Consilient evidence affirms expansive stabilizing ligaments in the tyrannosaurid foot

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Abstract: Tyrannosaurid dinosaurs were ecologically unique vertebrates as the sole clade of large terrestrial carnivores (adults >400 kg) in their continent-spanning habitats. Expanded ligaments between metatarsals, inferred by gross morphology of attachment correlates, have been hypothesized to have strengthened their specialized arctometatarsus. We tested the hypothesis of ligament presence with scanning electron microscopy and histological thin sections of putative attachment sites in a third metatarsal of the tyrannosaurid Gorgosaurus libratus, compared with a thin section from the unspecialized metatarsals of the early theropod Coelophysis bauri. In the Gorgosaurus metatarsal, Sharpey’s fibers and rough, pitted surface textures consistent with ligament coalescence occur at expansive distal regions and localized rugosities are ideally located for resisting torsional loading on the foot. Sparser Sharpey’s fibers occur at expected locations in other arctometatarsus-bearing coelurosaurs. In contrast, the Coelophysis metatarsal lacked Sharpey’s fibers or rugosity at the sectioned location, acting as a definitive negative control for identifying these features in tyrannosaurids. With soft-tissue correlates confirmed as ligament entheses, we conclude that tyrannosaurids possessed distinctive and specific ligament attachments to the third metatarsal lacking in other large carnivorous dinosaurs. Histological evidence for extensive distal intermetatarsal ligaments is consistent with greater inferred agility in derived tyrannosaurid dinosaurs than in earlier lineages of large theropods.

INTRODUCTION

Tyrannosaurs were large, ecologically prominent predators with continent-spanning ranges in North America and Asia during the Late Cretaceous (Brusatte et al. 2010). Unusually amongst terrestrial carnivores, adults of later tyrannosaurids were two orders of magnitude more massive than their next-largest adult competitors (Holtz 2002; Snively et al. 2019; Holtz 2021; Schroeder et al. 2021). Success of tyrannosaurids and relatives amongst the larger Tyrannosauroidea has been attributed to unique feeding adaptations, including fused, vaulted nasals (Hurum and Sabath 2003; Rayfield 2004; Snively et al. 2006), a broad skull resistant to torsion and bending (Snively et al. 2006), an expanded secondary palate (Holtz 2002), high bite and neck muscle forces (Snively and Russell 2007a, b; Bates and Falkingham 2012, 2018; Gignac and Erickson 2017; Cost et al. 2019) and robust bone-sundering teeth (Erickson et al. 1996). These adaptations evolved mosaically along the trend to greater adult body size (Erickson et al. 2004; Shychoski 2006; Snively et al. 2006; Li et al. 2010), and reached their greatest extents in Tyrannosaurus rex, Tarbosaurus bataar and Zhuchengtyrannus magnus (Brusatte et al. 2010; Hone et al. 2011), the last and largest tyranno-
saurs. In addition to feeding-related features, postcranial adaptations arising prior to tyrannosaurid diversification, when tyrannosauroids were relatively small (Nesbitt et al. 2019; Zanno et al. 2019), may have catalyzed the group's later ecological exclusivity as large predators (Schroeder et al. 2021; Holtz 2021). For example, derived tyrannosauroids (including tyrannosaurids proper) had anatomical features potentially consistent with greater agility (here defined as the ability to turn more rapidly) than other theropods, such as relatively large leg muscles (Hutchinson et al. 2012; Snively et al. 2019) effective for turning the body, and more compact bodies from nose to tail (Henderson and Snively 2003; Snively et al. 2019) for lower rotational inertia (Carrier et al. 2001; Henderson and Snively 2003; Paul 2005; Snively et al. 2019).

