single disproportionately large claw on the manus as a digging implement. The claws of *Trilophosaurus* also are laterally compressed. As noted by Gregory (1945), a fossorial animal would have broad claws that would maximize the surface area the claws contacted with each stroke. Laterally compressed claws would contact the least surface area per stroke. Scratch digging like that of the anteater *Cyclopes* could be suggested for *Trilophosaurus* but is unlikely due to the modifications of both the hind and forelimbs in the latter, whereas scratch diggers operate primarily with only their front limbs. Thus, the claw morphology of *Trilophosaurus* indicates it would have been a poor digger.

To further test the utility of the claws for terrestrial or arboreal use we undertook a quantitative analysis modified from Feduccia (1993) as described in the methods and materials section above. The claw curvature of *Trilophosaurus* ranges from 106.5° to 155.5° (Fig. 6B, Table 3). The data extend over both the perching and climbing claw curvature intervals established for extant birds by Feduccia (1993) and do not overlap with the ground dwelling birds (Fig. 6B). The *Trilophosaurus* claws we used were not articulated and could not be assigned to a digit (or even limb) with certainty. However, we distinguished two claw morphotypes based on claw curvature data, one that fell in the perching interval and the other that fell in the climbing interval. This is seen also in *Archaeopteryx*, and was used by Feduccia (1993) to support the arboreal interpretation of *Archaeopteryx*. Our results are comparable to Feduccia's (1993) study by virtue of the fact that all vertebrate claws are similar enough to allow for comparisons between species (Zani 2000). The data support the hypothesis that *Trilophosaurus* was arboreal, and our preliminary claw curvature measurements of ground-dwelling reptiles de-

