THE UNIVERSITY OF CALGARY

Functional morphology of the tyrannosaurid arctometatarsus

by

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ABSTRACT

The arctometatarsus is a metapodial structure exclusive to Cretaceous coelurosaurian dinosaurs. The central third metatarsal (MT III) of the arctometatarsus is proximally constricted between the second and fourth (MT II and MT IV). MT III is also triangular in distal cross section, with the apex towards the plantar surface. Descriptive morphology and Principal Components Analysis (PCA) segregate the arctometatarsus from other morphologies, and suggest hypotheses of function for tyrannosaurid metatarsi and similar forms. Through CT analysis of metatarsal shape, physical manipulation of casts, assessment of osteological correlates of ligaments, and comparison with the equid carpus, two hypotheses are evaluated for the tyrannosaurid arctometatarsus. First, ligament anatomy provides a mechanism for a previously proposed hypothesis, that axial locomotor energies were transferred from MT III to the outer elements. Second, the tensional keystone hypothesis holds that upon angled footfalls during linear locomotion, distal intermetatarsal ligaments would prevent anterodorsal displacement of MT III, and unify the metapodium. Finite element analysis of strain energy in Gorgosaurus libratus metatarsals strongly supports the energy transference hypothesis, and indirectly supports the tensional keystone hypothesis. From the perspective of this evaluation of the tyrannosaurid arctometatarsus, functional hypotheses are proposed for the metatarsi of other theropods. Mapping the arctometatarsus onto two phylogenies of theropods suggests a tentative scenario for the structure's evolution and biological role.

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INSTITUTIONAL ABBREVIATIONS

AMNH Gi	American Museum of Natural History, New York, New York. Geological Institute Section of Paleontology, Academy of Sciences,
	Ulan Bator, Mongolia.
HMN	Humboldt Museum of Natural History, Berlin, Germany.
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Bejing, China.
LACM	Los Angeles County Museum of Natural History, Los Angeles, California.
MOR	Museum of the Rockies, Bozeman, Montana.
NMC	Canadian Museum of Nature, Ottawa, Ontario.
OMNH	Sam Noble Oklahoma Museum of Natural History, U. of Oklahoma, Norman, Oklahoma,
PIN	Paleontological Institute, Academy of Science, Moscow,
	Russia.
PJC	Office of P.J. Currie, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta,
PVL	Paleontologia de Vertebrados de la Fundacion Miguel Lillo, Argentina.
RTMP	Roval Tyrrell Museum of Palaeontology, Drumheller, Alberta.
UCMP	Museum of Paleontology, U. of California, Berkeley, California.
UCMZ	U. of Calgary Museum of Zoology, Calgary, Alberta.
UCMP	Museum of Paleontology, U. of California, Berkeley, California.
UUVP	University of Utah Vertebrate Paleontology Collection, Salt Lake City, Utah.

CHAPTER 1: INTRODUCTION

Animals as integrated systems

The functional morphology of animals encompasses their operation as volitional machines within phylogenetic, developmental, and selective contexts (Lauder et al. 1989). Neurosensory feedback and motor control by the central nervous system, mediated by endocrine activity, impel the organism into coarse functions and behaviours (Zweers 1979). Multifariously interconnected subsystems (Bock 1989), such as an organ system consisting of bones, tendons, muscles, ligaments, and their nervous and vascular supplies, carry out functions of selective importance to the animal. **Function** may be defined as what an animal does with an anatomical structure, while **biological role** refers to a function's selective utility to the phenotype at the appropriate stage in its life history (Bock and von Wahlert 1965).

The study of animals as living systems benefits from a combination of reductionistic, synthetic, and expansive approaches. For example, the biomechanics of individual muscles and bones are assessed in relation to one another. These studies are ideally integrated with arthrology and innervation for an overall picture of function (Bock 1989, Lauder 1990, Zweers 1991). Variation in locomotor or feeding mechanisms can be placed under phylogenetic, biogeographic, and ecological purviews, in order to understand the evolution of a structure's biological role (Bock 1979, Russell 1979a, Liem 1989).

Five major approaches inform the investigation of integrated systems and evolutionary morphology (Lauder et al. 1989, Zweers 1991). Ontogenetic study

and constructional morphology reveal developmental and material capacities and constraints on structure. Phylogenetic analysis allows testing of evolutionary hypothesis that arise from apparent morphological similarity. Functional analysis entails the atomization and subsequent integration of biological subsystems in order to understand a more complex system. Finally, deductive methods involve quantitative modeling, which gives rise to predictions about how natural systems operate. These methods are readily applied to extant organisms.

Assessing functional morphology of extinct animals presents obvious constraints on some of the preceding approaches. Ontogenetic study is limited to evidence from hard tissues, and low sample sizes curtail developmental investigation of large fossil vertebrates. Constructional morphology of fossil hard tissues is readily amenable to study, but that of soft tissues requires inference of their presence and assumptions about their composition. This caution also overlies functional analysis of organs that include unpreserved components. Fossil systems can be modeled deductively, but falsifying such a model is even more difficult than with studies of extant organisms (Lauder 1995). Of these approaches, only phylogenetic analysis of fossil organisms attains full reciprocity with neontology. Phylogenetic study of extant biota requires a palaeontological perspective for falsification (Gauthier et al. 1988)

The common tripwire for many of these approaches is the required inference of unpreserved structures. This impediment is surmountable to some degree through careful examination of the fossil evidence, using principles of comparative anatomy.

Completing the system in fossil animals: inference of unpreserved structures

Two fruitful approaches facilitate inference of unpreserved soft tissues in vertebrate fossils. Both methods require anatomical comparisons, and assessments of correlates to soft tissue occurring on bones of extant vertebrates. One method involves inference from phylogeny, and the other approach entails extrapolation from histological and functional relationships between soft and hard tissues.

Recently the method of phylogenetic inference has been formalized (Bryant and Russell 1992, Witmer 1995), invoking comparison with living or wellpreserved extinct relatives of the fossil taxon. Phylogenetic inference mandates detailed anatomical examination of modern forms, and the framework of explicit cladistic hypotheses.

Soft tissue organs in fossil taxa are robustly inferable when derived and primitive modern outgroups (the extant phylogenetic bracket) possess osteological correlates to the structure also present in the extinct clade (Witmer 1995). For example, heads of extant dinosaurs (birds) and the nearest modern relatives of dinosaurs (crocodilians) have pneumatic diverticula or air sacs in the region anterior to the eyes, associated with fenestration or foramina in the skull bones. Extinct dinosaurs had these openings in their skulls; hence it is quite likely that these dinosaurs also had cranial air sacs (Witmer 1997).

Phylogenetic inference becomes less certain in taxa without the both elements of the extant bracket (Bryant and Russell 1992, Witmer 1995), or if correlates are ambiguous in any of the examined taxa (Nicholls and Russell 1985, Bryant and Seymour 1990). If a fossil taxon does not have a morphologically similar modern relative, or if it possesses a novel osteological feature not seen in extant vertebrates, inference of an unpreserved organ is still viable through the ahistorical extrapolatory approach (Bryant and Russell 1992).

Extrapolatory inference draws from biological generalizations of gross anatomy, histology, and constructional morphology. These universalities include the marks soft tissues leave on bone, such as scarring at the origins of tendons and ligaments, or the foramina through which blood vessels and nerves pass as bone grows around them. Examples of the extrapolatory approach include vascular evidence for nasal mucosal elaboration in herbivorous dinosaurs (Witmer and Sampson 1999), reconstruction of pelvic respiratory systems in ornithischians (Carrier and Farmer 2000), and histological inference of ligaments associated with the platelike armor of *Stegosaurus* (Buffrenil et al. 1986).

Thus unpreserved organs in fossil vertebrates are interpreted most reliably through consideration of homology, surface anatomy, and fine histology when possible. Osteological anatomy reveals marks of soft tissues that have developmental precedence over the skeleton (Witmer 1995), but that act in conjunction with bones. One example of a functionally integrated system of soft and hard tissues is the metatarsus of Mesozoic theropod dinosaurs, which incorporated bones, ligaments, and their associated vasculature and nervous supplies.

The arctometatarsus as an example of ligament-bone integration

During the Cretaceous, an unusual morphology of the metatarsus evolved in several taxa of the Theropoda, a predominately carnivorous clade of bipedal dinosaurs. Termed the **arctometatarsus** (Holtz 1994a), this structure displays a striking third metatarsal that is comparatively gracile towards the ankle and robust towards the toes. Figure 1.1 shows an example. The word "arctometatarsus" refers to the entire pedal metapodium of these theropods; **arctometatarsalian** describes the structure, or designates a taxon whose members possess an arctometatarsus.

There are four elements to the osteological definition of the arctometatarsus (Holtz 1994a). The third (central) metatarsal (designated herein as **MT III**) is constricted proximally relative to the condition in other theropods. **MT III** is also triangular in distal cross section, and thus constricted towards the plantar surface (flat of the foot). The outer weight bearing metatarsals, the second and fourth (**MT II** and **MT IV**), encroach towards the midsagittal plane of **MT III** where it constricts, and maintain contact with **MT III** distally and proximally. All three metatarsals therefore form a wedge-and-buttress morphology, in which buttressing surfaces of the outer metatarsals overhang and contact surfaces of the wedgelike third metatarsal (Holtz 1994a).

In addition to these osteological characteristics, several authors have commented on the likely presence of ligaments that bound the arctometatarsus together. Snively (1994) reported extensive rugosities on the metatarsal articular

surfaces of a *Tyrannosaurus rex* specimen, which were interpreted as sites for proximal and distal ligament attachment. Rugosity was especially prominent on the distal wedge and buttress surfaces of MT III and MT II. Snively (1994), Holtz (1994a) and Hutchinson and Padian (1997a) noted that such ligaments would have provided strong articulation between the metatarsals.