Convergently with other Cretaceous theropods (including ornithomimids, alvarezsaurids, troodontids, and some caenagnathids), tyrannosaurs evolved the actometatarsalian metatarsus, an elongate and relatively narrow, anteroposteriorly strong metapodium with a proximal splint and distal expansion of the third metatarsal, that conferred capabilities for greater stride length, and higher linear speeds, than was possible in theropods of similar size without such a structure (Holz 1995, 2001; Snively and Russell 2002, 2003; Snively et al. 2004). Such enhanced ground-covering ability (immediate or long distance: Carrano 1998; Dececchi et al. 2020) would have been valuable whether tyrannosaurids were primarily predators or scavengers. However, the most unusual aspects of actometatarsus morphology (Fig. 1) offer hints of immediate agility in tyrannosaurs: a wedge-and-buttress constriction of the central third metatarsal (MT III) between the outer bones (Coombs 1978; Holz 1995), and discrete areas of rugosity on surfaces where the metatarsals articulate with each other distally (Snively and Russell 2002, 2003). Ligaments hypothesized as emanating from these rugose surfaces would have induced kinematics reinforcing the foot during multi-directional maneuvering (Snively and Russell 2002, 2003). Snively and Russell (2003) established with physical testing that these kinematics would counteract splay at high footfall energies as the central metatarsal (MT III) is displaced anteriorly, and the outer metatarsals are drawn inwards towards the plantar midline of the foot. Other vertebrates put more loading on individual, splaying outer metatarsals, as occurs on the first digit of humans as they quickly accelerate or decelerate laterally during agility tests. In contrast, intermetatarsal kinematics in tyrannosaurids would distribute the loading and therefore forces more evenly amongst the metatarsals, enabling greater forces when maneuvering while maintaining similar stresses (force/area) and tissue safety factors (Snively and Russell 2003). Snively and Russell (2002) established the likely necessity of such ligaments for avoiding breakage of the central metatarsal’s proximal splint. These kinematic and structural mechanical hypotheses are subject to refined testing. If the hypotheses are borne out, such ligaments would be consistent with capability for successful prey capture in tyrannosaurids, as with adaptations that similarly enhance agility in predatory animals (Hadziselimovic and Savkovic 1964; Cox and Jeffery 2010; Snively et al. 2019). We refer the reader to these publications for further explication of agility.

Snively and Russell (2003) inferred intermetatarsal ligaments in tyrannosaurids based on gross-scale osteological correlates, but further lines of evidence can test this anatomical inference and form the basis for functional interpretations. We apply scanning electron microscopy and histology to 1) search for finer-scaled correlates of ligament attachment, potentially falsifying the hypothesis that ligaments were present, and 2) to assess whether the direction of ligament insertion is compatible with the splay-negating kinematics that Snively and Russell (2003) proposed. In addition to visually obvious surface rugosity at attachments that are subjected to high loads in life (Snively and Russell 2003, Tumarkin-Daratzian et al. 2007; Petermann and Sander 2013), ligaments and tendons produce microscopic traces of their attachment to bone (Hieronymus 2006; Petermann and Sander 2013) as fibroblasts under tension elongate within the periosteum (Fig. 2), and as parallel osteons form deep to the attachment surface. Ligament entheses also occur within transitional fibrocartilage, which leaves behind a rough bone surface. These histological traces can be used to test hypotheses of ligament presence, differentiating ligament and tendon entheses of attachment from other rough bone surfaces, such as vascularity-striated textures that appear during archosaur growth (Tumarkin-Daratzian et al. 2007; Tumarkin-Daratzian 2009; Brown et al. 2009). Scanning electron microscopy and histological preparations of an adult tyrannosaurid MT III (UALVP 49310) allowed us to assess whether intermetatarsal ligaments were present in a configuration consistent with enhanced tyrannosaur agility.

As a potential control for tyrannosaurid ligament inferences, we examined a metatarsal thin section from the early theropod Coelophysis bauri [AMNH FAR 7239], sampled where no gross enthesis correlates are present. The Coelophysis histology tests and potentially contradicts the hypothesis of extensive ligaments in tyrannosaurids. Falsifying evidence would include similar correlates in the Coelophysis and tyrannosaurid specimens, no microscopic correlates in either, or positive fine-scaled correlates in Coelophysis that are absent in the tyrannosaurid metatarsal. Additionally, in light of a previously described histological correlate for ligament attachments (Sharpey’s fibers) in the second metatarsal of an alvarezsaur (Qin et al. 2019),
we surveyed the literature for similar correlates in other coelurosaurus with arctometatarsalian or subarctometatarsalian (White 2009) pedes to test our predictions about their presence in tyrannosaurids.

MATERIALS & METHODS

Institutional Abbreviations

AMNH FARB, American Museum of Natural History Fossil Amphibians, Reptiles, and Birds collection, New York, New York, USA; BYU, Brigham Young University, Vertebrate Paleontology, Provo, Utah, USA; DINO, Dinosaur National Monument, Jensen, Utah, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; FPDM, Fukui Prefectural Museum, Katsuyama, Fukui, Japan; GI, Geological Institute, Section of Palaeontology and Stratigraphy, Academy of Sciences of the Mongolian People's Republic, Ulaan Bator, Mongolia; HMN, Museum für Naturkunde, Berlin, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; LPM, Lamington Park Museum, Lilley, Queensland, Australia; MPM, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan; NHMUK, Natural History Museum, London, United Kingdom; NSMT, National Science Museum of Thailand, Bangkok, Thailand; NMSU, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; NMV, Natural History Museum of Victoria, Melbourne, Victoria, Australia; OAM, Queensland Museum, Brisbane, Queensland, Australia; OSU, Oregon State University, Corvallis, Oregon, USA; PNGM, Papua New Guinea Museum of Natural History, Port Moresby, Papua New Guinea; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UCP, University of the Cumberlands, Hazard, Kentucky, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; USU, Utah State University, Logan, Utah, USA; WAM, Western Australian Museum, Perth, Western Australia; WNMNH, Westerdals Museum of Natural History, Oslo, Norway.