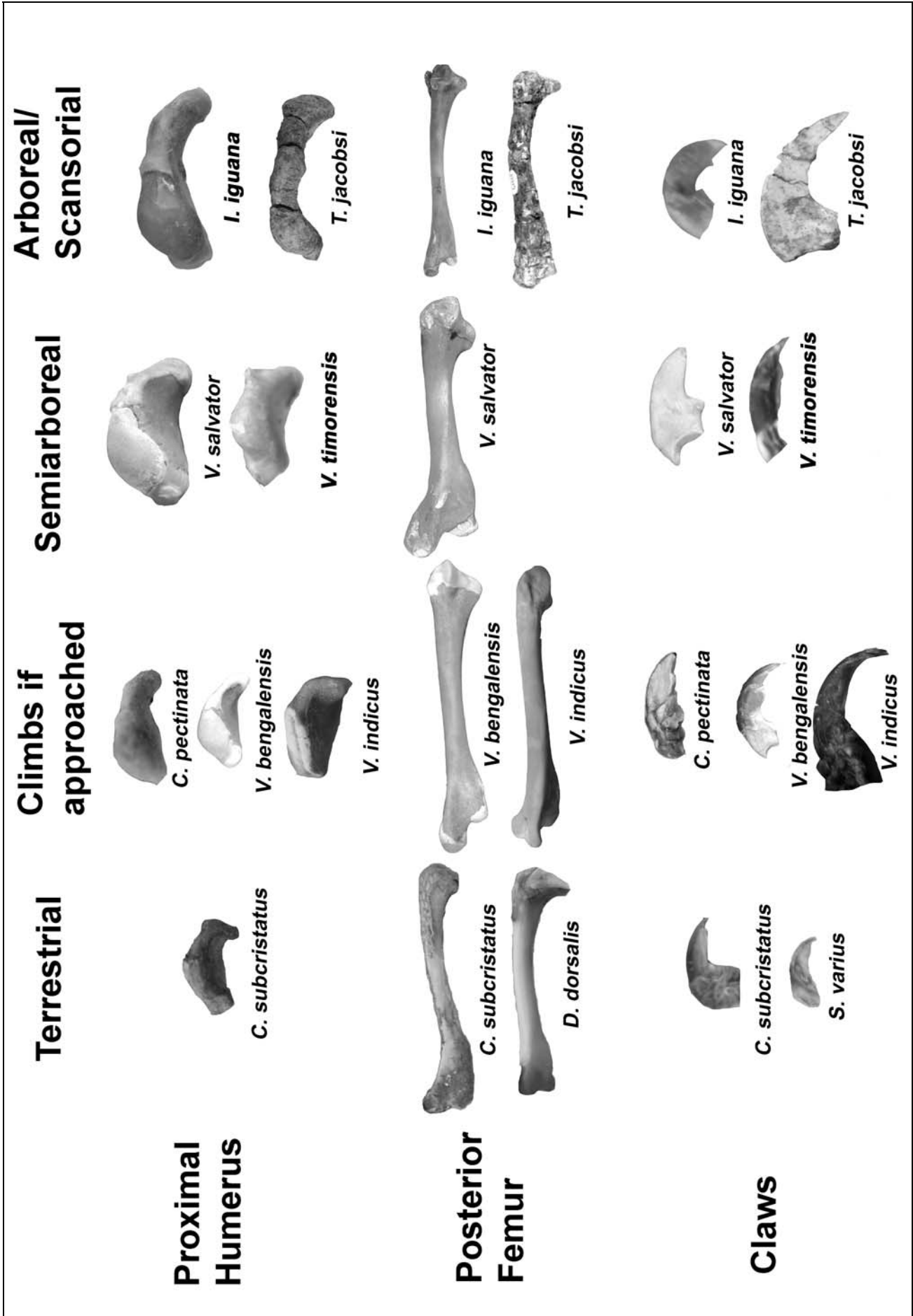


Fig. 7 - A table comparing the proximal humeri, posterior femora, and claws of terrestrial, semiarboreal, and arboreal varanids, iguanids, and *Trilophosaurus jacobsi*. Note the close similarity between the *T. jacobsi* and *I. iguana*.

monstrate a lesser degree of curvature by comparison. This follows Mertens (1942), who noted that among varanid species those which are arboreal have claws with increased curvature. Such a comparison between the claws of diverse arboreal animals is not without precedent. Renesto & Paganoni (1995) compared various drepanosaur claws with those of arboreal birds and mammals to further substantiate the idea that the drepanosaurs *Megalancosaurus* and *Drepanosaurus* were arboreal.

Comparisons with extant terrestrial and arboreal reptiles

When compared to terrestrial, semiarboreal, and arboreal reptiles, the morphology of *Trilophosaurus* is most similar to that of arboreal reptiles. Figure 7 compares the proximal humeri, posterior femora, and claws of *Trilophosaurus* with a variety of varanids and iguanids that range from terrestrial to arboreal.

The posterior proximal humeral head is larger in more arboreal animals and opens to form a wider arch in proximal view. The posterior femur of the terrestrial and semiarboreal reptiles has either tall or extensive internal trochanters, but not both; only *Trilophosaurus* and *Iguana iguana* share tall and extensive internal trochanters. The curvature of the claws of these terrestrial reptiles is fairly low with a small notch on the distal end with a sharp claw. More arboreal reptiles have much more curved claws that are more recurved. In all three areas of comparison *Trilophosaurus* groups with arboreal, not terrestrial or semiarboreal reptiles.

Mode of life

The problem of maneuvering in an angled to vertical environment must be solved by all arboreal animals. Various solutions are seen across numerous taxa. The osteological characteristics of *Trilophosaurus* indicate that it solved this problem in a manner like that of *Iguana iguana*.

We propose that *Trilophosaurus* moved up angled substrates quickly and with considerable power, using both its forelimbs and hindlimbs for propulsion. The forelimbs with the large pectoralis and extensive forelimb musculature helped to propel *Trilophosaurus* along substrates. The orientation of the digits of the manus, with its medially directed first digit, and the sharply curved claws of the manus, would give *Trilophosaurus* a solid grip, helping to retain its footing on substrates and aid in propulsion.

The hindlimbs served as the other primary propulsive force, based on the osteology and musculature of the femur. The quick, powerful retraction of the femur, via the caudifemoralis, with the medially-directed digits of the pes, was used to propel *Trilophosaurus*

against gravity and up substrates. The claws of the pes would interlock with the substrate and provide the friction needed to support *Trilophosaurus*. Any additional weight balancing or distribution needed to prevent toppling would be accomplished by the long tail, similar to an *Iguana*.

