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A new specimen of *Torvosaurus tanneri* originally collected by Elmer Riggs

Michael Hanson[a]* and Peter J. Makovicky[b1]

aDepartment of Biology, Loyola University Chicago, Chicago, IL, USA; bDepartment of Science & Education, Field Museum of Natural History, Chicago, IL, USA

A new specimen of the theropod dinosaur *Torvosaurus tanneri* discovered by Elmer Riggs in 1899 in the Freezeout Hills of Wyoming and held in the Field Museum of Natural History is described. This specimen demonstrates that unreported material of this species has been present in museum collections 80 years prior to the species' scientific description and it likely represents the first non-dental material of this species to be collected. This material comprises parts of the left foot and right hand, including phalanges which were previously unknown for *Torvosaurus*, and substantiates the possibility that other *Torvosaurus* material may be undiscovered in museum collections. Its occurrence in a multitaxon quarry is consistent with other skeletal finds of *Torvosaurus*, all or most of which occur in association with other, more common Morrison dinosaur taxa.

Keywords: dinosaur; Morrison Formation; Late Jurassic; Theropoda; Megalosauridae

1. Introduction

The megalosaurid megalosauroid *Torvosaurus tanneri*, described by Galton and Jensen in 1979, is among the largest of the theropods known from the Morrison Formation (approximately 9 m adult length, according to Britt 1991). It is the only North American member of the primarily European family Megalosauridae, which has eight other genera occurring in Middle Jurassic Europe and two others from Africa and Asia (see Sereno et al. 1994; Allain 2002, 2005; Allain and Chure 2002; Sadleir et al. 2008; Li et al. 2009; Benson 2010; Carrano et al. 2012; Rauhut et al. 2012). This species was originally described on the basis of disarticulated skeletal material from several individuals first collected in 1973 at the Dry Mesa locality in Colorado (Galton and Jensen 1979). It has since been recovered from sites in Utah, Colorado and Wyoming, and is stratigraphically restricted to the Brushy Basin and Salt Wash Members of the Morrison Formation, but occurs at many localities in the former widespread unit, while known from only a single occurrence in the latter (Britt 1991; Carrano 2000–2013). Furthermore, material described from the Lourinhã Formation of Portugal by Mateus and Antunes (2000), Mateus et al. (2006) and Araújo et al. (2013) has been referred to *T. tanneri*. Although Foster and Chure (2006) and Foster (2007) note that it is the second-most common theropod found in the Morrison Formation, it is far less common than *Allosaurus* and all specimens of this theropod are relatively fragmentary (Britt 1991). Britt (1991) suggested that more undescribed specimens of *Torvosaurus* may exist among the theropod materials historically collected from the Brushy Basin Member, and as an example noted a

large tooth likely collected in 1879 and figured by Lull in 1927. Here, we report another such overlooked *Torvosaurus* specimen, collected by an expedition led by Elmer Riggs in 1899 and accessioned in the Field Museum of Natural History in Chicago.

1.1 Institutional abbreviations

BYUVP, Brigham Young University Earth Sciences Museum, Vertebrate Paleontology, Provo, Utah; FMNH, Field Museum of Natural History, Chicago, Illinois; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; SGM, Ministère de l'Énergie et des Mines, Rabat, Morocco.

2. New specimen

FMNH PR 3060 (Figure 1): three midline fragments of gastralia, right metacarpal III, right manual phalanx III-2, left metatarsals II–IV, left pedal phalanx I-1.

2.1 New specimen locality, provenance and history

This specimen remained unprepared in the Field Museum's collections for decades following its collection in an 1899 expedition to the Morrison Formation conducted by Elmer Riggs and his field parties. During a collection inventory, it was identified as potentially important and prepared out of the matrix in 2005. While the specimen is doubtless from Riggs' Morrison Expeditions, its precise location and date of collection were undocumented. An examination of

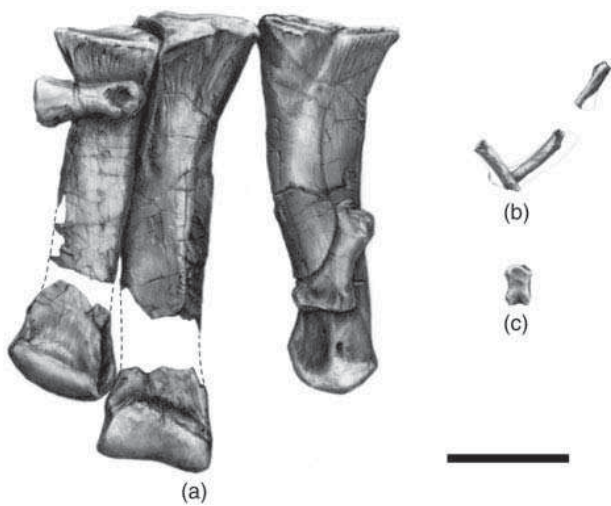*Corresponding author. Email: mhanson1@luc.edu

Figure 1. Illustration of specimen FMNH PR 3060, showing (a) the left metatarsus, left pedal phalanx I-1 and right metacarpal III, (b) the gastralia and (c) the right manual phalanx III-2. Unshaded regions delineated by dashed lines represent missing regions that have been reconstructed. Scale bar is 10 cm.