Figure 1. Contrasting morphologies of arctometatarsalian (a) and generalized (b) theropod metatarsals. a, metatarsus of a tyrannosaurid (Albertosaurus sarcophagus: TMP 81.10.1) in dorsal view showing proximally constricted MT (metatarsal) III, with plantar constriction evident in ventrolateral slope of the exposed distal MT II articular surface with MT III; b, metatarsus of Coelophysis bauri (LACM 153347 block) in dorso lateral view, showing proximally broad, anteriorly positioned MT III, unlike the interpretation depicted in Colbert (1989). Silhouette of Gorgosaurus libratus by Matthew Dempsey and silhouette of Coelophysis bauri by Scott Hartman, both available from Phylopic under a CC BY 3.0 license (https://creativecommons.org/licenses/by/3.0/).
Figure 2. a–b, Gross morphology of hypothesized ligament attachments; a, Gorgosaurus libratus (UALVP 49310) Metatarsal III (MT III), distal end. Outline around distal portion of large surface for articulation with MT II; b, close-up with low-angle light relative to MT II articular surface, showing rugosity indicative of a ligamentous enthesis. Arrow illustrates tension on enthesis, inferred as causing the rugosity; c, mechanism underlying enthesis rugosity in the femur of the lacertid lizard Podarcis hispanicus (H77, Collection of the Biology Department, Autonomous University of Madrid, Spain). Elongation of fibroblasts (*) under tension (muscular in this case) produces parallel bundles of collagen fibers at muscle and ligament attachments.
Angeles County, Los Angeles, USA; MOR, Museum of the Rockies, Bozeman, Montana, USA; MWC, Museum of Western Colorado, Fruita, Colorado, USA; NIGP, Nanjing Institute of Geology and Palaeontology, Academia Sincia, Nanjing, China; NMC Canadian Museum of Nature collections, Gatineau, Quebec, Canada; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; OMNH, Sam Noble Museum of Natural History, Norman, Oklahoma, USA; PVL, Paleontologia de Vertebrados Lillo, Universidad Nacional de Tucuman, Tucuman, Argentina; PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Neuquén Province, Argentina; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Methods
We reviewed macroscopic correlates for ligamentous attachments in comparative specimens that Snively et al. (2004) examined, with the addition of many recently-collected tyrannosaurid metatarsals at UALVP and TMP (Tab. 1). We also surveyed the literature for descriptions of histological correlates in additional coelurosaurian metatarsals. One tyrannosaurid specimen, UALVP 49310, was selected for paleohistological analysis. This specimen is a distal portion of metatarsal III of *Gorgosaurus libratus* collected from the Upper Campanian (Upper Cretaceous) Dinosaur Park Formation in Dinosaur Provincial Park, Alberta, Canada. Arctometatarsalian third metatarsals (MT III) are triangle-shaped in distal cross-sections (Holtz 1995), with a posterior constriction that forms a ridge (also called a plantar constriction; Snively et al. 2004). UALVP 49310 is identifiable as *Gorgosaurus* MT III by its curving, distally extended posterior constriction, differing from the contemporaneous *Daspletosaurus* which has a straighter, broader, oblong, and less edge-like constriction distally (Yun 2021).

Paleohistological analysis was conducted by cutting thin sections transversely through the entire diaphysis of the metatarsal (Fig. 3a, b). The section was initiated at the most protuberant region of the central rugosity on the lateral surface (attachment site for the metatarsal III-IV ligament). One-centimeter-diameter cores were also cut from the bone and divided sagittally to permit mounting on slides. The samples were stabilized via resin impregnation using Buehler EpoThin Low Viscosity Resin and Hardener prior

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**Figure 3.** a, b, distal portion of adult *Gorgosaurus libratus* (UALVP 49310) third metatarsal (right), in a, dorsal and b, ventral views, showing locations of whole-bone transverse section (transverse line) and histological core samples (i-iv). Core iv is from a smooth-surfaced scalloped area. Scale bar = 5 cm; c, d, Proximal portion of *Coelophysis bauri* (AMNH FARB 7239) third metatarsal (right) in lateral (c) and medial (d) views, showing location of whole-bone transverse section. Scale bar = 5 cm.
Table 1. Theropod metatarsal specimens examined. Ontogenetic stage is inferred based on striated (juvenile) or smooth (adult) subcutaneous bone texture, or assessments from original descriptions.