Besides holding joints together, ligaments also function in mechanoreception (Martin et al. 1998). As in modern tetrapods, ligament stretch receptors in the metatarsus of theropod dinosaurs probably were involved in reflex loops that mediated muscular response during locomotion. The ligament-bone system of the arctometatarsus therefore cannot be seen solely as a means of transmitting muscular force and absorbing stresses of locomotion. A probable neurosensory component to its function must be considered, which would have actively modulated locomotor activities.

The arctometatarsus in a whole organism context: the Tyrannosauridae and their relatives.

Mechanical and sensory functions of the arctometatarsus reflected the spectrum of behaviours the animals employed. These activities are unobservable, and hypotheses of behaviour are only testable through relatively high-order inference. Several lines of evidence inform our interpretations of theropod behaviour. The skeletal anatomy, paleoenvironments, ecological context, and phylogeny of theropods have been extensively studied (Weishampel et al. 1990, Currie and Padian 1997), and we have a broad although extremely incomplete picture of their appearance and possible habits.

Figure 1.1 shows a phylogeny of theropods, based on cladograms in Holtz (1996) and Currie and Padian (1997). All theropods with an arctometatarsus are within the clade Coelurosauria. The most famous coelurosaurs are the Tyrannosauridae, including the familiar *Tyrannosaurus rex*. Tyrannosaurids and some but not all other coelurosaurian clades with an arctometatarsus comprise the Arctometatarsalia (*sensu* Holtz 1996).

Tyrannosaurids, other arctometatarsalians (in the phylogenetic sense), and other taxa on the phylogeny are now introduced to place the arctometatarsus in a phenotypic context. Entries in Weishampel et al. (1990) and Currie and Padian (1997) provide more extensive treatment. Figures 1.2 through 1.4 show skeletal outlines of some members of these taxa.

- Tyrannosauridae (Figure 1.2): Tyrannosaurids were large to giant arctometatarsalians, often exceeding two tonnes in mass. Tyrannosaurids had relatively long hind limbs, extensive attachment sites for jaw musculature, and a broad muzzle and robust teeth, but had short forelimbs with only two functional fingers. Tyrannosaurid tooth marks on fossil bones (Ryan 1992, Erickson et al. 1996) and coprolitic evidence (Chin et al. 1998) indicate a macrocarnivorous diet, consisting of other large dinosaurs.
- Ornithomimidae (Figure 1.2): These were ostrich-like arctometatarsalians, whose hind limb length and element proportions indicate that they were among the fastest dinosaurs. Ornithomimids were toothless, and evidence of gastroliths and other stomach contents indicates they may have been herbivorous (Kobayashi et al. 1999).

- Troodontidae (Figure 1.2): Troodontids were arctometatarsalians the size of humans or smaller, with finely grasping hands, a hyperextesible claw on their second toe, and possibly an omnivorous diet (Holtz et al. 2000, Ryan et al. 2000). Together with the Ornithomimidae, troodontids constitute the clade Bullatosauria, the arctometatarsalian sister taxon to Tyrannosauridae.
- 4. Oviraptorosauria (Figure 1.3): Oviraptorosaurs were small theropods with long grasping hands; several specimens have short tails. Known oviraptorosaur skulls are toothless, with a parrot-like anterior arching of the lower jaws. They were at least partially carnivorous; bones of neonate dromaeosaurids were discovered in the nest of one oviraptorosaur. Two families of oviraptorosaurs are shown on the phylogeny, the Oviraptoridae and Elmisauridae. Members of the Elmisauridae possess an arctometatarsus (Currie 1990).
- 5. Therizinosauridae (Figure 1.3): Therizinosaurs were bizarre coelurosaurs with broad and deep bellies, short legs, and long forelimbs with very large claws (Maryanska 1997). Their coarsely serrated or crenellated teeth are similar to those of herbivorous lizards. *Ornitholestes hermani* (Figure 1.3): *Ornitholestes* was a small coelurosaur with long hands and conical premaxillary teeth, rather than the blade-like teeth of most other theropods (Paul 1988). This may indicate a microcarnivorous diet of relatively small prey.
- 6. Dromaeosauridae (Figure 1.3): The sister group to birds (or Aves on the phylogeny), dromaeosaurids were dog- to bear-sized macrocarnivorous

coelurosaurs with an enlarged trenchant claw on their second toe and a stiffened tail, indicating an agile macropredaceous habit (Ostrom 1969

- 7. Ornitholestes hermani (Figure 1.3). Ornitholestes was a small coelurosaur with long hands and conical premaxillary teath, rather than the blade-like teeth of most other theropods (Paul 1988). This may indicate a microcarnivorous diet of relatively small prey. The relationship of Ornitholestes to other coelurosaurs is unclear (Figure 1.1).
- 8. Carnosauria (Figure 1.4): Carnosaurs were large to giant macrocarnivorous theropods. They had proportionally shorter legs but longer and more robust arms than tyrannosaurids (Hutchinson and Padian 1997b). The phylogenetic diagram positions Carnosauria as the sister group to the Coelurosauria.
- Elaphrosaurus bambergi (Figure 1.4): Elaphrosaurus is a member of the Ceratosauria, the sister group to the carnosaur-coelurosaur clade. It had proportionally gracile lower limbs and a long thoracic region (Galton 1982; Holtz 1994b); its skull and probable diet are unknown.
- 10. Herrerasaurus ischigualastensis (Figure 1.4): Herrerasaurus was a primitive theropod in some characteristics, with a long fifth toe and a craniocaudally short hip. Some cladograms place Herrerasaurus as an outgroup to other saurischian dinosaurs, but it has the long raptorial hands and jointed lower jaw of theropods (Novas 1993). Herrerasaurus had about the same mass as a lioness (Paul 1997).
- 11. Prosauropoda (Figure 1.4): Prosauropods are primitive members of the Sauropodomorpha, the herbivorous sister taxon to the Theropoda known for

their long necks and massive bodies (Galton 1990). Unlike more advanced and larger sauropodomorphs, most prosauropods share with theropods the primitive dinosaurian condition of three weight bearing metatarsals.

The arctometatarsus thus appears in coelurosaurs that were diverse in trophic habit. Their diet often converged with that of more distantly related saurischians than with taxa similarly endowed with an arctometatarsus. Herbivory in ornithomimids may have paralleled that of therizinosaurids and prosauropods, while tyrannosaurids were apparently the trophic analog of large carnosaurs.

Regardless of putative diet, all members of the Arctometatarsalia share proportionally longer lower limbs than expected in other theropods of the same mass (Holtz 1994a, 1994b); the metapodia are especially elongate. A relatively long metatarsus occurs in arctometarsalians over their complete range of adult sizes (Figure 1.5). Long lower limbs are associated relatively high speeds in living tetrapods with a parasagittal gait (Hildebrand 1988). Presumably, the elongate hind limbs of arctometatarsalians imparted the same functional advantage as in their modern analogs (Holtz 1994a). The biological role of increased relative speed is harder to assess, but may well have varied with the dietary needs of the animal.

While the proportional length of the arctometatarsus has many analogs among cursorial vertebrates (Stein and Casinos 1997, Carrano 1999), the proximally pinched MT III is a unique morphology. Workers have proposed several possible functions for this unusual feature, but there have been few tests of their hypotheses.

Hypothesized functions of the tyrannosaurid arctometatarsus

Hypotheses of arctometatarsus function have usually centered on its utility for rapid locomotion. Coombs (1978) proposed that snap ligaments stored and returned energy as MT III pistoned along the long axis of the metatarsus. Norman (1985) observed that the metatarsals were tightly interlocked, perhaps for increased strength. Wilson and Currie (1985) noted that the distal portion of MT II in *Troodon inequalis* appeared free to pivot anteriorly as the thin proximal portion rotated posteriorly. They hypothesized that proximal ligaments running between the metatarsals would damp this rotation (Wilson and Currie 1985).

Holtz (1994a) reviewed the pistoning and rotational hypotheses of Coombs (1978) and Wilson and Currie (1985), and found that while either might be reasonable for certain taxa, neither hypothesis was satisfactory for all forms. Holtz amplified a second hypothesis proposed by Wilson and Currie (1985), that the wedge-and-buttress morphology of the arctometatarsus facilitated a transfer of locomotor energy, from MT III to the outer metatarsals and thence to the astragalar condyles (Holtz 1994a). The energy transference hypothesis is applicable to more taxa, and thus perhaps is better supported than the alternatives (Hutchinson and Padian 1997a).

These workers have prudently avoided assigning energy transference or strengthening functions to a specific biological role. Carpenter (1997) suggested that one role of the arctometatarsus was to increase the stability of the foot when

the animals ran on uneven ground. This is an intriguing possibility, although Carpenter (1997) did not offer a detailed morphological analysis.

Hypotheses of biological role or function of the arctometatarsus must derive from thorough assessment of the observed inter-relatedness of its parts. Therefore, this thesis attempts a large-scale analysis of arctometatarsus function and its selective implications, through study of basic morphology, systematic variation of the arctometatarsalian pes, and possible connectivities (Bock 1989) between this organ system's constituent structures.

Elicitation and testing of hypotheses: atomization, synthesis, and extrapolation

The salient features of the arctometatarsus are the proximal and plantar constriction of MT III. These observations alone suggest a general primary hypothesis and null hypothesis:

H(a): MT III constriction imparted functional differences between the arctometatarsus and other theropod metatarsus morphologies.

H(o): The constricted **MT** III of the arctometatarsus functioned identically to unconstricted theropod third metatarsals.

Superficially these hypotheses appear overly broad. However, generating hypotheses of specific function or performance advantage requires more comprehensive observation. When these focused hypotheses are supported or falsified, the validity of the more general hypothesis can be upheld or discounted.

This thesis seeks out and tests more specific hypotheses of arctometatarsus function through the following methods:

1. Atomization (Chapters 2 and 3). The tyrannosaurid arctometatarsus is chosen as a basis for comparison with other morphologies. The third metatarsals of theropods are described in detail, and quantitative variation in MT III morphology is assessed through a Principal Components Analysis of shape. Individual bones and soft structure correlates are assessed for the tyrannosaurid arctometatarsus.