Riggs' field notes from these expeditions show that of the nine quarries that Riggs documented collecting dinosaurian material (Quarries 1, 2, 3, 5, 6, 12, 13, 14 and 15) over the course of three expeditions from 1899 to 1901, only one appears to have produced material from multiple genera and any theropod material, Quarry 6 from the Freezeout Hills of Wyoming. According to Riggs's field notes, this site was originally 'discovered by Williston's party from Kansas University' and Riggs and Menke excavated the site during the 1899 expedition. This site is likely the same described by Logan (1900). All other quarries that Riggs excavated reportedly only produced material from *Camarasaurus*, *Apatosaurus* and *Brachiosaurus*, with never more than a single genus found per site. Quarry 6, on the other hand, produced a large number of 'miscellaneous dinosaurs', and many of specimens went unidentified in the field notes while those identified include *Camarasaurus*, *Stegosaurus* and *Allosaurus*. It is therefore most parsimonious to assume that unrecorded theropod material from Riggs's expeditions derives from his Freezeout Hills Quarry 6. In addition, the fossil material and the matrix of the new specimen compare favourably to other Freezeout Hills specimens, with deep black fossil bones and greyish, grainy clay matrix and some reddish iron deposits occurring adjacent to the bones or in cracks. This corresponds to the description that Logan (1900) gives for Stratum 23, the horizon of the site discovered by Williston's party, which in turn corresponds to Riggs's Quarry 6 (in addition, Logan's faunal listing for Stratum 23 is the same as that given in Riggs's field notes).

Logan's Stratum 23 is described as the uppermost layer of the Jurassic formations of the Freezeout Hills and, today, it would be considered to belong to the Brushy Basin Member of the Morrison Formation, which dates approximately to the early Tithonian, i.e. ~150–148 Ma (Kowallis et al. 1998). The specimen's occurrence is consistent with the distribution thus far known for North American *T. tanneri*, which Britt (1991) suggested 'may range throughout the Brushy Basin Member of the Morrison, but is a very rare member of the fauna'. Virtually all North American *Torvosaurus* specimens have been recovered from quarries in Colorado, Utah and Wyoming belonging to the Late Kimmeridgian to Early Tithonian (Late Jurassic) Brushy Basin Member, a single specimen has been documented from the earlier Kimmeridgian Salt Wash Member of the Morrison Formation (Carrano 2000–2013; Carrano et al. 2012).

3. Description and comparisons

3.1 Description

In the following, we make comparisons to material already known for *Torvosaurus* in order to document individual variation and offer new observations based on elements that are better preserved in this specimen than in previously described or figured material. Elements previously unknown in *Torvosaurus* are compared with other large tetanuran theropods. Measurements were taken in millimetres with digital callipers or a tape measure (for measurements in excess of 20 cm), some are approximate due to missing and restored sections of the specimen.

3.1.1 Preservation

This specimen consists of a largely complete metatarsus with the second and third metatarsals close to a natural articulation, although the second metatarsal is slightly shifted anteriorly relative to the third. The fourth metatarsal has shifted outwards from its natural position and is not articulated with the other metatarsals, but is separated by only 9 cm or less from metatarsal III (maximum distance between elements, at the distal region of the specimen). The third metatarsal lacks a portion of its shaft immediately proximal to the condyle that is equivalent to approximately one-sixth of the element's estimated length. Similarly, metatarsal II is missing a portion proximal to the condyle that would have comprised around one-twelfth of the original length of the bone, and part of the posterior projection of the proximal face has broken off and is missing. The proximal and distal sections were collected *in situ* permitting accurate restoration of these sections with Apoxie® Sculpt (Aves Studio, River Falls, WI, USA). All metatarsals exhibit some minor cracking and crushing, but the overall shapes of the elements are not heavily distorted, although Metatarsal IV shows a greater degree of crushing than the other two metatarsals in the anteroposterior aspect.

In addition to the metatarsals, the specimen preserves the left first phalanx of the hallux, a right-third metacarpal and the second phalanx of the right-third manual digit. The latter phalanx has been completely prepared out of the matrix and is almost entirely complete, only missing a small region of the edge of the lateral condyle. The pedal phalanx and the metacarpal still remain attached with matrix to the extensor surfaces of the proximal end of the second metatarsal and the distal half of the fourth metatarsal, respectively.

Finally, three fragments of gastralia are preserved in association with the pedal and manual elements. These fragments exhibit heavy cracking and are still partially in the original matrix. Two gastral fragments overlap each other and represent articulated ends of a medial and lateral gastralia pair, while the other section is preserved on its own. Histological thin sections of two of the gastralia were made, as gastralia have been useful for ageing some theropod specimens (Erickson et al. 2004, 2007; Grellet-Tinner and Makovicky 2006). Unfortunately, all three sections are completely remodelled with Haversian canals and erosional lacunae obliterating the growth history.