| Taxon                                      | Specimen number | Ontogenetic stage   |
|--------------------------------------------|-----------------|---------------------|
| Albertosaurus sarcophagus                  | AMNH 5432       | Adult               |
| Albertosaurus sarcophagus                  | TMP 1999.050.0025 | Subadult           |
| Albertosaurus sarcophagus                  | TMP 1981.010.0001 | Adult              |
| Albertosaurus sarcophagus                  | TMP 1986.064.0001 | Juvenile-subadult |
| Albertosaurus sarcophagus                  | TMP 1999.050.0012 | Juvenile           |
| Albertosaurus sarcophagus                  | TMP 1988.016.0022 | Subadult-adult     |
| Allosaurus jimmadseni                      | MOR 693         | Adult               |
| Allosaurus fragilis                        | ROM 5091        | Adult               |
| Allosaurus jimmadseni                      | DINO 11541      | Subadult-adult      |
| Allosaurus maximus                         | OMNH 01708      | Adult               |
| Bambiraptor feinbergi                      | AMNH 30556      | Subadult            |
| Carcharodontosauridae                     | PVPH 108-31     | Adult               |
| Chirotosmetes pergacilis                   | NMC 8538        | Adult               |
| Coelophysis bauri                          | TMP block       | Adult               |
| Daspletosaurus sp.                         | TMP 2001.036.0001 | Subadult-adult   |
| Daspletosaurus sp. or Gorgosaurus libratus | TMP 1994.172.0099 | Juvenile          |
| Daspletosaurus sp. or Gorgosaurus libratus | TMP 1999.055.0113 | Subadult-adult   |
| Daspletosaurus sp. or Gorgosaurus libratus | TMP 1968.003.0001 | Adult              |
| Deinonychus antirrhopus                    | MOR 947         | Adult               |
| Deinonychus antirrhopus                    | YPM 5205        | Adult               |
| Elaphrosaurus bambergi                     | HMN Gr.S. 38–44 | Adult               |
| Elmisaurus sp.                             | TMP/PJC, photographs | Adult            |
| Fukuiraptor kitadaniensis                  | FPDM V9712224   | Subadult-adult      |
| Gorgosaurus libratus                       | TMP 1994.012.0602 | Adult            |
| Gorgosaurus libratus                       | TMP 1979.014.0704 | Adult            |
| Gorgosaurus libratus                       | TMP 1967.014.0022 | Juvenile         |
| Gorgosaurus libratus                       | TMP 1986.144.0001 | Juvenile-subadult |
| Gorgosaurus libratus                       | TMP 1991.036.0500 | Juvenile-subadult |
| Gorgosaurus libratus                       | TMP 1981.039.0021 | Adult            |
| Gorgosaurus libratus                       | TMP 1973.030.0001 | Adult            |
| Gorgosaurus libratus                       | TMP 1967.010.0041 | Juvenile         |
| Gorgosaurus libratus                       | UALVP 10        | Adult               |
| Gorgosaurus libratus                       | UALVP 49310     | Subadult-adult      |
| Herrerasaurus ischigualestensis            | PVL 2566        | Adult               |
| Ingenia yanshini                           | GI 100/34       | Adult               |
| Ingenia yanshini                           | GI 100/32       | Adult               |
| Ornitholestes hermanni                     | AMNH 619        | Adult               |
to sectioning. Cutting and grinding followed procedures for standard petrographic sections. Sections were ground to a thickness of 60–80 μm (measured using interference colors), depending on the visibility of internal structures of interest. The sections were examined using a Nikon ECLIPSE E400 POL Polarizing Microscope in plane polarized (PPL) and cross-polarized (XPL) light.

Scanning electron microscopy was performed to image the surface texture of the four cores used for histologic analysis (Fig. 3a, b). The cores were coated with approximately 100 Ångstroms of gold and examined using a JEOL 6301 FE scanning electron microscope. The accelerating voltage was 5.0 kv and the working distance was 15 mm.