2. Synthesis (Chapters 3 and 4). These chapters address possible integrated functions for the ligaments and bones of the arctometatarsus. The extent and orientation of soft tissue correlates in the metatarsus of tyrannosaurids are compared with those of the carnosaur *Allosaurus fragilis*, which lacks a constricted third metatarsal. Range of movement in the metatarsi of several tyrannosaurids is tested through computed tomographic (CT) scans, and physical manipulation of casts. This kinematic and morphological data is synthesized into a model of arctometatarsus function in tyrannosaurids, which is compared with the function of an extant analog, the equine wrist.

The hypothesized model of tyrannosaurid metatarsus function, and the energy transference hypothesis (Holtz 1994a), are tested with finite element stress analysis. The computer model integrates the suggested kinematics of the qualitative hypotheses, and assumptions of material properties based on measurements of modern bones.

3. Extrapolation (Chapter 5). The preceding results for tyrannosaurid metatarsals are applied comparatively to potential functions in other theropods, in a revisiting of variation revealed in Chapter 2. Metatarsal morphology is placed in

an evolutionary context, in an effort to track the origination and biological role of the arctometatarsus in Mesozoic theropods.

These methods provisionally explicate the arctomatatarsus as a part of an integrated phenotypic system, and tentatively suggest its possible roles in ecological interactions and in theropod evolution. Ultimately, the goals of this thesis are to understand the bones and ligaments of the arctometatarsus as a locomotor subsystem, and to explore the implications of its function for tyrannosaurids. This study begins with the qualitative and quantitative morphology of the metatarsus of tyrannosaurids and their relatives (Chapter 2).

Figure 1.1. Phylogenetic diagram of the Saurischia (topology after Holtz 1996). In addition to the terminal taxa, the following taxa are designated at nodes:

- 1 Saurischia
- 2 Theropoda
- 3 Tetanurae
- 4 Coelurosauria
- 5 Oviraptorosauria
- 6 Arctometatarsalia
- 7 Bullatosauria

A right arctometatarsus of the tyrannosaurid *Albertosaurus* sarcophagus is shown in anterior view. Taxa with members that possess an arctometatarsus are marked with an asterisk

(*). All terminal taxa are described in the text. Note that this figure is not a cladogram because it lacks explicit characters for all nodes.



Prosauropoda

Figure 1.2. Phylogenetic diagram of the Saurischia (topology after Holtz 1996). Representatives of the Arctometatarsalia (*sensu* Holtz 1996) are illustrated.

A The troodontid *Sauromithoides mongoliensis*, after Paul (1988).

B The ornithomimid Struthiomimus altus, after Paul (1988).

C A composite skeleton of the tyrannosaurid *Tyrannosaurus rex*, after Paul (1988).


Figure 1.3. Phylogenetic diagram of the Saurischia (topology after Holtz 1996). Representatives of several coelurosaurian clades are illustrated.

A The small coelurosaur *Ornitholestes hermani*, after Paul (1988); parts of the hand and trunk are conjectural.

B The dromaeosaurid Velociraptor mongoliensis, after Paul (1988).

C Composite therizinosaur; the majority of the skeleton is based on *Nanshiungosaurus brevispinus* (after Paul 1997).

D The oviraptorosaur Oviraptor philoceratops, after Paul (1988).



Figure 1.4. Phylogenetic diagram of the Saurischia (topology after Holtz 1996). Non-coelurosaurian saurischians are illustrated.

A The prosauropod *Plateosaurus engelhardti*, after Paul (1997).

B The basal theropod Herrerasaurus ischigualastensis, after

Paul (1997).

- C The ceratosaur Elaphrosaurus bambergi, after Paul (1988).
- D The carnosaur Allosaurus fragilis, after Paul (1988).



Figure 1.5. Skeletal restorations of *Tyrannosaurus rex* and *Sauromithoides mongoliensis* (after Paul 1988) demonstrate the great size range of adult arctometatarsalian theropods. The *Tyrannosaurus rex* figure is scaled to the size of the largest documented specimen. Its femur length is 1380 mm, while the femur length of the *Sauromithoides mongoliensis* specimen is 200 mm.



CHAPTER 2: Descriptive and quantitative morphology of the arctometatarsalian third metatarsal

INTRODUCTION

As explained in Chapter 1, Holtz (1994a,b) investigated the phylogenetic and functional implications of the proximal constriction of the third metatarsal (MT III) in several clades of Cretaceous coelurosaurs. He designated the arctometatarsus, in which MT III is proximally pinched, as a character state present in taxa that also display relatively long lower limb elements (see Figures 1.1, 1.2, and 1.5. Chapter 1). Those taxa that Holtz qualitatively assessed to have a full arctometatarsus are the Tyrannosauridae, Ornithomimidae, Troodontidae, and Elmisauridae (Holtz 1994a). This chapter explores qualitative differences between the third metatarsals of these taxa, to extend Holtz's work on pedal variation within "arctometatarsalian" clades. Building upon this qualitative framework, a Principal Components shape analysis statistically crystallizes divisions between theropod metatarsal morphologies. I then synthesize and discuss statistical and qualitative data for resultant subgroupings of metatarsal shape. Once the comparative morphology of the tyrannosaurid arctometatarsus has been established observationally and statistically, the thesis logically proceeds into detailed questions of its function and evolution (Chapters 3-4 and Chapter 5, respectively).

Conceptions of arctometatarsus morphology

The term arctometatarsus has been used imprecisely in the literature and in public scientific discourse. This confusion arises primarily because Holtz (1994b)

did not quantify the degree of proximal constriction of MT III that differentiates an arctometatarsus from other morphologies. A theropod MT III with any degree of proximal constriction, such as that displayed by *Allosaurus* (Figure 2.1: e), could qualify as arctometatarsalian if the definition is interpreted with some latitude (for example, Hutchinson and Padian 1997). This unquantified morphological definition has become conflated with the hypothesis of a polyphyletic origin of the structure, given the controversial constituency of Holtz's Arctometatarsalia (Tyrannosauridae + Bullatosaura; Holtz 1994b, Hutchinson and Padian 1997, Sereno 1999). Sereno challenged the monophyly of the Arctometatarsalia (Holtz 1994b) at the 1994 Society of Vertebrate Paleontology meeting, in part because *Deinonychus* and *Allosaurus* appear to display some proximal narrowing of MT III.

Most parties to this controversy initially overlooked Holtz's (1994a) character of plantar constriction of MT III, which separates the arctometatarsus from other theropod morphologies. Thus, Holtz's (1994a,b) characterization of MT III morphology that typified the Arctometatarsalia was a three dimensional assessment, and accounted for more than a simple narrowing of the proximal end of this element. Sereno (1999) redressed this imbalance by incorporating plantar constriction and further qualitative character states into a phylogenetic analysis. This systematic reassessment of the Theropoda (Sereno 1999) disrupted the monophyly of Holtz's (1994b, 1996) Arctometatarsalia.

Regardless of the ultimate phylogenetic distribution of the arctometatarsus, the ambiguity surrounding its morphology invites further elucidation. The definition of the arctometatarsus has so far relied upon comparative qualitative study, which has spurred quantitative investigation of biomechanics (Holtz 1994a) and phylogeny (Holtz 1994b, 1996, Sereno 1999). A thorough assessment of theropod MT III diversity must precede efforts to place the arctometatarsus in a systematic and functional framework, and thus to explicate its roles in theropod evolution and ecology. Both descriptive and quantitative techniques are useful in addressing these issues.

Description provides a salutary prerequisite to mathematical inquiries into morphological diversity. While quantitative analysis is ostensibly a more objective starting point, a grounding in qualitative data is necessary for assessing previous morphological perceptions, and for interpretation of statistical results (Pimentel 1979). Statistical methods must yield wholly to morphological description when sample size is very low (often the case with palaeontological specimens: Kemp 1999). Description and observation are the primary methods for arriving at phylogenetic characters when morphology is the only criterion available (Grande and Bemis 1998). In addition, subtleties of morphology may be missed when a worker chooses landmarks for morphometric study (see conclusions to this chapter for examples).

Therefore, this chapter proceeds from descriptive to quantitative assessment of theropod third metatarsals. The development and province of MT III affected that of both adjacent weight bearing metatarsals (Holtz 1994a). Morphological segregation of MT III by description and statistical clustering has the potential to elucidate variation in the entire pes of a wide array of taxa. Because the initial qualitative debate over arctometatarsus shape concentrated on its anterior outline, I apply morphometric analysis of theropod metatarsi in anterior view in an attempt to uncover potential patterns of systematic and functional diversity.

Promisingly, clustering of elements by planar outline has elucidated questions of both function and phylogeny in extant taxa. Lombard et al. (1986) quantitatively assigned the ectopterygoids of colubroid snakes to shape classes. Their classification of ectopterygoid morphology corresponded with differences in feeding mechanics specific to colubroid subtaxa. The shape of the ectopterygoid informs the function and ontogeny of the articulating maxilla and pterygoid in snakes; all three bones form an integrated anatomical system (Lombard et al. 1986). The ectopterygoid is especially enlightening in this regard, because it functions as the central element in the system, and influences both neighboring bones and the elements they contact. This neontological precedent reinforces the utility of the theropod third metatarsal in explicating pedal morphology in a diversity of taxa.

To quantitatively sort snake ectopterygoids by shape, Lombard et al. (1986) employed Principal Components Analysis (PCA; see Appendix 1 for the rationale and methodology behind PCA). Often applied in ecology to determine community structure (Pielou 1984), researchers have also used PCA to cluster modern and extinct taxa according to morphological variables (Cundall and Rossman 1984, Lombard et al. 1986, Weishampel and Chapman 1990, Forster 1995, Smith 1998, Carrano 1999). Other methods of visual data clustering, such as bivariate plots (Holtz 1994a) and ternary diagrams (Gatesey and Middleton 1995), can informatively map specimens onto graphs of two or three pertinent variables. Principal Components Analysis has two major advantages over these approaches. First, because PCA consolidates multiple variables, it distills trends and correlations in voluminous data more expeditiously than juxtapositions of only two or three measurements (Weishampel and Chapman 1990). Second, PCA also calculates the relative contribution of specific measurements to overall variation. Specimens are plotted onto graphs of the most important constituents of variation, which can be interpreted as important differences in shape or size.