Many similarities exist between the limbs of *Trilophosaurus* and the arboreal *Iguana iguana*. The large deltopectoral crest, entepicondyle, and ectepicondyle of the humerus are shared by both genera (Fig. 3). Also, both have very large internal trochanters, suggesting similar musculature and powerful hindlimb movement (Fig. 5).

Trilophosaurus was able to utilize its method of climbing on various large trees that were distributed throughout what is today the southwestern United States during the Late Triassic. Two large varieties of trees from the Late Triassic, *Araucarioxylon arizonicum* and *Schilderia adamanica*, both grew to diameters that would easily accommodate an adult *Trilophosaurus*. *Araucarioxylon arizonicum* reached a maximum diameter of 1.72 meters and *Schilderia admanica* reached a maximum diameter of 0.9 meters (Ash & Creber 2000; Creber & Ash 2004).

Swinging among branches, as in primates, requires long arms, a mobile scapula, and a high degree of movement of the humerus relative to the pectoral girdle (Hildebrand 1974). While *Trilophosaurus* does have long forelimbs it is due to the length of the manus, not the extended humerus, radius, and ulna seen in swinging primates. The tight associations of the bones of the pectoral girdle of *Trilophosaurus* would not allow any movement of the scapula, thus making it impossible for swinging. A high degree of humeral mobility is impossible for *Trilophosaurus* based on the glenoid fossa bounding the humeral head on three sides. Thus, the osteology of *Trilophosaurus* strongly contrasts with that of an arboreal swinger.

In order to leap from one branch or one tree to the next, a specialized vertebral structure is needed. Leaping animals have an increased number of presacral dorsal vertebrae whose centra are elongated compared to related non-leaping species (Hildebrand 1974). The dorsal vertebral series of *Trilophosaurus* has no elongation of any centra and has a number of vertebrae comparable to other archosauromorphs. Thus, *Trilophosaurus* has an axial skeleton that makes it impossible for it to leap.

A unique manus and pes can give an animal a novel way to move along substrates. The manus of *Trilophosaurus*, while unique among archosauromorphs, does not share key characteristics with some other highly specialized climbing mammals and reptiles. Such climbing mammals and reptiles have clefts in their manus and pes that allow their digits to oppose each

other, as in chameleons. There is no evidence for such a cleft in the manus or pes of *Trilophosaurus* or in extant iguanids like *Iguana iguana*. While *Trilophosaurus* did have a unique orientation of digits, that appears relatively well-suited for an arboreal habitat, its manus and pes do not have opposing digits as in some other climbing mammals and reptiles.

Conclusion

The body proportions of *Trilophosaurus* distinguish it among archosauromorphs, especially the relative size of the manus and pes compared to the trunk. The functional morphology of the pectoral girdle, forelimbs, pelvic girdle, hind limbs and unguals indicate that *Trilophosaurus* possesses numerous characteristics that suggest it was arboreal, an idea left unexplored for nearly 60 years. When compared to extant terrestrial

and arboreal reptiles *Trilophosaurus* appears morphologically most similar to arboreal reptiles. A model for its movement along the trunks of large trees is based on the osteology of the animal and suggests that like living *Iguana iguana*, it used both its forelimbs and hindlimbs for propulsion and its tail for balance.

Acknowledgments. Bob Kahle of Midland, Texas, donated his extensive collections of *Trilophosaurus* specimens to the NMMNH, making this study possible. Laura Abraczinskas helped to coordinate the loan of the various herpetological specimens from the Michigan State University Museum. J. T. Giermakowski facilitated viewing of the Museum of Southwestern Biology specimens. Kate Zeigler and Vincent L. Morgan read early drafts of this manuscript and made helpful comments. Larry Rinehart provided input on our statistical methods. Silvio Renesto and James Farlow offered insightful reviews. The Dartmouth Senior Fellowship Program provided one of us (JAS) funding in order to complete this study.