A *Coelophysis bauri* metatarsal, AMNH FARB 7239, was previously sectioned by one of us (DEB) for display in the 2016-2017 AMNH Dinosaurs Among Us special exhibition and proved useful for comparison in the current study. We identified it as a right metatarsal III based on the presence of articular facets on two sides, a large anterior tuberosity, a laterally offset proximal depression for a distal tarsal, and a sharp ventral constriction between the expanded proximal end and the diaphysis (Fig. 3c, d). Though unfused to metatarsal II, unlike the fused condition in some *C. bauri* (e.g., NMMNH P-42200) (Rinehart et al. 2009, fig. 80A, D), the element nevertheless shares these similarities with the third metatarsal of NMMNH P-42200 and those of the coelophysoids ‘Syntarsus’ kayentakatae and *Powellvenator podocitus* (Tykoski 2005:fig. 102C, E; Ezcura 2017:fig. 9). AMNH FARB 7239 was sectioned transversely across its entire diaphysis, near the proximal end (Fig. 3c, d). The sampled fragment was embedded in epoxy, sectioned with a Buehler Isomet 11-1180 low speed saw, ground until optically transparent and imaged with a Nikon Optiphot 2 petrographic microscope in plane polarized (PPL) and cross-polarized (XPL) light.

### RESULTS

The proximal portions of the tyrannosaurid MT III examined in this study exhibit large ligament scars similar to those previously reported in other theropod specimens. Unlike other large theropods however, tyrannosaurid MT III bear enormous, rugose ovoid facets distally along MT III-IV and MT II-III articular surfaces (Fig. 4a) as reported by Snively and Russell (2003).

Other features flank this scar distally, or contribute to its topography. A regularly-oriented, oblong tuberous ridge (the primary tuberosity) occurs along the anterior border of the large, distal scar in tyrannosaurids regardless of individual age and taxonomic variation. The extent of rugose surface texture related to the primary tuberosity appears age-dependent, and is typically less developed and covers less surface area in smaller tyrannosaurid MT III interpreted as juveniles (Tab. 1). A smooth scalloped area is noticeable distal to the primary tuberosity and dorsal to the posterior collateral ligament pit, but the overall size and depth of the scalloped surface is expressed to a lesser degree in *Tyrannosaurus rex* than in other tyrannosaurids.
In observed specimens of albertosaurine tyrannosaurids (*Gorgosaurus libratus* and *Albertosaurus sarcophagus*), a secondary tuberosity commonly accompanies the posterior border of the scallop and all juvenile tyrannosaurids show deeper scalloping with clearly demarcated borders. A smaller, circular, accessory tuberosity, frequently found near the posterior base of the primary tuberosity (Fig. 4c), is exaggerated in specimens of *Tyrannosaurus rex*.

Parallel, linear assemblages of microscopic fibrocartilaginous ligament-bundle insertion pits (individual ‘entheses’, Shaw and Benjamin 2007) align with the long axis of each tuberosity (Figs. 5, 6). Scanning electron microscopy reveals distinct differences in surface texture, enthesis pit morphology and distribution between regions that relate to the extent of ligament involvement (Fig. 6). The deepest pits, as well as the majority of pits, are found immediately bordering the tuberosities. No pitting is observed where ligaments are not predicted to attach (Fig. 6d).

The outermost cortex of three of the four core samples is characterized by periosteal bone. Sharpey’s fibers reveal that ligaments penetrated the periosteal surface at angles of 20–50°, although their direction relative to the periosteal surface is consistent within each core (Fig. 7). At the roughest surfaces (Fig. 7b, c), Sharpey’s fibers are multidirectionally angled relative to the bone surface, as common in strong entheses (Apostolakos et al. 2014). Sharpey’s fibers occur with consistent direction at the external surface and deep to lines of arrested growth when LAGs are evident in the thin section, as seen in extant *Alligator* (Petermann and Sander 2013).

In addition, the enthesis histology directly resembles that occurring at smaller ligament and tendon attachments in *Alligator* (Hieronymus 2006; Tumarkin-Deratzian et al.).

![Figure 4.](image)

*Figure 4.* a, Adult *Gorgosaurus libratus* (UALVP 10) left MT III, distal portion, lateral view. The proximal 18% of the element is missing. The red outline traces the full, rugose distal surface of articulation with MT IV; b, inset box highlights a broad region of rugosity for attachment of the MT III–IV ligament; c, more distal attachments of the MT III–IV ligaments, including the primary tuberosity (i); accessory tuberosity (ii); scalloped region and secondary tuberosity (iii). Scale bar = 5 cm. The Roman numerals here do not correspond with those in Figures 3 and 6.