3.1.2   Elements

Left metatarsal II. Metatarsal II possesses a 'D'-shaped proximal articulation as in *Torvosaurus* (Britt 1991) and *Eustreptospondylus* (Sadleir et al. 2008) (Figure 2(a)–(f)). The lateral margin of the proximal articulation is slightly more flared than in BYUVP 5147, which appears more squared off. The diaphysis is flat laterally and rounded medially, and it bears a low, mound-like insertion for the *M. gastrocnemius* (Carrano and Hutchinson 2002) approximately three quarters of the distance from the proximal end. This muscle scar is more pronounced in FMNH PR 3060 than in BYUVP 5147. The distal articulation is subspherical rostrally, but terminates in two unequal hemicondyles caudally, with a wide and helical notch on the caudal face of the bone. The collateral ligament fossae are shallow as in other specimens of *Torvosaurus* (Britt 1991), but unlike the deep pits of allosauroids and ceratosauroids. The lateral ligament fossa is broad and expanded across most if the lateral face of the distal end, but the medial fossa is delimited by a low crest rostrally.

Left metatarsal III. The proximal end is more block-like with less of a constriction than in *Allosaurus* or coelurosaurs (Figure 2(g)–(l)). It is almost straight medially and modestly indented laterally. The rostral and caudal edges of the proximal articulation are not parallel and both overhang the shaft. The shaft exhibits a twisted appearance as it is deeper than wide rostrally, but has opposite proportions adjacent to the distal articulation. The distal articulation is broad and deeper medially than laterally in rostral aspect. Although it extends beyond the rostral face of the shaft, there is no extensor fossa above the distal articulation as in many coelurosaurs. As in the other metatarsals, the ligament pits are wide and shallow on both sides. The rostral rim of each fossa bears a low tuber, a feature also observed in *Allosaurus* (FMNH PR 25114).

Metatarsal III of FMNH PR 3060 is extremely similar to BYUVP 5147, except that the proximodorsal corner of the proximal surface is less ventrally displaced.

Left metatarsal IV. The proximal articulation is tear-drop shaped with a broad, rounded rostral edge and a pinched caudal end (Figure 2(m)–(r)). The shaft is deflected laterally towards its distal end. The distal articulation is narrower than deep, subspherical and the notch between the posterior hemicondyles is very wide and shallow. Compared to BYUVP 5147, the plantar ridge in this specimen appears narrower, but this is likely accentuated by the mediolateral crushing of the shaft.

FMNH PR 3060 described here provides some new information on the anatomy of *Torvosaurus*. The fourth metatarsal illustrated in Britt (1991, figure 24), BYUVP 5278, was heavily restored with plaster, while FMNH PR 3060 is completely preserved and, despite the crushing, gives a better example of the overall shape of this element. It reveals that the proximal articulation is not slanted as reconstructed in BYUVP 5147, but is nearly perpendicular to the diaphysis.