REFERENCES

- Ash S.R. & Creber G.T. (2000) - The Late Triassic *Araucarioxylon arizonicum* trees of the Petrified Forest National Park, Arizona, USA. *Palaeontology*, 43: 15-28, Cambridge.
- Benton M.J. (1983) - The Triassic reptile *Hyperodapedon* from Elgin: Functional morphology and relationships. *Phil. Trans. R. Soc. London*, B, 302: 605-718, London.
- Benton M.J. (1990) - The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Phil. Trans. R. Soc. London*, B, 328: 213-306, London.
- Benton M.J. & Walker A.D. (2002) - *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zool. J. Linnean Soc.*, 136: 25-47, London.
- Calzavara M., Muscio R. & Wild, R. (1980) - *Megalancosaurus preonensis* n. g. n. sp., a new reptile from the Norian of Friuli. *Gortania*, 2: 59-64, Udine.
- Cartmill M. (1985) - Climbing. In: Hildebrand M., Bramble D. M., Liem K. F. & Wake D. B. (eds.) - Functional Vertebrate Morphology. Harvard University Press, 73-88, Cambridge.
- Case E. C. (1928) - Indications of a cotylosaur and of a new form of fish from the Triassic beds of Texas, with remarks on the Shinarump Conglomerate. *Univ. Michigan Contr. Museum Paleont.*, 3: 1-14, Ann Arbor.
- Chatterjee S. (1974) - A rhynchosaur from the Upper Triassic Maleri Formation of India. *Phil. Trans. R. Soc. London*, B, 267: 209-261, London.
- Chatterjee S. (1985) - *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of Tyrannosaurs. *Phil. Trans. R. Soc. London*, B, 309: 395-460, London.
- Colbert E. H. (1970) - The Triassic gliding reptile *Icarosaurus*. *Bull. Am. Museum Nat. Hist.*, 143: 87-142, New York.
- Coombs M.C. (1983) - Large mammalian clawed herbivores: a comparative study. *Trans. Am. Phil. Soc.*, 73 (7): 1-96, Philadelphia.
- Creber G. T. & Ash S. R. (2004) - The Late Triassic *Schilderia adamanica* and *Woodworthia arizonica* trees of the Petrified Forest National Park, Arizona, USA. *Palaeontology*, 47: 21-38, Cambridge.
- Crush P. J. (1984) - A late Upper Triassic sphenosuchid crocodylian from Wales. *Palaeontology*, 27: 131-157, Cambridge.
- Demar R. E. & Bolt J. R. (1981) - Dentitional organization and function in a Triassic reptile. *J. Paleont.*, 55 (5): 967-984, Lawrence.
- Elder R. L. (1978) - Paleontology and paleoecology of the Dockum Group, Upper Triassic, Howard County, Texas. *M.S. thesis, University of Texas at Austin*, 205 p.
- Evans S. E. & Haubold H. (1987) - A review of the Upper Permian genera *Coelurosauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). *Zool. J. Linnean Soc.*, 90: 275-303, London.
- Ewer R. F. (1965) - The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Phil. Trans. R. Soc. London*, 248: 379-435, London.
- Feduccia A. (1993) - Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science*, 259: 790-793, Washington, D.C.
- Gower D. J. (1996) - The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. *Zool. J. Linnean Soc.*, 116: 347-375, London.
- Gower D. J. (2003) - Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. *Ann. South African Museum*, 110 (1): 1-88, Cape Town.