![Figure 5.](image)

*Figure 5.* Adult *Gorgosaurus libratus* (UALVP 49210) distal right MT III, partial ventral view. Bracket and insets highlight the primary tuberosity and individual ligament pits, which form oblique linear assemblages. Scale bar = 5 cm.
Figure 6. a, scanning electron micrographs (SEM) of *Gorgosaurus libratus* (UALVP 49310) core sample iii showing linear, parallel assemblages of ligament pits, scale bar = 2.5 mm; b, SEM detail of linearly-arranged ligament pits, scale bar = 250 μm; c, SEM of isolated ligament pit, scale bar = 25μm; d, Contrasting SEM of core sample iv (Fig. 4) showing non-ligamentous surface (scale bar = 250 μm).

Figure 7. a, histological sections from *Gorgosaurus libratus* (UALVP 49310) MT III core sample i, Sharpey’s fibers (white arrow) insert are parallel, consistent with a tight periosteum; b, Core histology for sample ii (primary tuberosity with ligament pits); multi-directional Sharpey’s fibers correspond to superficial rugosity, consistent with anchoring function of ligament attachment; c, Core histology for sample iii (primary tuberosity with ligament pits), Sharpey’s fibers inserting irregularly into bone surface (intermediate between a and b); d, Core histology for sample iv (non-ligamentous bone surface), which is depauperate of Sharpey’s fibers. All histological sections viewed under cross-polarized light with periosteal (superficial) surface to the left of each panel. Scale bar = 1 mm.

Figure 8. a, Right side of entire section through the entire MT III of *Gorgosaurus libratus* (UALVP 49310) at the location indicated in Figure 3. Dorsal is towards the bottom. Scale bar = 1 cm; b, c, insets with different polarizing filters show undulations characteristic of fibrocartilaginous ligament entheses (Tumarkin-Deratzian et al. 2007; Apostolakos et al. 2014), outlined in c. Scale bar = 2 mm.
in which an undulating subperiosteal structure is evident in thin section (Fig. 8), and differs from the histology of other rough bone surfaces in that taxon (Tumarkin-Deratzian et al. 2007). Furthermore, Sharpey’s fibers in the *Gorgosaurus* MT III resemble those at femoral muscle attachments in *Alligator mississippiensis*, the rabbit *Oryctolagus cuniculus*, and turkey *Meleagris gallopavo* (Petermann and Sander 2013), but in *Gorgosaurus* are consolidated into more robust bundles than in these smaller tetrapods. The enthes histology and pitting occurs across both expansive and localized attachment sites (Figs. 4, 5) in the tyrannosaurid metatarsal, indicating great cross-sectional areas of ligaments with high aggregate stiffness and strength. The dorsal side of the *Coelophysis bauri* proximal metatarsal III (AMNH FARB 7239) lacks Sharpey’s fibers and comprises largely woven bone surrounding primary osteon lined by lamellar bone (Fig. 9). The vasculature is primarily reticulate to longitudinal, with some vascular spaces forming large cavities at this plane of section. An inner circumferential layer of lamellar bone lines the medullary surface. The outermost cortex shows greatly reduced vascularity, and may consist of parallel-fibered bone, despite being somewhat opaque, likely reflecting diagenetic alteration and/or increased thin section thickness towards the periosteum. Nevertheless, no Sharpey’s fibers are seen anywhere in the section.

**DISCUSSION**

**Ligament Inferences in the Context of Theropod Metatarsal Histology**

Correlates suggestive of distal intermetatarsal ligaments in tyrannosaurids are not present in their extant bracket (birds and crocodylians, Witmer 1995). Characterizing these soft tissues therefore requires high-order inference (Bryant and Russell 1992; Witmer 1995) and additional lines of evidence, such as our comparative SEM and bone histology. These methods enable microscopic assessment of soft-tissue traces universal amongst vertebrates, such as Sharpey’s fibers evident in ground thin sections.