Left pedal phalanx I-1. This element is previously unknown in *Torvosaurus* and is preserved here in its entirety, although the lateral aspect could not be examined (Figure 3(a)–(e)). The proximal end is almost elliptical, but with a straight ventral edge that imbues it with a more triangular outline than that of *Allosaurus* (Madsen 1976a, Plate 54). The shaft is short and thick and the distal articulation is twisted relative to the proximal one. The distal ginglymus is much wider ventrally than dorsally in distal aspect, and not dorsally directed as they are in *Allosaurus*. In comparison with *Poekilopleuron bucklandii* (Eudes-Deslongchamps 1838, Plate VIII, figure 8), this phalanx has a more triangular proximal outline in *Torvosaurus*, the anterior condyles are more mediolaterally compressed in *Torvosaurus* and the ventral surfaces of the distal condyles remain restricted compared to *Poekilopleuron*, in which they extend farther proximally so that the anterior condyles extend over a third of the length of the bone.
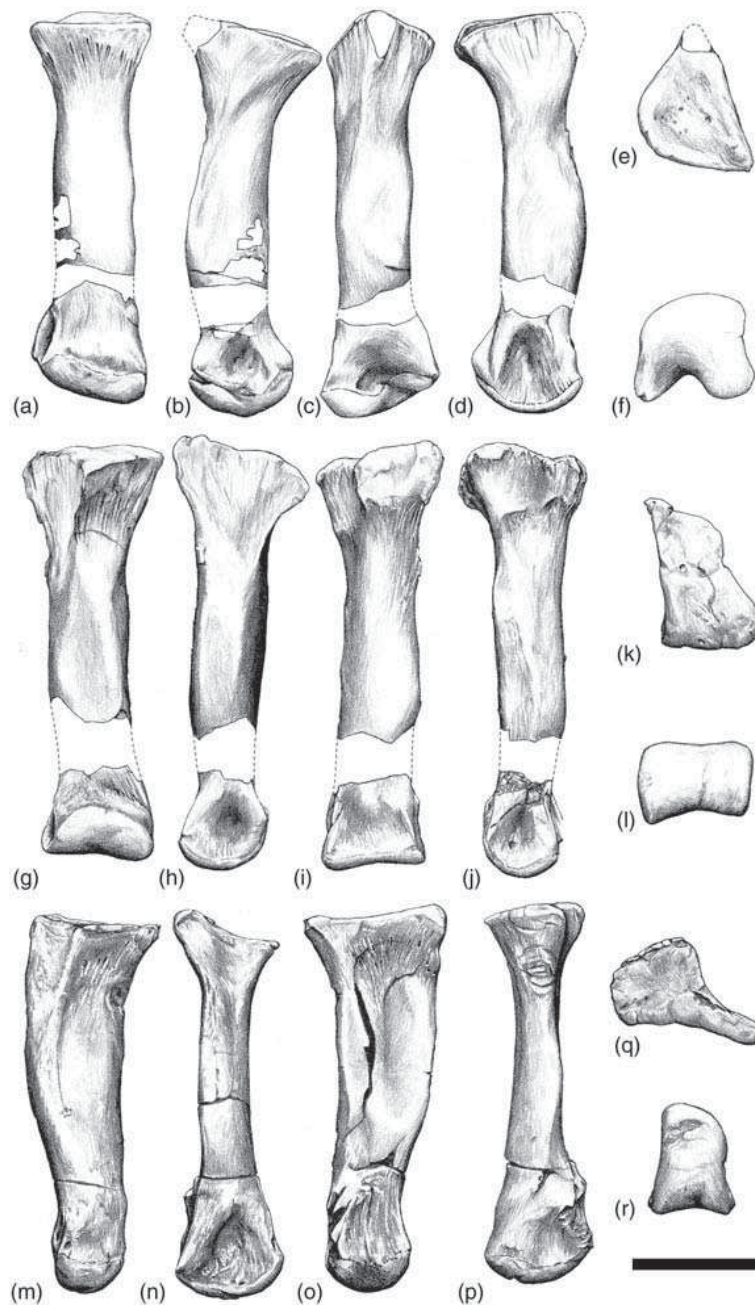
Figure 2.   Left metatarsal elements of FMNH PR 3060: metatarsal II (a–f), metatarsal III (g–l) and metatarsal IV (m–r) in anterior (a, g, m), medial (b, h, n), posterior (c, i, o), lateral (d, j, p), proximal (e, k, q) and distal (f, l, r) views. Unshaded regions delineated by dashed lines represent missing regions. Scale bar is 10 cm.

Right metacarpal III. Despite being completely preserved, the ventral aspect of this metacarpal could not be examined (Figure 3(f)–(j)). The proximal end forms a broad, low triangle in end view. The shaft is pinched between the proximal and distal articulations, and slightly curved so that the distal end is twisted relative to the proximal one. A shallow extensor fossa lies adjacent to the distal articulation, which has a blocky outline in distal view interrupted by a deep ventral concavity. Collateral ligament fossae are absent. Several slight differences are noted compared to previously described specimens (Galton and Jensen 1979; Britt 1991): the distal condyle is less curved in lateral view and more square in distal view; the shaft is more elongated, proximal end is not as expanded, particularly so ventrally.

Right manual phalanx III-2. This element is previously unknown in *Torvosaurus* and the only other megalosauroid for which it is known is *Sciurumimus albersdoerferi*,
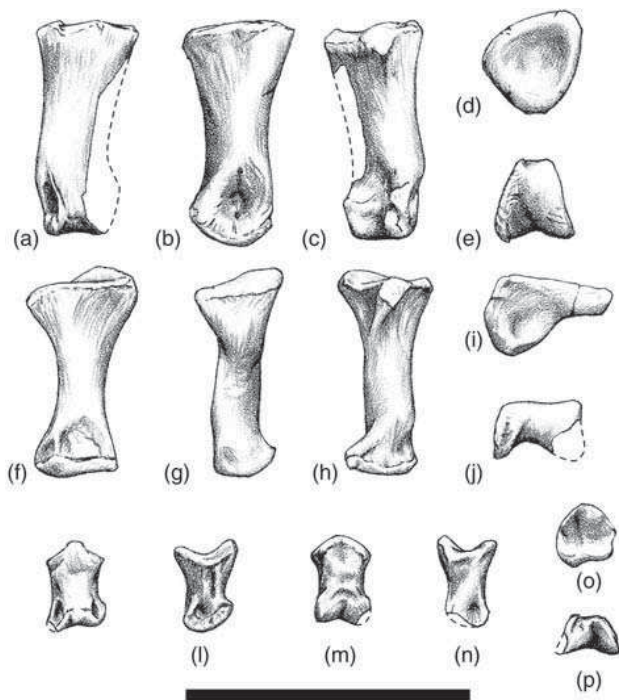
Figure 3. Metacarpal and phalangeal elements of FMNH PR 3060: left pedal phalanx I-1 (a−e), right metacarpal III (f−j) and right manual phalanx III-2 (k−p) in anterior (a, f, k), medial (b, g, l), posterior (c, m), lateral (h, n), proximal (d, i, o) and distal (e, j, p) views. Unshaded regions delineated by dashed lines represent regions obscured by matrix (in a, c and j) or missing regions (in k, m, n and p). Scale bar is 10 cm.