- Gozzi E. & Renesto S. (2003) - A complete specimen of *Mystriosuchus* (Reptilia, Phytosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). *Riv. It. Paleont. Strat.*, 109: 475-498, Milano.
- Gregory J. T. (1945) - Osteology and relationships of *Trilophosaurus*. *Univ. Texas Publ.*, 4401: 273-359, Austin.
- Gregory W. K. & Camp C. L. (1918) - Studies in comparative mycology and osteology. No. III. *Bull. Am. Museum Nat. Hist.*, 38: 447-563, New York.
- Heckert A.B. (2004) - Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern U.S.A.. *New Mexico Museum Nat. Hist. Science Bull.*, 27, 170 p., Albuquerque.
- Heckert A.B., Lucas S.G., Kahle R. & Zeigler K. E. (2001) - New occurrence of *Trilophosaurus* (Reptilia: Archosauromorpha) from the Upper Triassic of West Texas and its biochronological significance. *New Mexico Geol. Soc. Guidebook*, 52: 115-122, Socorro.
- Heckert A.B., Lucas S.G., Rinehart L.F., Spielmann J.A. & Kahle R. (2003) - *Trilophosaurus jacobsi* is not a procolophonid: data from a new quarry from the Upper Triassic Chinle Group, West Texas. *Geol. Soc. America Abstr. Progr.*, 35 (7): 497.
- Heckert A.B., Lucas S.G., Rinehart L.F., Spielmann J.A., Hunt A.P. & Kahle R. (in press) - Revision of the archosauromorphs reptile *Trilophosaurus*, with a description of the first skull of *Trilophosaurus jacobsi*, from the Upper Triassic Chinle Group, West Texas, USA. *Palaentology*, 49, Cambridge.
- Hildebrand M. (1974) - Climbing. In: Hildebrand M. & Goslow Jr. G. (eds.) - Analysis of Vertebrate Structure. John Wiley and Sons Inc., 543-563, Hoboken.
- Hopson J. A. (2001) - Ecomorphology of avian and nonavian theropod phalangeal proportions: Implications for the arboreal versus terrestrial origin of bird flight. In: Gauthier J. & Gall L. F. (eds.) - New Perspectives on the Origin and Early Evolution of Birds: *Proc. Intern. Symp. in Honor of John H. Ostrom*. Yale University Press, 210-235, New Haven.
- Hunt A. P. & Lucas S. G. (1991) - A new rhynchosaur from West Texas, (USA) and the biochronology of Late Triassic rhynchosaurs. *Paleontology*, 34: 927-938, Cambridge.
- Kaye F. T. & Padian K. (1994) - Microvertebrates from the *Placerias* quarry: a window on Late Triassic vertebrate diversity in the American Southwest. In: Fraser N.C. & Sues H.-D. (eds.) - In the shadow of dinosaurs: Early Mesozoic tetrapods. Cambridge University Press, 171-196, Cambridge.
- Long R. A & Murry P. A. (1995) - Late Triassic (Carnian and Norian) tetrapods from the southwest United States. *New Mexico Museum Nat. Hist. Bull.*, 4, 254 p, Albuquerque.
- Lucas S. G., Hunt A. P. & Kahle R. (1993) - Late Triassic vertebrates from the Dockum Formation near Otis Chalk, Howard County Texas. *New Mexico Geol. Soc. Guidebook*, 44: 237-244, Socorro.
- Lucas S. G., Zeigler K. E. & Heckert A. B. (2003) - Invertebrate paleontology of the Upper Triassic Snyder quarry, Chinle Group, Chama Basin, New Mexico. *New Mexico Museum Nat. Hist. Science Bull.*, 24: 63-66, Albuquerque.
- Merck Jr. J. W. (1995) - The cranial anatomy of *Trilophosaurus buettneri* as revealed by high resolution computer aided tomography. *J. Vert. Paleont.*, Abstracts, 15 (3): 49A.
- Mertens R. (1942) - Die Familie der Warane (Varanidae): Abhandlungen Senckenberg. Naturf. Ges., 1-3 (465), 1-399, Stuttgart.
- Middleton K.M. & Gatesy S.M. (2000) - Theropod forelimb design and evolution. *Zool. J. Linnean Soc.*, 128: 149-187, London.
- Murry P. A. (1986) - Vertebrate paleontology of the Dockum Group. In: K. Padian (ed.) - The Beginning of the Age of Dinosaurs. Cambridge Univ. Press.
- Murry P. A. (1987) - New reptiles from the Upper Triassic Chinle Formation of Arizona. *J. Paleont.*, 61: 773-786, Lawrence.
- Parks P. (1969) - Cranial anatomy and mastication of the Triassic reptile *Trilophosaurus*. *M.S. thesis, University of Texas at Austin*, 100 p.
- Parrish J. M. (1983) - Locomotor adaptations in the hindlimb and pelvis of the Thecodontia (Reptilia: Archosauria). *Ph.D. Dissertation, University of Chicago*.
- Parrish J. M. (1986) - Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. *Hunteria*, 1 (2): 1-34, Boulder.
- Pinna G. (1980) - *Drepanosaurus unguicaudatus*, nuovo genere nuova specie di Lepidosauo del Trias Alpino (Reptilia). *Atti Soc. It. Sc. Nat.*, 121 (3):181-192, Milano.
- Pinna G. (1984) - Osteologia di *Drepanosaurus unguicaudatus*, Lepidosauo Triassico del sottordine *Lacertilia*. *Mem. Soc. It. Sc. Nat.*, 24:7-28, Milano.
- Pinna G. (1986) - On *Drepanosaurus unguicaudatus*, an Upper Triassic Lepidosaurian from the Italian Alps. *J. Paleont.*, 60: 1127-1132, Lawrence.
- Renesto S. (1994) - *Megalancosaurus preonensis*, a possibly arboreal archosauromorph from the Norian (Late Triassic) of Northern Italy. *J. Vert. Paleont.*, 14: 38-52, Lawrence.
- Renesto S. (2000) - Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of Northern Italy. *Riv. It. Paleont. Strat.*, 106: 157-180, Milano.
- Renesto S. & Paganoni A. (1995) - A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of Northern Italy. *N. Jahrb. Geol. Paläont., Abh.*, 197: 87-99, Tübingen.
- Rinehart L. F., Lucas S. G. & Heckert A. B. (2003) - An early eubranchyuran (Malacostraca: Decapoda) from the Upper Triassic Snyder quarry, Petrified Forest Formation, north-central New Mexico. *New Mexico Museum Nat. Hist. Science Bull.*, 24: 67-70, Albuquerque.
- Romer A. S. (1949) - The vertebrate body. - W. B. Saunders Company, 624 pp., Philadelphia.
- Romer A. S. (1956) - Osteology of the Reptiles. - University of Chicago Press, 772 pp., Chicago.