This statistical segregation of metatarsal morphologies, complemented by thorough description, potentially suggests analogous and/or homologous pedal biomechanics within various groups. If discrete morphologies can be classified statistically and qualitatively, the separation fosters the development of biomechanical, functional, and phylogenetic hypotheses. The work in this chapter therefore integrates descriptive and mathematical approaches in order to derive such hypotheses.

General approach and hypotheses

Qualitative methods elucidate subtleties of morphology apparent in theropod third metatarsals, and PCA is then used to circumscribe morphologies on the basis of anterior silhouette. Specifically, the goals and approaches are as follows:

 Results from qualitative description of specimens are applied to the following hypothesis:

Ha: The tyrannosaurid **MT** III is qualitatively differentiable from similar forms in ways not predictable from simple allometry.

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This hypothesis focuses on tyrannosaurids, in the hope of eliciting morphologically important characteristics not strictly uncovered by PCA. All specimens are examined and described, but mainly in explicative comparison with MT III of tyrannosaurids.

2) Ordination of variance and covariance components by PCA quantitatively address a fundamental hypothesis:

Hb: Metatarsi classified as arctometatarsalian (Holtz 1994a,b) have a significantly greater degree of proximal MT III constriction than do those of other theropods.

Hypothesis b denotes that the arctometatarsus is proximally narrower relative to overall length than are alternate morphologies. If this hypothesis is corroborated, arctometatarsalians will cluster together on bivariate plots of major principal components. Non-arctometatarsalian specimens sharing homogeneous morphologies will cluster separately from the arctometatarsalian group.

MATERIALS AND METHODS

Materials

Twenty-three saurischian third metatarsals (Table 2.1, Figures 2.1-2.4), isolated and from complete metatpodia, were chosen for description and Principal Components Analysis. Because the analysis tested for correlations between proximal constriction versus overall length, only complete specimens (physical or from figures) were deemed suitable. Specimens from the groups introduced in the phylogeny in Chapter 1 were included, without presuppositions about clustering by metatarsal morphology. Specimens from a wide phylogenetic spectrum show the diversity of included morphologies (Figure 2.1). Constituents of each phylogenetic group are listed below, and specimen information is given in Table 2.1.

- 1. Tyrannosauridae: Albertosaurus sarcophagus, Gorgosaurus libratus, Tarbosaurus bataar, Tyrannosaurus rex.
- 2. Ornithomimidae. cf. Ornithomimidae.
- 3. Troodontidae: Troodon formosus.
- 4. Oviraptorosauria: Elmisauridae: *Elmisaurus* sp., Oviraptoridae: *Ingenia* yanshini, Rinchenia mongoliensis.
- 5. Ornitholestes hermani.
- 6. Dromaeosauridae: Deinonychus antirrhopus.
- 7. Therizinosauridae: Segnosaurus ghalbinensis.
- 8. Carnosauria: Allosaurus fragilis, Allosaurus (Saurophaganax) maximus, Sinraptor dongi.
- 9. Elaphrosaurus bambergi.
- 10. Herrerasaurus ischigualastensis.
- 11. Prosauropoda: Plateosaurus engelhardti.

When available, physical specimens of these taxa were photographed for further measurement and analysis. Figures 2.2 through 2.4 depict examined fossil or cast specimens; all are displayed with a 10 cm scale bar; the grouping of Table 2.1. Theropod and *Plateosaurus* third metatarsals examined for descriptive morphology and Principal Components Analysis., including specimen numbers. The table adheres to the following conventions:

1. An asterisk (*) signifies that a specimen displays proximal constriction connoting an arctometatarsus (Holtz 1994).

2. Under the heading "Specimen/photo PJC," the symbol ***** indicates that a physical specimen was examined. The designation *****photo indicates that confirmed measurements and observations pertain to a photograph in the collections of P. J. Currie (PJC).

3. In the column labeled "Reference: Figure/photo," the slide number or volume in the collection of P.J. Currie is cited as PJC (number or volume).

4. If measurements were taken from a figure, the reference is cited under "Reference: Figure/photo."

Taxon (arctometatarsus*)	Specimen number	Specimen/ photo PJC	Reference: Figure/photo	
Albertosaurus sarcophagus*	TMP 81.10.1	*		
Albertosaurus sarcophagus*	TMP 86.64.1	*		
Gorgosaurus libratus*	MOR 657	*		
Gorgosaurus libratus*	AMNH 5432		Holtz 1994a	
Tarbosaurus bataar*	PIN 552-1		Maleev 1974	
Tyrannosaurus rex*	LACM 7244/23844	*		
Tyrannosaurus rex*	MOR 555	*		
cf. Ornithomimidae*	TMP 87.54.1	*		
Troodon formosus*	MOR	*		
<i>Elmisaurus</i> sp.*	PJC	*		
Ingenia yanshini	GI 100/34	*photo	PJC 1998 II	
Ingenia yanshini	GI 100/32	#photo	PJC 1998 II	
Rinchenia mongoliensis	GI 100/42	#photo	PJC 89.9.233	
Ornitholestes hermani	AMNH 619		Paul 1988	
Deinonychys antirrhopus	MOR 793	*		
Segnosaurus ghalbinensis	GI SPS 100182		Perle 1979	
Allosaurus fragilis	MOR 693	*		
Allosaurus fragilis	UUVP 6000 right	*		
Allosaurus fragilis	UUVP 6000 left	*		
Allosaurus (Saurophaganax) maximus	OMNH 01708		Chure 1995	
Sinraptor dongi	IVPP 10600	*		
Elaphrosaurus bambergi	HMN dd		Janensch 1925	
Herrerasaurus ischigualestensis	PVL 2566		Reig 1963	
Plateosaurus engelhardti	?		Huene 1907-8	

specimens in the figures reflects anatomical or methodological distinctions, that I now describe in detail.

Figure 2.1 shows specimens measured from figures in the literature. These were included to broaden the outgroup context for arctometatarsalian theropods, but only if the original figures and their scales were clear, and if the reference made no mention that the metatarsal was incomplete or distorted.

In addition, P.J. Currie provided slides and length measurements of metatarsals from *Ingenia* and *Rinchenia* (Figure 2.3: a, b, and c), representing all of the oviraptorid third metatarsals employed in this study.

Methods for morphological description

Specimens at RTMP, MOR, and UCMZ were analyzed in detail and photographed. Photographs later served to corroborate or clarify notes taken at these institutions. Figure 2.5 shows the conventions used to describe position and direction. To facilitate comparison between specimens and between observations and measurements, I concentrated on three regions of each metatarsal:

- a) The ginglymus, which is the roller joint surface of the metatarsal where it articulates with its proximal phalanx. The descriptions also refer to the ginglymus as the phalangeal articular surface.
- b) The shaft of the metatarsal, from the most proximal extent of the ginglymus to the most distal extent of articular surfaces with MT II and MT IV. I noted contours, apparent relative width, and possible regions of distal joint contact with MT II and MT IV.

c) Region of proximal articulation with MTs II and IV. On isolated specimens the intermetatarsal joint surfaces were examined, as well as MT III in proximal view. In the descriptions below, I also refer to the proximal aspect of the metatarsal as the proximal cross section, or the mesotarsal articular surface.

If a specimen was unavailable for direct assessment but was figured in the literature, only those aspects of morphology discernible in the figure were described. In some cases examination of incomplete specimens, mounted specimens unavailable for measurement, and photographs in the author's collection supplemented qualitative information from figures. For example, metatarsals of *Segnosaurus* were unavailable, but a cast partial MT III of the therizinosaur *Alxasaurus* (RTMP skeletal mount) was examined. Skeletal mounts and photographs of the metatarsals of *Plateosaurus* (AMNH), *Herrerasaurus* (FMNH), and *Ornitholestes* (RTMP) clarified qualitative assessments from figures.

Methods for Principal Components Analysis

Table 2.1 and Figures 2.1-2.4 document the specimens measured for PCA, according to the template (Figure 2.6) showing landmarks and measured distances between them. I measured overall length (LTOTAL), distal and proximal widths (WDIST and WPROX), several evenly spaced transverse widths, and the distoproximal extent of the ginglymus in anterior view (HGINGL). For both physical and figured specimens, a minimum of three averaged measurements (in mm) were taken for each distance. Ambiguous measurements

were not attempted. While this limited the sample size, a PCA matrix does not permit missing data.

Metatarsals were measured at RTMP and MOR, with Mitutoyo digital calipers or tape measure for larger specimens. I also photographed the elements with a scale bar. To obtain measurements of the *Ingenia* and *Rinchenia* specimens (Figure 2.3), slides provided by P.J. Currie were scanned. The images were measured on printouts scaled to the sizes of the original specimens, according to measurements provided by Dr. Currie.

In order to assess the accuracy of measurements from slides or figures, photographs of RTMP and MOR specimens were traced, and scaled-up measurements of the tracings were checked against physical measurements. The accuracy was within +/- 2%. The accuracy was consistent for all measurements on a given photograph; thus proportions remained consistent from specimen to photograph. The primary variable contributing to inaccuracy appears to be the position of the scale bar relative to the anterior surface of the metatarsal. This indicates that absolute measurements from figures are even less accurate than my measurements from photographs, because the illustrator's preferred position for a scale bar is usually indeterminable. However, the consistency of proportions shows that ratios obtained from figure measurements are likely to be within acceptable limits of measurement error.

All measurements (Table 2.2) were recorded in mm in Microsoft Excel 98 for Macintosh, and saved as WK1 Quattro Pro files for compatibility with statistical software. An asterisk indicates arctometatarsalian forms. Log transforms of these

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measurements are shown in Table 2.3. Principal Components Analysis results below reflect the log transformed data matrix. The PCA was run on the matrix in SYSTAT for DOS.