Our inferences of ligamentous soft tissues in *Gorgosaurus* at the sampled locations are consistent with histological evidence for Sharpey’s fibers in other theropods. The histology of the proximal portion of metatarsal III of both *Coelophysis bauri* and the coelophysoid *Powellvenator* (Ezcurra 2017) reveals no evidence of Sharpey’s fibers. Therefore, we can state that Sharpey’s fibers are not ubiquitously distributed throughout individual metatarsals of these early diverging theropods, which fails to falsify our hypothesis that Sharpey’s fibers are only concentrated at localized ligamentous attachment sites. We predict that further sampling will show that the distal portions of early diverging theropod metatarsals also lack Sharpey’s fibers consistent with ligament attachment, in contrast with our finding of distal Sharpey’s fibers in *Gorgosaurus*. Non-tyrannosauroid coelurosaur, including maniraptorans, provide further data for comparison. Sharpey’s fibers do not appear present in the subarcmetatarsal metatarsals of troodontids sectioned to date (Varricchio 1993; Erickson et al. 2007; Sellés et al. 2021), nor have they been reported from midshaft thin sections of ornithomimosaur fourth metatarsals (Watanabe et al. 2013; Cullen et al. 2014). To date the only published, histologically confirmed occurrence of Sharpey’s fibers in a theropod metatarsal are those of the distal end of metatarsal II of *Xixianykus zhangi*, an alvarezsaur which also has an arctometatarsalian pes (Qin et al. 2019). Additionally, the elmisaaurine oviraptorosaur *Leptorhynchos elegans* appears to have sparsely distributed Sharpey’s fibers along the periosteal surface of the anteromedial corner of metatarsal III (Funston et al. 2016:fig. 9G) deep to its surface of articulation with metatarsal II. This position is consistent with predicted ligamentous entheses in arctometatarsalian pedes and concurs with our observation of localized Sharpey’s fibers at ligamentous attachments in tyrannosaurids.

**Function of Tyrannosaurid Arctometatarsus Ligaments**

As in extant vertebrates, ligament surface pitting and Sharpey’s fibers in the *Gorgosaurus* metatarsal are inferred to have arisen from a mechanobiologic process relating directly to stress transfer at the ligament-bone junction (Fig. 2; Carter and Beaupré 2001). Why are these entheses particularly extensive and robust in the arctometatarsus of tyrannosaurids, and what selective factors shaped their likely adaptive roles? As proposed in the Introduction, we posit that the confirmed ligaments played a direct role in locomotor agility in long-footed tyrannosaurids.

Distal regions of the limbs of large, extant vertebrates routinely experience complex loads and can fail when overloaded during fast, agile locomotion, as seen in horses (Ely et al. 2009). Attempted maneuvering at larger body sizes imposes greater torsional loadings that critically stress specific regions of the skeleton unless changes in size, shape, material properties and/or function occur to accommodate these loads; these adaptive allometries become more prominent as body mass exceeds 300 kg (Biewener 2005). Consistent with relatively compact body proportions and large leg muscles suggestive of enhanced agility in tyrannosaurids (Snively et al. 2019), the arctometatarsus displays architectural (Wilson and Currie 1985; Holtz 1995; Snively and Russell 2003) and ligamentous modifications (Snively and Russell 2002, 2003; current study) that can be deduced from the macro- and microscopic soft-tissue traces that remain.
We interpret the ligament attachment correlates with the maintenance of agile maneuvers, for which regions of calcified ligamentous attachments are effective at withstanding greater stresses at the ligament-bone interface (Shaw and Benjamin 2007). Parallel assemblages of microscopic entheses would have permitted local transduction of foot compressive forces to tension with a tensegrity-style mechanism (Snively and Russell 2003; Sellers et al. 2017). Collectively these large ligament attachments would have distributed regional tensile stresses to enhance strength in the tyrannosaurid foot (Shaw and Benjamin 2007). The expanded extent of the distal scar that approached the

**Figure 9.** Thin section through anterior cortex of *Coelophysis bauri* metatarsal III (AMNH FARB 7239), at the location in Figure 3. The lower image depicts the section traversing from endosteal to periosteal surfaces, and the upper image is modified to better show osteocyte lacunae. No Sharpey’s fibers or other enthesis correlates are present that would indicate ligament attachment, in contrast with the *Gorgosaurus libratus* MT III sections (Figs. 7, 8). A “Dehaze” filter was applied to the lower figure to compensate for opacity of its superficial portion (see text).
collateral ligament pits indicates reinforcement of the tyrannosaurid limb to a greater extent than that conferred by the ligaments of other theropods. This is especially true for adult *Tyrannosaurus rex*, in which the scars are further expanded proximally to capture greater relative surface areas (Snively and Russell 2003). The three distinctly oriented tuberosities furnish even greater surface area as ligament anchors, thereby enhancing the effectiveness of the ligaments by transferring regional torsional stresses to minimize intermetatarsal splay (lateral spreading of the bones from each other, Snively and Russell 2003). These distal attachments are not present in allosauroids similar in size to adult *Tyrannosaurus* (Snively et al. 2004), including *Mapusaurus*, *Acrocanthosaurus*, and an examined large carcharodontosaurid (PVPH 108-31). Relatively large ligaments in adult *T. rex* are, therefore, not solely attributable to weight bearing, and as in its smaller relatives likely assisted in high maneuverability relative to body size (Snively et al. 2019).