- Sander P.M. (1989) - The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with description of a new species. *Phil. Trans. R. Soc. London*, 325/1230: 561-670, London.
- Sereno P. C. (1991) - Basal archosaurs: phylogenetic relationships and functional implications. *Soc. Vert. Paleont. Mem. 2, J. Vert. Paleont.*, 11 Supplement to (4), 53 p., Northbrook.
- Sues H.-D. & Olsen P. E. (1993) - A new procolophonid and a new tetrapod of uncertain, possibly procolophonian affinities from the Upper Triassic of Virginia. *J. Vert. Paleont.*, 13: 282-286, Northbrook.
- Sues H.-D., Olsen P. E., Carter J. G. & Scot D. M. (2003) - A new crocodylomorph archosaur from the Upper Triassic of North Carolina. *J. Vert. Paleont.*, 23: 329-343, Northbrook.
- Unwin D.M. (1996a) - Pterosaur tracks and the terrestrial ability of pterosaurs. *Lethaia*, 29: 373-386, Copenhagen.
- Unwin D.M. (1996b) - First record of Pterosaurs from the Early Cretaceous Tetori Group: a wing-phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan. *Bull. Natn. Sci. Mus., Ser. C*, 22 (1,2): 37-46, Tokyo.
- Williston S.W. (1914) - The osteology of some American Permian vertebrates. *J. Geol.*, 22: 364 - 419, Chicago.
- Xu X., Zhou Z. & Wang X. (2000) - The smallest known non-avian theropod dinosaur. *Nature*, 408: 705-708, London.
- Zani P.A. (2000) - The comparative evolution of lizard claw and toe morphology and clinging performance. *J. Evolut. Biol.*, 13 (2): 316-325, Basel.
- Zeigler K. E., Heckert A. B. & Lucas S. G. (2003) - The vertebrate fauna of the Upper Triassic (Revueltian) Snyder Quarry. *New Mexico Museum Nat. Hist. Science Bull.* 24, 71-79, Albuquerque.
- Zhang F., Zhou Z., Xu X. & Wang X. (2002) - A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften*, 89: 394-398, Berlin.