QUALITATIVE RESULTS

These descriptions follow the sequence of taxa as introduced in Chapter 1 and on page 31 of this chapter. Trends evident in larger groups are noted, and then individual specimens are described. Description proceeds from distal to proximal along the long axis of the metatarsus. Because proximal features of the MT III specimens are often more superficially striking, this progression ensures that distal variation receives due consideration. Specimens that were examined physically are given more extensive treatment than those examined from figures gleaned from the literature. Because this thesis deals primarily with the tyrannosaurid metatarsus, I devote a plurality of space to description of the tyrannosaurid MT III.

Theropod third metatarsals have several features in common. There are usually deep subcircular fossae on the distolateral and -medial surfaces. (These indentations are shallow on the medial surface of MT IV, and often absent on the fourth metatarsal's lateral surface.) In living amniotes, the fossae mark the attachment sites of collateral ligaments between the metatarsal and the first phalanx. Complementary fossae occur on all phalanges, save the ungual, in most forms. Proximally, the articular surfaces for MT II and MT IV are rugosely striated in tyrannosaurids, carnosaurs, and *Deinonychus*, possibly indicating intermetatarsal ligaments in this region (see Discussion of this chapter, and Chapter 3). I now address variations and similarities in MT III morphology, starting with tyrannosaurids.

1.Tyrannosauridae.

a) Ginglymus (Figures 2.7 and 2.8). The third metatarsal of tyrannosaurids is robust distally. The surface of the ginglymus extends farther proximally than it does in other taxa. The dorsal edge of this surface is curved, but inclines more gradually dorsomedially, so that the apex is medially offset. A deep, anterior reniform indentation (flexor notch: probably the MT III head of M. extensor brevis digiti III) occurs just proximal to the phalangeal articular surface. In tyrannosaurids the insertion follows the contour of the edge of the articular surface, and thus inclines distolaterally towards the fourth metatarsal.

On the posterior surface, the phalangeal articulation comes to a point, forming a triangular shape (Figure 2.8).

b) Shaft. Proximal to the flexor notch on the anterior surface, the metatarsal constricts somewhat medially (Figure 2.7) before expanding again. This slight anterior constriction, and the posterior apex of the ginglymus, mark the distalmost position of plantar constriction of the metatarsal. The plantar constriction continues proximally for about 60% of the length of the metatarsal (Figure 2.8), giving it a triangular cross section in this region.

Surfaces that incline midsagittally towards the edge of this plantar constriction articulate with the third and fourth metatarsals. Holtz (1994a) revealed that distal articular facets of MT II and MT IV dorsally buttressed these complementary surfaces on MT III. Table 2.2. Measurements of theropod and *Plateosaurus* third metatarsals (in mm), according to the template shown in Figure 2.6. Arctometatarsalian forms are designated with and asterisk (*).

lateosurus engelhardti	71.001	44 32	2°98	33.66	11.05	43.89	14'92
kerrerasaurus ischigualestensis	524,58	14.66	56.56	56.24	56.42	46.27	18.02
Elaphrosaurus bambergi	36.505	58.83	56.46	55.43	58.52	37.6	55'28
Sinraptor dongi	412'36	81.69	54.03	<u>9</u> 9'99	60.72	4.97	8°9Z
sumixem (xenegendonue2) .A	462.75	7 6.96	80.69	74 ,86	75.68	127.76	60.35
silipert zuruezollA	£7£	81.24	63.63	17.89	18.07	£0 [°] 26	91.43
siligerî zuruezollA	78.67	82.73	58.32	78.78	Z9.92	96 ⁻ 62	41.25
siligent suruesollA	341.84	96.36	20.62	91.64	97.87	71.47	5.14
sisnenidledg surussongeS	584.4	99°EZ	98.43	96.02	96'19	47.ET	56.32
suqohiina syhoynoni90	135.56	G.8	10.54	78.11	13.09	19.12	9.8
Ornitholestes hermani	112.11	7.245	7.42	96'9	6.7	21.11	69'6
sizneilognom einedoniA	180	9°.36	11.25	96.91	29.61	51.23	78.41
inidaney sinegul	159.36	81.9	11.64	91	12,42	53'36	12.8
inidanev einegal	74.97	99°Z	8.2	£8.8	9 7'6	11.4	9 7`Z
tas suruesimi∃,*	11,991	13'32	99'9	7.8	13.94	54.94	13,67
*suzomioi nobooiT	433,25	14.63	5.8.3	12.14	79.72	50.52	34.61
*esbimimontinnO	304,31	15.71	6,12	14.33	27.47	51.25	18.81
_xəx snınesouue.k	67.748	65,28	37.46	26.53	92'901	148.19	9'06
_xəı snınesouueıλ⊥	268.23	44.61	79.97	51.63	64'3	128.08	79.18
Tarbosaurus bataar*	178	37.26	33 [.] 69	30.92	15.88	106.46	16,82
eorgosaurus libratus*	069	36.21	56.83	22.57	93`29	81.08	\$ 0,23
*supertoores suruesoftedA	484'32	92.52	96.91	£7.61	64.73	73.57	37,21
*superiqostes suruesofiedlA	244.23	34'34	32.72	29.64	66.69	£0 [.] 03	5.82
Specimen	LATOTA	MPROX	M75-LTU-DE	Msol, TU-DE	MS2 I DE	TSIQW	1011101H

(mm) finemenu seeM :S.S eldeT

Table 2.3. Log-transforms of measurements (in mm) of theropod and *Plateosaurus* third metatarsals. Arctometatarsalian forms are designated with and asterisk (*).

Specimen	LTOTAL	WPROX	W75%TU-DE	W50%TU-DE	W25%TU-DE	WDIST	HGINGL
Albertosaurus sarcophagus*	2.73578248	1.53542072	1.43536651	1.4718782	1.80611211	1.95438725	1.76492298
Albertosaurus sarcophagus*	2.6851593	1.37584644	1.30016054	1.29512709	1.73822545	1.86670076	1.57065967
Gorgosaurus libratus*	2.77085201	1.55882853	1.41214122	1.35353156	1.80318389	1.90406605	1.79267179
Tarbosaurus bataar*	2.75663611	1.57124285	1.52750101	1.35353156	1.94600989	20.2718646	1.77018902
Tyrannosaurus rex*	2.78175538	1.67052416	1.52100725	1.72246939	1.98475228	2.11882666	1.91694974
Tyrannosaurus rex*	2.81143424	1.81478015	1.57356777	1.75227899	2.02428038	2.1708189	1.9571282
Ornithomimidae*	2.48331622	1.23829707	0.95999484	1.15624619	1.45438747	1.50691073	1.26740642
Troodon formosus*	2.63673857	1.16524433	0.76566855	1.08421869	1.44669247	1.70346334	1.5392016
Elmisaurus sp.*	2.22039578	1.12548127	0.82347423	0.93951925	1.14426277	1.39689645	1.13257985
Ingenia yanshini	1.87488751	0.88422877	0.91381385	0.9459607	0.97543181	1.05690485	0.87273883
Ingenia yanshini	2.11180001	0.96284268	1.06595298	1.17609126	1.24104815	1.3494718	1.10720997
Rinchenia mongoliensis	2.25527251	0.97081161	1.05115252	1.2291697	1.29159083	1.32899086	1.17231097
Ornitholestes hermani	2.05076631	0.86003839	0.87040391	0.84260924	0.89762709	1.04805317	0.98181861
Deinonychys antirhopus	2.1224125	0.92941893	1.02284061	1.07445072	1.11693965	1.28148789	0.93449845
Segnosaurus ghalbinensis	2.45392959	1.86664172	1.81197694	1.70722942	1.71566914	1.97786073	1.42028588
Allosaurus fragilis	2.53382288	1.98389679	1.72484909	1.69161187	1.68538341	1.87022828	1.6180481
Allosaurus fragilis	2.5782609	1.83110156	1.76581752	1.75868485	1.7775718	1.90287279	1.61542395
Allosaurus fragilis	2.57170883	1.90976991	1.80366192	1.83701995	1.85009459	1.98690603	1.73367866
A. (Saurophaganax) maximus	2.66534643	1.98650302	1.83935233	1.87424982	1.95119176	2.1063949	1.78067727
Sinraptor dongi	2.61908289	1.83998056	1.73263497	1.74546517	1.75656004	1.88309336	1.41161971
Elaphrosaurus bambergi	2.48280215	1.45984464	1.42258984	1.40534636	1.45514952	1.57518784	1.35391623
Herrerasaurus ischigualestensis	2.35137108	1.52387648	1.42422807	1.40208935	1.42193281	1.65581049	1.25575479
Plateosaurus engelhardti	2.27914201	1.64708943	1.56466606	1.52711411	1.47871076	1.64236558	1.17464119

Table 2.3: Log-transformed values for measurements

The distal intermetatarsal articulation surfaces of MT III are not symmetrical about the edge of the plantar constriction (Figure 2.8). The articular surface of MT III with MT IV displays a compound curvature. It is slightly concave, and twists from a nearly sagittal orientation distally to a more mediolaterally transverse orientation proximally. Compared with the MT II facet, the surface of MT III articulating with MT IV is relatively vertical.

In contrast, most of the facet contacting MT II inclines proximolaterally towards the midsagittal axis of the metatarsal. This is reflected in anterior view by a high medial curvature adjacent to MT II (Figure 2.7). The distal surface of MT III that articulates with MT II consists mostly of a broad surface in one plane, which twists slightly when the metatarsal approaches its narrowest width. The distal surface adjacent to MT II is more rugose than that articulating with MT IV, especially in *Tyrannosaurus rex*.