**Synthesis 1: Musculoskeletal Evidence of Tyrannosaurid Agility is Consistent with Semicircular Canal Morphology**

Expansive foot ligaments and dynamics calculations (Snively et al. 2019) suggest competent agility in tyrannosaurids that is consistent with their neurosensory morphology. The semicircular canals of tyrannosaurids are expanded, especially the lateral canal (e.g., *Tyrannosaurus* CMNH 7541, AMNH FR 5117) versus other large theropods (*Allosaurus* UMNH VP18050, *Ceratosaurus* MWC 1.1, Witmer and Ridgely 2009; Sampson and Witmer 2007). This expansion suggests the capability for enhanced vestibulo-ocular and vestibulocollic reflexes important for tracking and striking prey (Witmer et al. 2008; Witmer and Ridgely 2009; Bronzatti et al. 2021).

The inner ear structure of mammals, birds, and large dinosaurs has been broadly linked to locomotor agility based on the sizes and shapes of the semicircular canals (Hadziselimovic and Savkovic 1964; Money et al. 1974; Spoor et al. 2007; Cox and Jeffery 2010) and their neural connections with the visual system to stabilize gaze. Although quantitative studies of comparable scope to those done for mammals have not been done for dinosaurs, the finding that canals are relatively elongate in agile mammals (such as cheetahs and bats, Cox and Jeffery 2010, brachiating primates, Spoor et al. 2007; Cox and Jeffery 2010) and birds (Hadziselimovic and Savkovic 1964) is fully consistent with our evidence for rapid maneuvers in tyrannosaurs. As in other small coelurosaurians, juvenile tyrannosaurids would benefit more from synapomorphically large canals (Witmer and Ridgely 2009) for full-body maneuvers than would slower reacting, slower turning tyrannosaurid adults (More et al. 2010, Snively et al. 2019). Once in range, tyrannosaurid adults could engage vestibular reflexes for rapid and controlled head-neck movements (Snively and Russell 2007; Witmer and Ridgely 2009).

**Synthesis 2: Ecological and Evolutionary Implications of Tyrannosaurid Agility**

Whereas tyrannosaurids were the only large carnivorous dinosaurs in latest Cretaceous (Campanian and Maastrichtian) terrestrial communities of Asia and North America (Fig. 10), earlier dinosaur-dominated ecosystems typically had representatives of various theropod clades (ceratosaurs, megalosauroids, allosauroids, and various coelurosaur groups) separately occupying different adult size classes (Fig. 10; Farlow and Holtz 2002; Holtz 2004; Schroeder et al. 2021; Holtz 2021). The Tyrannosauroidea, the more inclusive clade of which the giant Tyrannosauridae are the last, largest, and most derived (Holtz 2004, Brusatte et al. 2010), was present from the Middle Jurassic onward (Brusatte et al. 2010), are represented by small- and medium-sized components of these diverse assemblages (Nesbitt et al. 2019; Zanno et al. 2019). At present, there is little direct evidence to determine whether the transition from ecosystems of numerous large theropod families to those dominated by tyrannosaurids is reflective of competitive displacement, or decline and opportunism. Regardless of the scenario, the modifications of the arctometatarsus that permitted greater agility evolved initially in the context of smaller body size (Nesbitt et al. 2019; Zanno et al. 2019) and became effective even in the largest individuals of the derived forms. The unique tyrannosaurid arctometatarsus would have enhanced the tyrant dinosaurs’ potential in prey acquisition.

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Figure 10. Campanian and Maastrichtian tyrannosaurids are the only large, toothed theropods of continental Laurasia. In contrast, theropods of other times and regions are more phylogenetically diverse, within single formations and even individual quarries. a, extant diurnal carnivorous theropods of two clades common at Devil’s Tower National Monument, Wyoming, USA; b, derived tyrannosauroids are the only large theropods in eastern Asia, Laramidia, and Appalachia; c, giant allosauroids, large megaraptorans, and abelisaurid ceratosaurs span the Candeleros and Huincul Formations of Argentina; d, Ceratosaurus, Allosaurus (predominantly), megalosauroid, and tyrannosaurid fossils occur in the Cleveland Lloyd Quarry of the Morrison Formation.

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Author contributions
L.A.S. conceived the research and carried it out with M.B. and D.E.B. All authors co-wrote and/or edited iterations of the paper. L.A.S interpreted macro- (osteological) and microscopic (SEM analysis; enthesis) morphology. M.B.
and D.E.B. contributed histological and micro-CT analysis and interpretation, and A.P.R. prepared and contributed extant material for comparisons, from previous research. L.A.S, M.B., E.S., L.M.W., D.E.B., and T.R.H. wrote the manuscript, and P.J.C. provided facilities.

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