a species based on a juvenile specimen (Rauhut et al. 2012) (Figure 3(k)−(p)). At 34 mm in length, the phalanx described here is substantially smaller than the first phalanx of the first manual digit (BYUVP 2021) described by Galton and Jensen (1979) (where the scale given in figure 4 indicates an approximate length of 65 mm) and has a distinctive 'twisted' morphology with the distal condyles oriented at an angle to the proximal end, which the element described here lacks, thus the identity as manual phalanx I-1 may be ruled out. Phalanges II-1 and II-2 may also be ruled out as these tend to be closer in size to manual phalanx I-1 and in megalosauroids that preserve phalanges of the second digit – *Leshansaurus qianweiensis* (Li et al. 2009), *Sciurumimus albersdoerferi* (Rauhut et al. 2012) and possibly *Baryonyx walkeri* (Charig and Milner 1997) – these phalanges have a long, narrow dorsoventral and anteromedial profile where the length is greater than twice the maximum width, this is also true for other large theropods such as *Allosaurus* (Madsen 1976a, Plate 45) and *Acrocanthosaurus* (Currie and Carpenter 2000, figure 12). Of the third manual digit phalanges, phalanx 3 is typically the most elongated and narrowest in dorsal profile, with a length only slightly more or less than twice the width as in *Allosaurus*. Among megalosauroids,

Afrovenator abakensis (Sereno et al. 1994), *Leshansaurus* and *Sciurumimus* conform to this morphology, and pending the discovery of further material it is most likely that *Torvosaurus* was not different in this regard. Finally, the phalanx III-1 may be ruled out as the phalanx described here has two facets at its proximal articular surface to articulate with a more proximal phalanx, whereas the first phalanx typically has a single facet to articulate with the metacarpal (Charig and Milner 1997). The asymmetry of this phalanx, where the larger (i.e. lateral) hemicondyle occurs on the right side, indicates that it belongs to the right manus, as in other theropods (see Madsen 1976a, Plate 44; Currie and Carpenter 2000, figure 12). In lateral view, this phalanx is very similar to the same element in *Sciurumimus* (Rauhut et al. 2012, figure 1(c)), where it is the shortest phalanx, with a subtriangular profile and a highly reduced diaphysis.

Compared with *Allosaurus fragilis*, this element in *T. tanneri* is proportionately much shorter and stouter, its maximum width being two-thirds of its maximum. This element is more similar to that of *Acrocanthosaurus atokensis* in being short and robust compared to *Allosaurus*, although the distal condyles in *Acrocanthosaurus* are more similar in structure to *Allosaurus* (i.e. more rounded and less inclined).

The phalanx is almost entirely complete, only missing a small part of the lateral condyle. The proximal articulation is divided by a faint, vertical ridge that is obliquely oriented. It is much deeper than the distal articulation in lateral view. The shaft is short and barely constricted between the articular ends. A shallow pit marks the medial face of the shaft adjacent to the proximal articulation. Small, but distinct ligament pits are present distally and are positioned close to the dorsal edge rather than being centred on the lateral face of each hemicondyle. The distal articulation is ginglymoid with the hemicondyles converging dorsally in end view.

3.2 Comparisons

Despite Britt (1991) listing the absence of collateral pits as a diagnostic feature of *T. tanneri*, this trait, properly described as very broad and shallow ligament pits, is observed more broadly among megalosauroid theropods including *Eustreptospondylus* (Sadleir et al. 2008) and *Piatnitzkysaurus* (MACN Ch-895). Britt (1991) also recognised that *Torvosaurus* could be distinguished from other large Morrison theropods in having both larger and proportionately wider metatarsals than any other Morrison theropod. FMNH PR 3060 can be confidently assigned to *T. tanneri* based on the size and proportions of the metatarsals, which are unique to *Torvosaurus* among Morrison theropods (see Table 1; Gilmore 1920; Madsen

Table 1.   Measurements of FMNH PR 3060 (in millimetres).

Element	Total length	Minimum shaft width	Proximal anterio-posterior thickness	Proximal latero-medial width	Distal anterio-posterior thickness	Distal latero-medial width
Left metatarsus II	306[a]	58[a]	93[a]	92	80	90
Left metatarsus III	356[a]	59[a]	117	73	59	89
Left metatarsus IV	287	57	109	70	60	81
Left pedal phalanx I-1	80	24	39	38	35	26
Right metacarpal III	85	19	48	35	31	47
Right manual phalanx III-2	34	16	25	22	16	21

[a] An approximate measurement.

1976a; lengths of the metatarsals range from two to three times the maximum proximal end widths of the respective metatarsals in *Torvosaurus*, versus three to four times in *Allosaurus* and *Ceratosaurus*), in combination with the shallow ligament pits, a trait with a restricted distribution among megalosauroids.