Proximal to these articular facets with MT II and MT IV, MT III narrows to a uniform width in anterior view (Figure 2.7). This constitutes the gracile, proximally constricted region of the metatarsal, and continues for about 30% of the element's length. The third metatarsal continues to display plantar constriction for most of this portion of the shaft (Figure 2.8).

c) Region of proximal articulation (Figures 2.7 and 2.8). The third metatarsal expands again to articulate proximally with MT II and MT IV. As in *Allosaurus fragilis* and *Ornitholestes hermani*, the proximal portion of the tyrannosaurid MT III that articulates with MT II and MT IV is hooked in cross section. From the plantar to the flexor surfaces, the metatarsal is first sagittally oriented, and then

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experiences a sharp laterally inclined bend. MT III is therefore constrained anteriorly by a projection of MT II, and posteriorly by a projection of MT IV.

Variation in tyrannosaurid third metatarsals appears to be largely a matter of scaling; gross differences in the qualitative morphology just described are not apparent. MT III becomes less gracile with increasing body size, as judged by estimates of mass (Paul 1988, Holtz 1994a, Christiansen 1999). *Tyrannosaurus rex* has the most robust MT III among tyrannosaurids in the sample, and specimens of *Albertosaurus* and *Gorgosaurus* are more gracile. Curiously, the *Tyrannosaurus bataar* MT III specimen (Figure 2.1: a) appears more robust than a longer MT III of *Gorgosaurus libratus* (AMNH 5432; Figure 2.1: b).

2. Ornithomimidae. The isolated ornithomimid MT III is very similar in overall morphology to that of the Tyrannosauridae (Figure 2.9). The specimen appears fairly narrow distally, but the metatarsal is quite slender overall. Only three differences are apparent that are not congruent with scaling trends in tyrannosaurids. MT III does display a slight proximal re-expansion in the ornithomimid, but this region is not hooked as it is in the tyrannosaurids. The ornithomimid MT III also lacks the deep flexor notch that occurs in even small tyrannosaurids (Hutchinson et al. 1997: UCMP V72085-112003).

Additionally, in anterior view the ornithomimid MT III appears roughly symmetrical in the robust region between the proximal splint and the ginglymus. The edge along the articular surface with MT IV is slightly straighter than that along MT II (Figure 2.9). This differs from the condition in the tyrannosaurid MT III, which has a pronounced medial deflection in anterior view in this region (Figure 2.7). Ornithomimid third metatarsals examined in skeletal mounts at RTMP corroborate these observations.

3. *Troodon formosus*. The *Troodon formosus* specimen (Figure 2.10) was a complete articulated metatarsus, and some aspects of morphology on the lateral and medial surfaces could not be assessed. However, its MT III displayed several differences with that of the tyrannosaurids and ornithomimid.

a) Ginglymus. The phalangeal articular surface of the *Troodon* third metatarsal forms a gentle symmetrical arch, and its proximal apex lacks the medial deflection seen in ornithomimids and tyrannosaurids. The flexor insertion is shallow, as it is in the ornithomimid (Figure 2.10).

b) Shaft (distal to proximal). The distal articular surfaces for MT II and MT IV are not as proximally extensive as they are in other arctometatarsalians. In contrast to the condition in tyrannosaurids and ornithomimids, the distal joint contact with MT II is vertical and the contact with MT IV is angled proximomedially (Figure 2.10). The proximal laterally constricted portion of the metatarsal is much longer and thinner than those of the aforementioned taxa.

c) Region of proximal articulation. There is little proximal re-expansion of MT III of *Troodon formosus*, as was noted by Wilson and Currie (1985) for *Troodon inequalis*.

4. Oviraptorosauria. These constitute the most diverse phylogenetic assemblage in terms of third metatarsal morphology. I begin with the *Elmisaurus* specimen,

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because it can be cursorily classified as arctometatarsalian on the basis of proximal constriction.

Elmisaurus sp.: This MT III is similar overall to the tyrannosaurid and ornithomimid forms, but has several readily distinguishable characteristics.

a) Ginglymus. The phalangeal articular surface has laterally expansive condyles, and its proximal edge has a reniform contour (Figure 2.11a). The flexor insertion appears shallow, yet is extensive in area and is somewhat medially offset. The posterior surface of the ginglymus is triangular, with a proximal apex (Figure 2.11b), as it is in tyrannosaurids and the ornithomimid. Unlike the situation in these taxa, however, in *Elmisaurus* distinct ridges demarcate the laterally and medially inclined sides of the triangle, giving the posterior surface of the ginglymus more relief.

b) Shaft (distal to proximal). In anterior view, the shaft of the metatarsal gradually tapers proximally until it reaches its point of greatest proximal constriction. Unlike in *Troodon*, this point is somewhat more proximal than it is in tyrannosaurids, and the thin portion of the metatarsus is shorter in relative length (Figure 2.11a). The *Elmisaurus* MT III displays less plantar constriction than the condition in larger arctometatarsalian morphologies (Figure 2.11b). The plantar surface is flat, and the metatarsal is not triangular in cross section distally, as it is in tyrannosaurids. Proximally, however, the metatarsal is narrower anteriorly and broader posteriorly (Figure 2.11a, 2.11b). Thus the cross section of the metatarsal changes proximally from a wedge that is truncated posteriorly, to one truncated anteriorly.

c) Region of proximal articulation. As noted elsewhere (Currie 1990), the metatarsus of *Elmisaurus* is fused proximally. In posterior view, the proximal articular surfaces between MT III and MT II are completely obliterated by ankylosis (Figure 2.11: b).

The remaining oviraptorosaur specimens were examined solely by way of photographs. Their descriptions are restricted to those features visible in anterior view.

Rinchenia mongoliensis (distal to proximal): This metatarsal appears very gracile overall (Figure 2.3b). The phalangeal articular surface resembles that of *Elmisaurus*. The metatarsal tapers very gradually from distal to proximal. The oviraptorid MT III is therefore somewhat narrower at the proximal end than at the distal end, but not to the same relative degree as with the anterior face of *Elmisaurus* (Figure 2.11a). This specimen differs fundamentally from *Elmisaurus* and other arctometatarsalian morphologies in that the taper is continuous along the length of the metatarsal, and does not display a dramatic narrowing about halfway along the element.

Ingenia yanshini (distal to proximal; Figure 2.3c, 2.3d): Both MT III specimens of this oviraptorosaur have phalangeal articular surfaces that are unexpanded distally. In two specimens the proximal edge of this surface slopes gently proximomedially, but in one specimen the contour resembles that previously described for tyrannosaurids (Figure 2.3c, Figure 2.7). Compared with

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arctometatarsalian specimens, the *Ingenia* MT III have only slight narrowing evident where MT II proximally articulates with MT II and MT IV. There is no appreciable plantar constriction.

5. Ornitholestes hermani (Figure 2.1c). For these descriptions, figures in Paul (1988) supplement observations of *O. hermani* cast skeletal mounts at RTMP.

a) Ginglymus. The dorsal edge of the ginglymus is shallow laterally, but comes to a sharp peak medially before sloping steeply towards the distomesial corner of the metatarsal's anterior face (Figure 2.1c). The ginglymus does not appear to extend as far proximally in anterior view as it does in tyrannosaurids.

b) Shaft (distal to proximal). The entire metatarsal has a very slight medial bowing. There is a very modest degree of constriction towards the longitudinal center of the element (Figure 2.1c).

c) Region of proximal articulation. This third metatarsal is hook shaped in proximal view, as described for tyrannosaurids. In lateral or medial view, MT III expands craniocaudally in this region. In concert with the hook-like bowing, this expansion increases the apparent area of articulation with MT II and MT IV.

6. *Deinonychus antirrhopus*. Ostrom (1969) described the MT III of *Deinonychus* in some detail, but the present account stresses different and complementary aspects of morphology.

a) Ginglymus. Unlike the situation in *Ornitholestes*, the ginglymus is spoolshaped in anterior view, with the proximal edge showing a midsagittal depression. The entire ginglymus is inclined proximomedially (Figure 2.12). The inclination is not as great as that of the ginglymus of MT II, which articulates with a hyperextensible phalanx. Above the phalangeal articular surface of MT III is a very shallow subtriangular flexor depression.

b) Shaft (distal to proximal). There is little narrowing of the metatarsal along its long axis, although the anterior surface of the proximal 20% of MT III is somewhat constricted relative to the posterior face.

Notably, the MT III of *Deinonychus* has an elongate distal articular facet for MT II, which angles slightly towards the plantar surface. This facet recalls the distal MT II articular surface of arctometatarsalians, although the plantar angulation is much less striking, and the facet does not incline proximally and midsagittally as it does in tyrannosaurids and bullatosaurians.

c) Region of proximal articulation. In lateral view, the proximal 15% of the metatarsal flares to become somewhat elongate anteroposteriorly at the mesotarsal articular surface (Figure 2.12).

7. Segnosaurus ghalbinensis. The MT III of Segnosaurus (Figure 2.1g) reveals a highly unusual morphology among theropods.

a) Ginglymus. In anterior view the upper edge of the ginglymus is W-shaped (dilambdoidal). At the proximalmost level of the ginglymus, small lateral and medial projections flare out from the metatarsal shaft (Figure 2.1g. The medial flaring is more prominent than the lateral.

b) Shaft and region of proximal articulation (distal to proximal). The metatarsal attenuates proximal to the lateral and medial projections, but remains thick mediolaterally. At a point about 60% of the length from the distal end, the metatarsal begins to flare laterally and somewhat medially to become very wide at its proximal end. Other information could not be reliably obtained from the figure.

8. Carnosauria. Four out of five carnosaur third metatarsals examined are from *Allosaurus*. I consider the elements by species and specimen number.

Allosaurus fragilis (UUVP 6000; TMP cast): There are minor qualitative differences between left and right MT III on this skeleton.

a) Ginglymus. In anterior view the ginglymus is fairly broad distally. Its proximal edge resembles those of the tyrannosaurids and ornithomimids on the left MT III, recalling a medially inclined arch (Figure 2.4b). On the right MT III, the proximal edge of the ginglymus is low medially, but has a higher lateral arch (Figure 2.4c). The flexor indentation is symmetrical and moderately deep on the right side (although not as deep as in the tyrannosaurids), and is very shallow on the left MT III.

b) Shaft (distal to proximal). The shafts of both metatarsals have a small medial curvature. A poorly defined distal facet marks part of the articulation surface with MT II, and extends to roughly the apex of the medial curve.

c) Proximal articular sufaces. The proximal part of the MT II articulation surface, and that articulating with MT IV, are rugose and expand into the hooked contours seen in Ornitholestes. The metatarsal is thus very similar to that of Ornitholestes in proximal view.

Allosaurus fragilis (MOR 693): The left MT III of this specimen differs little from the metatarsals of UUVP 6000.

a) Ginglymus. The complex shape of the proximal ginglymus edge is like that of the right MT III of UUVP 6000, but the shallow flexor notch more resembles that of UUVP 6000's left MT III (Figures 2.13, 2.4c). Plate 53 in Madsen (1976) indicates that MOR 693 is typical of *Allosaurus* in this region.

b) Shaft and region of proximal articulation. The general contours are the same as in UUVP 6000, with a hooked cross section in proximal view.

The MOR third metatarsal is unusual, however, in two notable features (Figure 2.13). The proximal portion, where the element articulates with MT II and MT IV, is relatively wide in anterior view. There is also a pathology in the form of an small exostosic bump, just proximal to midshaft on the lateral surface.

Allosaurus (Saurophaganax) maximus: This large MT III was figured by Chure (1995), and in anterior view closely resembles the other Allosaurus specimens (Figure 2.1e). It appears to be much more robust, but proximally is proportionally narrower than the smaller metatarsals. The figure does not facilitate discernment of other marked distinguishing features.

Sinraptor dongi: The Sinraptor MT III appears to be more gracile than that of the Allosaurus specimens.

a) Ginglymus. Figure 2.14 shows the contours of the ginglymus; its proximal edge is more of a continuous arc than the bipartite shape found in most *Allosaurus* specimens (see above). The flexor notch is large and subtriangular, but shallow.

b) Shaft (distal to proximal). The shaft of the metatarsal has a small medial bend. The area of demarcation for the MT II articular surface is better delineated in *Sinraptor* than it is in the other carnosaurs, and is at least as evident as the corresponding surface in *Deinonychus*. Rugosity on MT II in this region implies distal ligamenture between MT II and MT III. This articulation is similar although less extensive than it is in tyrannosaurids. *Sinraptor*'s MT III does not share the extreme plantar angulation of tyrannosaurid third metatarsals; while there is a slight medial slope towards the plantar surface, it is even less marked than the condition in *Deinonychus*.

c) Region of proximal articulation. The proximal articulations with M TII and MT IV are similar to those in *Allosaurus*. The *Sinraptor* MT III angles more anterolaterally in proximal view (Figure 2.14), and the cross section is shaped more like a posteriorly truncated hourglass than the L or hook shape in *Allosaurus*.

9. *Elaphrosaurus bambergi* (distal to proximal). The *Elaphrosaurus* MT III was unavailable for examination, and figures (Janensch 1925) allow only a cursory description (Figure 2.1f). The ginglymus is the widest part of the element. The distalmost surface of the ginglymus curves proximolaterally, and its upper edge

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has a very shallow U-shape. The shaft of the metatarsal is fairly slender, and narrows only slightly to a point about 85% along its distoproximal axis. From there the metatarsal widens again, but its proximal width is less than the width at midshaft.

10. Herrerasaurus ischigualastensis

a) Ginglymus. The ginglymus of MT III appears reniform in anterior view, and its distal edge inclines somewhat proximomedially (Figure 2.1g). The flexor notch is proximodistally compressed and becomes sharply defined laterally, so that a thin ridge overhangs the dorsolateral edge of the ginglymus (Figure 2.1g).

b) Shaft and region of proximal articulation (distal to proximal; Figure 2.1g). The narrowest point along the long axis of the metatarsal occurs at 20-25% of its length from the distal end. The shaft varies little in width, but twists laterally where it articulates with MT II and MT IV. In this region, figures of all three metatarsals indicate that the MT III of *Herrerasaurus* is slightly wider along its posterior border than along its anterior face (Novas 1994).

11. Plateosaurus engelhardti.

a) Ginglymus. The ginglymus is quite low, and the flexor notch is only a shallow indentation. Distal to the main shaft, the metatarsal is somewhat wider posteriorly than anteriorly. Consequentially, the collateral ligament fossae are visible in anterior view (Figure 2.1h).

b) Shaft and region of proximal articulations (distal to proximal). The figured MT III that was subject to measurement (Huene 1907-8: Figure 2.1h) and the photographed specimen have a medial curvature. A more robust specimen lacks this curvature (*Gresslyosaurus robustus* in Heune 1907-8; referred to *P*. *engelhardti* by Galton 1986).

Two proximal features of the MT III of *Plateosaurus* differ greatly from the condition seen in theropods. The mesotarsal articular surface comes to a point anteriorly, making the proximal face of the metatarsal subtriangular in cross section. A keel extends distally from this apex, about 15-20% of the metatarsal's length along the anterior surface (Figure 2.1h).

These qualitative assessments delineate morphological variation along the longitudinal axis of the theropod MT III. The results and accompanying figures leave the impression of striking disparity in proximal robustness between the arctometatarsalian morphologies (typified by the tyrannosaurids, the ornithomimid, *Troodon*, and *Elmisaurus*) and the other specimens. The quantitative results below provide an independent appraisal of the foregoing descriptive elucidation.

QUANTITATIVE RESULTS

Numerical results from PCA

Table 2.4 displays the loading of each measurement along the first three principal components, the percentages the measurements contribute to each component, and component correlations. The first three principal components account for 98.29% of total variance: PC1 explains 86.65%, PC2 10.614%, and
PC3 1.026%. Other components contribute negligible amounts to overall variation. Because PC3 also accounts for so little variance, it yields little information about significant differences in shape or size. Therefore, this section concentrates on PC1 and PC2.

Variable loadings for each principal component (Table 2.4a) inform the type of variance the components represent. All loadings on PC1 are positive, which indicates that this component primarily describes overall size variation. PC2, on the other hand, shows a pattern of positive and negative loadings. Values for measurements representing proximal width are all negative, while loadings for other measurements are positive. This indicates that PC2 describes shape variation in the frontal plane, and that proximal width scales negatively compared with overall length in many specimens.

Loadings on variables for PC2 show that proximal constriction plays a quantitatively significant role in overall variation in theropod third metatarsals. The high negative loading of W75%TU-DE (-0.517) reveals that relative width, at about 75% of the distance from the phalangeal to mesotarsal articulations, is the most important contributor to frontal shape variation. The proximal width, and width about half way along the metatarsal (W50%TU-DE), are about equal in their contribution (with loadings of -0.328 and -0.335, respectively).

The percentage contribution of PC1, 2 and 3 to the variance of each measurement (Table 2.4b) corroborates the relative significance of these proximal width measurements. PC2 accounts for 17.7% of variation in W75%TU-DE, 6.2% for WPROX, and 9.6% for W50%TU-DE. More distal

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measurements of width (W25%TU-DE and WDIST) contribute less to variance among the specimens. Two considerations indicate that variation in distal width tracks linear size, and varies less relative to overall size than measures of proximal width. First, loadings are positive for these measurements in PC 2. Second, and more importantly, PC1 accounts for a higher percentage of variation in distal width measurements than in proximal measures, and PC2 for a lower percentage (Table 2.4b). PC1 describes size variance and PC2 primarily indicates shape variation, so a higher percentage contribution by PC1 indicates that size discrepancy is more important than shape for variance in a given measurement.

Component correlations (Table 2.4c) provide congruent evidence for these trends in width variance. As with loadings, correlations for proximal width measurements are negative for PC2, but correlations are positive for distal width. This confirms the unique contribution of proximal width to shape variation. Also, correlations between proximal width variables and their loadings have higher absolute values for PC2 (correlations of WPROX =-0.248, W75%TU-DE=-0.418, and W50%TU-DE=-0.305, versus correlations of 0.201 and 0.179 for W25%TU-DE and WDIST). This indicates that, in addition to being negatively correlated with size, proximal width contributes strongly to overall variation along PC2.

Interestingly, Table 2.4a reveals that HGINGL has a high positive loading on PC2 (0.461), and PC2 is an important element of the variance for the measure (accounting for 16.9% of variance: Table 2.4b). Differing signs for HGINGL and proximal width loadings may indicate that the height of the ginglymus correlates

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Table 2.4. Loading, variance, and correlation results for PCA.

- Table 2.4a. Normalized loadings of each variable on each of the first three principal components, and also the eigenvalues and corresponding percentage of total sample variance explained by each component. Positive loadings indicate that a measurement contributes to size variation for a component. Negative loadings indicate that a measurement explains shape variation for a component.
- Table 2.4b. The percentage of variance for a given measurement that a component explains.
- Table 2.4c. Component correlations. A positive correlation indicates a contribution to size variance. A negative correlation indicates a contribution to shape variance.