The foot of *Torvosaurus* is distinguishable from that of *Allosaurus* in that the second metatarsal is not as strongly angled medially (as described in Britt 1991) and has a proximal articular surface that is teardrop-shaped to almost semicircular in outline, rather than subtriangular with a medial groove (as in *Allosaurus*, see Madsen 1976a, Plate 54), the third metatarsal has a somewhat more trapezoidal proximal surface and lacks the postero-medial extension seen in *Allosaurus*, and the fourth metatarsal has a shaft that is straight rather than strongly angled laterally and a proximal articulation with a narrower, more triangular shape than in *Allosaurus*. It should be noted that this specimen demonstrates that the fourth metatarsal actually is angled distally in the lateral direction to a slightly greater degree than described in Britt (1991), nonetheless, the angle is not nearly as great as that seen in *Allosaurus*, and the robustness of this element is distinguishable from *Allosaurus*.

FMNH PR 3060 can be distinguished from *Ceratosaurus nasicornis* (see Gilmore 1920, Plates 24 and 25; Madsen and Welles 2000, figure 10) in that the proximal articulation of the third metatarsal is more trapezoidal, with a slight degree of mediolateral constriction as in tetanurans. In *Ceratosaurus*, the articulation is nearly rectangular with the anterior portion slightly narrower than the posterior. Also, the proximal face of the fourth metatarsal in *Torvosaurus* exhibits a narrow, subtriangular shape whereas in *Ceratosaurus* it is trapezoidal. As Britt (1991) noted, the metatarsus in *Torvosaurus* lacks the deep pits at the site of attachment for the collateral ligaments that occur in *Ceratosaurus* and other ceratosauroids (e.g. *Deltadromaeus agilis* SGM Din-2). Like *Ceratosaurus*, however, the metatarsals are more robust and less curved in *Torvosaurus* than in *Allosaurus*.

No metatarsals of the considerably smaller (~5 m estimated length according to Madsen 1976b) Morrison piatnitzkysaurid megalosauroid *Marshosaurus bicentesimus* are known (Benson 2010; Carrano et al. 2012), but it likely shared its metatarsal anatomy with the other piatnitzkysaurids *Piatnitzkysaurus floresi* (Bonaparte 1986, figure 27) and *Condorraptor currumili* (Rauhut 2005, figure 14). Both of these species exhibit a far more gracile metatarsal morphology with relatively small epiphyses and a much longer, narrower diaphysis such that the total length of any major metatarsal is at least four to five times the maximum width of the proximal ends versus a length that ranges from approximately two to three times the maximum proximal width in *Torvosaurus* (Table 1). The third and fourth metatarsals in *Piatnitzkysaurus* exhibit much stronger latero-medial curvature along the diaphysis than in *Torvosaurus*. The fourth metatarsal of *Condorraptor* also has similar curvature and has a distal condyle that is rounder, and semicircular in lateral profile, whereas that of *Torvosaurus* is flatter. Thus, while metatarsal material remains unknown from *Marshosaurus*, it is expected to be smaller and morphologically distinct from *Torvosaurus*.

There is no overlap between the new specimen and the material originally assigned to *Edmarka rex*, which Bakker et al. (1992) described as a second megalosauroid species in the Morrison, and which recent workers (Rauhut 2003; Holtz et al. 2004; Carrano et al. 2012) consider to be a junior synonym of *T. tanneri* based on studies of other specimens, an opinion we follow here.

No other large tetanuran theropods with preserved metatarsi are known from the Morrison Formation, and the only remaining large theropod taxon of comparable size, *Saurophaganax*, is a sister taxon to *Allosaurus* (Carrano et al. 2012) and is likely to have shared its pedal anatomy

3.3   Size and proportions

Manual and pedal elements in megalosaurids, especially the phalanges, are poorly documented and the specimen

described here provides previously unknown elements for *T. tanneri*. Comparison of manual to pedal proportions with other megalosauroids remains difficult as the only megalosauroid that preserves significant portions of both the manual and pedal elements is *Sciurumimus albersdoerferi*, which is only known from an immature specimen. According to Rauhut et al. (2012), the proportions of *Sciurumimus* are 'remarkably similar' to those of juvenile coelurosaurs such as *Juravenator*, and among these proportional characteristics is a 'relatively long manus'. Based on the figures provided in Rauhut et al. (2012), the length of the second digit of the manus, including the metacarpal and excluding the ungual, is subequal to the length of the third metatarsal, the first manual digit (including the metacarpal and excluding the ungual) to be subequal to approximately half this length and the third manual digit (including the metacarpal and excluding the ungual) to be subequal to approximately 75% of the metatarsus length. These proportions may not be applicable to adult megalosauroids. Britt (1991) points out that the metacarpal and non-manual forelimb material of *Torvosaurus* is relatively short and stout for a theropod.

The new specimen is similar in size to previously described specimens. The length of metatarsal III (the longest metatarsal in *Torvosaurus*) in the specimens described by Jensen (1985) ranges from 320 to 365 mm, and the reconstructed metatarsal III length of FMNH PR 3060 (356 mm) falls within that range. The length of the pubis described by Galton and Jensen (1979) is about 85% smaller (736 mm) than that described by Bakker et al. (1992) (866 mm). It is noteworthy that all documented Morrison *Torvosaurus* specimens including FMNH PR 3060 are from similarly sized, likely adult individuals (Britt 1991; Bakker et al. 1992).

There may be several reasons for a lack of sampling immature individuals, none of which are mutually exclusive. For many Morrison vertebrates, large individuals preserve better and are more likely to be collected than small ones, especially if abundance is factored out (Foster 2007). Another possibility is that immature individuals may have occupied a different ecological niche from adults in habitats where their remains were likely to preserve as fossils. Hone and Rauhut (2010) suggest that if dinosaur predation behaviour and population structures were comparable to modern predatory tetrapods, a reason for the universal scarcity of juveniles in the fossil record may be due to juveniles being the prey of choice for larger predators. A fourth option is that *Torvosaurus* experienced Type B_1 population survivorship as has been found in other dinosaurs (Erickson et al. 2006, 2009), with mortality increasing after sexual maturity was achieved leading to an abundance of mature individuals in the fossil record. A final possibility is that immature *Torvosaurus* remains could be misidentified, as young megalosauroids were

very similar in proportion to coelurosaurs (Rauhut et al. 2012). This may especially bias against the recognition of juveniles of a large taxon such as *Torvosaurus*, which is most readily identified based on size and robustness when diagnostic characters are not preserved (Britt 1991).

3.4   Other comparative remarks

Megalosauroids with pedal material known that is comparable to the *Torvosaurus* material described here include the piatnitzkysaurids *Condorraptor* (Rauhut 2005) and *Piatnitzkysaurus* (Bonaparte 1986), the spinosaurid *Baryonyx* (Charig and Milner 1997) and megalosaurids *Eustreptospondylus* (Sadleir et al. 2008), *Megalosaurus* (Benson 2010), *Afrovenator* (Sereno et al. 1994), *Poekilopleuron* (Eudes-Deslongchamps 1838) and *Sciurumimus* (Rauhut et al. 2012), and *Torvosaurus* remains distinct in that the elements described here being more robust than in any of these other megalosauroid. The piatnitzkysaurids have distinctly gracile and curved metatarsals. The metatarsals of *Baryonyx* are far too poorly preserved to conclusively identify, but unusually for a megalosauroid, Charig and Milner (1997) note that it possesses 'well-developed ligament pits'. The remaining megalosaurids are relatively uniform and more gracile in their morphology. Comparable manual material is limited among megalosauroids to the spinosaurid *Suchomimus* (Sereno et al. 1998) and megalosaurids *Leshansaurus* (Li et al. 2009) and *Sciurumimus*. The *Suchomimus* material, limited to the third metacarpal, is yet to be described or illustrated in detail. The third metacarpals of *Leshansaurus* and *Sciurumimus* are, like their metatarsi, gracile compared with *Torvosaurus*. Charig and Milner (1997) described phalangeal material for the manus of *Baryonyx*, but apart from phalanx I-1, they were unable to establish to which digit the remaining material belonged and more spinosaurid material is still needed to make a conclusive determination, leaving *Sciurumimus* as the only megalosauroid with phalangeal material that can be compared to the *Torvosaurus* material described here. It should be noted that while the holotype of *Sciurumimus albersdoerferi* is the most complete megalosauroid known and all elements described here for *Torvosaurus* are known in *Sciurumimus*, its ontogenic stage and small size make any further comparison between the elements described here and those in *Sciurumimus* problematic as of this writing.

4.   Occurrence

Torvosaurus tanneri specimen FMNH PR 3060 was likely found in a multitaxon quarry that included, according to Riggs' 1899 field notes, '*Morosarus* [*Camarasaurus*], *Creosaurus* [*Allosaurus*], and other small forms' as well as a 'plate of *Stegosaurus*'. This is generally consistent with other reported findings of *Torvosaurus* in the

Morrison Formation, almost all of which co-occur with several other dinosaur taxa, most notably *Camarasaurus* and *Allosaurus* (Table 2; Foster and Chure 2006; Foster 2007). Only a single quarry is listed on *The Paleobiology Database* (Carrano 2000–2013) as yielding only *Torvosaurus* remains, yet this is adjacent to other quarries at Garden Park, which yield specimens of more common species. Another unpublished partial skeleton unassociated with other taxa is known from Emery County, Utah (Carpenter, pers. comm.). At many sites such as the Dana Quarry, *Torvosaurus* is only represented by shed tooth crowns (Galiano and Albersdörfer 2010), and the occurrence of skeletal material seems to be almost exclusively from multidominant Morrison Formation bonebeds, such as Dry Mesa Quarry, Dinosaur National Monument and the Cleveland-Lloyd Quarry, with *Torvosaurus* as a minor component. The Calico Gulch Quarry appears to be the only multitaxon quarry from which *Torvosaurus*, represented by a single first manual ungual[2] (Galton and Jensen 1979), has been documented in the absence of *Allosaurus*. This pattern has been interpreted as indicative of *Torvosaurus* sharing habitats with other predators, most notably *Allosaurus*, but at much lower abundances (Foster and Chure 2006; Foster 2007). Riggs' Quarry 6 may thus represent the only locality yet reported, in which *Torvosaurus* and *Allosaurus* are each represented by only a single partial skeleton each. Reported occurrences in Portugal (Mateus and Antunes, etc.) are notably different in that the findings of *Torvosaurus* are not associated with other faunal elements. Whether this difference is related to taphonomy, palaeoenvironment or taxonomy is not yet clear.

5.   Historical significance

FMNH PR 3060 likely represents the first non-dental material of *T. tanneri* ever collected, and second only to some unusually large teeth described by Lull (1927), and later referred to the species by Britt (1991). Postcranial material of *Torvosaurus* can be identified with far greater certainty, because in comparison with contemporaneous theropods, *Torvosaurus* material is distinctive in its size and robustness. The discovery of this specimen in the Field Museum's collections demonstrates that non-dental material that demonstrably belongs to *T. tanneri* has been collected decades before the species' 1979 description thereby confirming the possibility raised by Britt (1991) that *Torvosaurus* elements would be found among the large Morrison theropod materials 'housed in various institutions, but in many cases [. . .] never [. . .] studied in detail or even prepared'.

There may yet be more such specimens to be uncovered in museum collections, possibly collected under the presupposition of being material of an already-

Table 2.   Faunal composition of quarries reported to yield remains of *T. tanneri*.

Locality	*Camarasaurus*	*Allosaurus*	*Stegosaurus*	*Apatosaurus*	*Dipolodocus*	*Barosaurus*	*Camptosaurus*	*Dryosaurus*	*Brachiosaurus*
Calico Gulch/Lily Park	×				×			×	
Dry Mesa	×	×	×	×	×	×		×	
Dinosaur National Monument	×	×	×	×	×	×		×	
Meyer Site 2	?	?		?	?				
Nail Quarry	×	×	×	×	×				
Louise Quarry	×	×	×	×					
Red Canyon Ranch	×	×	×						
Dana Quarry	×	×		?	?	?	×		×
Freezeout Quarry	×	×	×	×					

Notes: Data from The Paleobiology Database (Carrano 2000–2013) and taxa ordered from left to right according to approximate abundance as reported by Foster (2007). Presence of a taxon is indicated by '×' and '?' indicates possible presence based on fragmentary remains.

known theropod species such as *Allosaurus* or *Ceratosaurus*, or of being scrappy, and thus not worthy of further scientific inquiry. The overlooking of a taxon for nearly 80 years exposes the risks of disregarding scrappy material (though certainly it is no less fragmentary than the holotype humerus[3] of *T. tanneri*). This specimen is also the first non-dental material documented from the Freezeout Hills. Britt (1991) reported a tooth from Gilmore's Quarry N, and the new specimen described here strengthens the evidence for the presence of *T. tanneri* in the Freezeout hills and throughout the Brushy Basin Member.

Notes

1. Email: pmakovicky@fieldmuseum.org
2. Allain et al. (2012) referred this exceptionally large ungual (BYUVP 2020) to an indeterminate spinosaurid, reasoning that enlarged first-digit manual unguals are only known in spinosaurids and the specimen was not found in association with any other skeletal material that could point to its origin. They also suggested that the specimen should not be used to diagnose Spinosauroidea *sensu* Sereno et al. 1998 (= Megalosauroidea). We do not follow this position and consider the ungual to belong to *Torvosaurus* for the following reasons: Allain et al. (2012) recovered Megalosauridae and Spinosauridae as sister taxa in their phylogenetic analysis in spite of their position on this specimen and in agreement with other studies (e.g. Benson 2010; Carrano et al. 2012). Furthermore, as discussed in this work, megalosaurid manual anatomy remains poorly understood. It is possible that the spinosaurid ungual morphology may have been more widely distributed in Megalosauria. Both Allain et al. (2012) and Carrano et al. (2012) recover *Torvosaurus* as either basal or sister to the clade containing *Afrovenator* and *Dubreuillosaurus*, which lacks the enlarged first-digit ungual. Given the current state of knowledge, it is still reasonable to view the spinosaurid condition a possible basal synapomorphy for Megalosauria, and its loss in other Megalosaurids as a derived condition. Finally, Allain et al. (2012) acknowledge that, in the absence of this ungual, no distinctly spinosaurid dental or skeletal material has been recorded from the Morrison Formation. Pending the discovery of such material, it is most parsimonious to regard the specimen as belonging to a taxon already known from the Morrison Formation's Brushy Basin Member, and *Torvosaurus* remains the best candidate.
3. The holotype humerus of *Torvosaurus tanneri* belongs to a local accumulation of cranial, vertebral, pelvic and limb material from several individuals of the same species in the Dry Mesa Quarry. Galton and Jensen (1979) considered a set of left and right humeri, a right radius, and left and right ulnae (BYUVP 2002) to belong to a single individual and designated the assemblage as the holotype. Britt (1991) saw no reason to presume that the elements belonged to the same individual and designated the left humerus as the holotype, regarding the other bones as part of the paratype series.

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