Measurement	PC 1	PC 2	PC 3
LTOTAL	0.2806069	0.4400111	-0.201246
WPROX	0.4411288	-0.328262	-0.760263
W75TUDE	0.3896637	-0.516838	0.2795085
W50TUDE	0.3590298	-0.335247	0.4024922
W25TUDE	0.3957905	0.2339741	0.3242299
WDIST	0.4019173	0.2095291	-0.078262
HGINGL	0.3578044	0.460964	0.1229837
Eigenvalue	0.666	0.082	0.008
Percent of Total Variance	86.65	10.614	1.026

Table 2.4a Loading of variables for each component

Table 2.4b Variance/measurement each PC explains

Measurement	PC 1	PC 2	- PC 3
LTOTAL	0.7639895	0.2312903	0.0047202
WPROX	0.9059136	0.0617643	0.0323221
W75TUDE	0.8178047	0.1771409	0.0050545
W50TUDE	0.8909102	0.0956404	0.0134494
W25TUDE	0.9513948	0.040936	0.0076692
WDIST	0.967195	0.0323645	0.0004405
HGINGL	0.8293437	0.1694793	0.0011769

Table 2.4c Correlation of components with variables

Measurement	PC 1	PC 2	PC 3
LTOTAL	0.8609023	0.4736842	-0.067669
WPROX	0.9498681	-0.248021	-0.17942
W75TUDE	0.8983051	-0.418079	0.0706215
W50TUDE	0.9301587	-0.304762	0.1142857
W25TUDE	0.96997	0.2012012	0.0870871
WDIST	0.9761905	0.1785714	-0.020833
HGINGL	0.8957055	0.404908	0.0337423

positively with relative metatarsal gracility, while proximal width decreases with gracility. However, a high positive loading for HGINGL may reflect the relatively high values for this measurement in the large tyrannosaurid specimens (see Discussion), and therefore may be correlated more with overall metatarsal length than with proximal narrowing.

Grouping of specimens by PCA

Table 2.5 gives statistics for all specimens measured for PCA, including the total variance for each specimen, the amount of each specimen's variance explained by each PC (Varcomp), and the distance of the specimen from the origin of all PC axes. The last quantity gives the degree of deviation from a hypothetical average morphology in size and shape as determined by the constituency of the entire data base. The value of distance from the origin is simply the square root of the variance, and is the number of standard deviation units (SD) a specimen plots away from the origin.

The distribution of standard deviations (Distance: Table 2.5) facilitates the general identification of unusual and typical morphologies. Because PC1, a size related component, explains 86.65% of total variance, distance from the origin in SD primarily shows deviations in overall size from the average of the sample. At 0.15 SD, the *Elaphrosaurus* MT III is closest to the average in linear dimensions. By far the most aberrant are *Ornitholestes* and the smaller *Ingenia* specimen, at distances of 1.474 and 1.480 SD, respectively. These are the smallest specimens in overall length. At the other extreme, *Allosaurus* (Saurophaganax) *maximus* (1.08 SD) and the larger *Tyrannosaurus rex* specimen (1.04 SD) have

the largest sum of linear measurements. Standard deviation distance values are useful for finding where organisms cluster relative to the morphological mean of the sample, but clustering by specific morphological traits requires plots of specimens against important eigenvectors.

Figure 2.15 shows plots of specimens along these principal component axes. With PCA of morphological data, PC1 is usually associated with variation in linear size. Figure 2.15 illustrates the interpretation that PC1 is size-related for the examined theropod metatarsals. Tyrannosaurids, all of which have metatarsals with large absolute size, have high component scores along PC1. Carnosaurs, which are also quite large animals, likewise have high loadings for PC1. These large theropods plot far to the right in along PC1 (the x axis). By contrast, one *Ingenia* specimen and the *Ornitholestes* metatarsal are smallest in overall length, and have the lowest eigenvalues along PC1. All other specimens plot appropriately for PC1 depending on their absolute size and general robustness.

Figure 2.15 also shows evident demarcations between subgroupings of metatarsal morphology, with clustering along PC2 (an index of proximal gracility). Figures 2.16 through 2.19 align clades from the phylogeny introduced in Chapter 1 with MT III clusterings revealed by PCA. I now outline these clusterings in detail.

1. "Arctometatarsalian" third metatarsals (Figure 2.16). Tyrannosaurids and bullatosaurians, the third metatarsals of which have relatively narrow proximal measurements (Tables 2.2 and 2.3), all have eigenvalues for PC2 above 0.22.

Table 2.5. Statistics for specimens measured for PCA. The first column gives the figure number in which a specimen is highlighted on a plot of PC1 versus PC2. Distance is the number of standard deviations a specimen sits from the origin of all PC axes. Total variance is given for each specimen, and the fraction of variance accounted for by PC1, PC2, and PC 3 are designated by the Varcomp statistics.

Specimen	Figure	Distance	Variance	Varcomp1	Varcomp2	Varcomp3
Albertosaurus sarcophagus*	2,16	0,5530086	0.3058185	0.7147519	0,2801177	0.0051304
Albertosaurus sarcophagus*	2.16	0,355655	0.1264905	0.1444969	0.8512326	0.0042705
Gorgosaurus libratus*	2.16	0.5537515	0.3066407	0.5883366	0.4080698	0.0035937
Tarbosaurus bataar*	2.16	0.6597609	0.4352844	0.7439737	0.2544735	0.0015528
Tyrannosaurus rex*	2.16	0.9088764	0.8260562	0.8840475	0.0997535	0.016199
Tyrannosaurus rex*	2,16	1.0408658	1.0834016	0.9389227	0.0596432	0.0014341
Ornithomimidae*	2,16	0.5814915	0.3381323	0.830386	0.148997	0.020617
Troodon formosus*	2.16	0.764133	0.5838992	0.342511	0.6305173	0.0269718
Elmisaurus sp.*	2.16; 2.17	1.0236163	1.0477903	0.9537784	0.0162656	0.029956
Ingenia yanshini	2.17	1.4797775	2.1897415	0.976256	0.0227774	0.0009665
Ingenia yanshini	2.17	0.929745	0.8644258	0.9630605	0.0053579	0.0315816
Rinchenia mongoliensis	2.17	0.8385277	0.7031287	0.9567793	0.0005779	0.0426428
Ornitholestes hermani	2.17	1.4739739	2.1725992	0.9982476	0.0011667	0.0005857
Deinonychys antirhopus	2.17	1.1249073	1.2654165	0.9838395	0.0112622	0.0048983
Segnosaurus ghalbinensis	2.17	0.7300281	0.5329411	0.7110034	0.2871364	0.0018602
Allosaurus fragilis	2.18	0.7375907	0.5440401	0.814883	0.1467556	0.0383614
Allosaurus fragilis	2.18	0.7367215	0.5427586	0.901861	0.0965832	0.0015558
Allosaurus fragilis	2,18	0.9069353	0.8225317	0.9418661	0.0557587	0.0023753
A. (Saurophaganax) maximus	2,18	1.0842314	1.1755578	0.978329	0.0213214	0.0003496
Sinraptor dongi	2.18	0.6768732	0.4581574	0.8070133	0.1907049	0.0022818
Elaphrosaurus bambergi	2.19	0.158441	0.0251036	0.4328608	0.555731	0.0114082
Herrerasaurus ischigualestensis	2.19	0.2755659	0.0759366	0.2204489	0.7156195	0.0639317
Plateosaurus engelhardti	2.19	0.4503833	0.2028451	0.0002991	0.9870327	0.0126682

Table 2.5: Specimen statistics

Troodon, with the most gracile metatarsal proximally, has the highest eigenvalue for PC2 at 0.607. *Elmisaurus* has the lowest PC2 value among proximally gracile forms, at 0.13. Because *Elmisaurus* is a member of the oviraptorosaur clade, its position relative to others in that group is noted below.

2. Oviraptorosauria (Oviraptoridae (*Ingenia*, *Rinchenia*) + Elmisauridae (*Elmisaurus*)), Therizinosauridae (*Segnosaurus*), Dromaeosauridae (*Deinonychus*), and *Ornitholestes* (Figure 2.17). These coelurosaurs show a great diversity in MT III shape. *Elmisaurus*, which is qualitatively considered arctometatarsalian (Holtz 1994a, b), shows the highest value for PC2 among oviraptorosaurs. The oviraptorid *Ingenia* shows high variability (PC2 values of -.22 and -0.06), while *Rinchenia mongoliensis* is intermediate between *Ingenia* and *Elmisaurus*. The dromaeosaurid *Deinonychus* and *Ornitholestes* are undifferentiable from the oviraptorosaur cluster.

In contrast, the therizinosaurid *Segnosaurus* is set apart from its oviraptorosaur sister group in both size (PC1) and shape (PC 2). Its PC1 value is fairly high at 0.61, and its PC2 value is the lowest of any of the examined theropods, at -0.39.

3. Carnosauria (Figure 2.18). Carnosaurs, all of which are relatively large, cluster strongly along PC1. They show more variation in shape than the similarly large tyrannosaurids, however, and are spread out further along PC2. The carnosaur MT III appears to become more gracile proximally with increasing linear size; the highest PC2 values occur for the large *Allosaurus* (*Saurophaganax*) *maximus*

and *Sinraptor dongi* specimens. Without a larger sample size, it is premature to draw conclusions from this trend.

4. Outgroups to Carnosauria + Coelurosauria, collectively the Tetanurae as defined in Chapter 1 (Figure 2.19). *Elaphrosaurus* has a PC2 value almost identical to that of *Deinonychus* (-0.118 versus –0.119, respectively), which is surprising since the metatarsus of *Elaphrosaurus* has been considered relatively gracile (Osmolska 1990). *Deinonychus* and *Elaphrosaurus* do not group together, however, because MT III in *Elaphrosaurus* has a higher size loading along PC1. *Herrerasaurus* and *Elaphrosaurus* group closely along PC1, but the lower PC2 score of *Herrerasaurus* reveals that its MT III is more robust proximally.

The prosauropod *Plateosaurus* plots very low along PC2, with by far the lowest value (-0.45). Table 2.2 confirms that *Plateosaurus* has the highest relative measurements of proximal width.

DISCUSSION

Are the hypotheses corroborated or falsified?

The results provide evidence for testing hypotheses based on qualitative and quantitative approaches. This first hypothesis relied on descriptive evidence: **Ha:** The tyrannosaurid **MT III** is qualitatively differentiable from similar forms in ways unpredictable from simple allometry.

Testing this hypothesis requires evidence of variation or homogeneity among examples of the "arctometatarsalian" MT III. Proximally constricted third

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metatarsals, including those of tyrannosaurids, ornithomimids, troodontids and elmisaurids, are morphologically diverse. The tyrannosaurid MT III appears more robust than those of the other proximally attenuated forms, as would be expected given the tyrannosaurids' much larger overall size (Hildebrand 1988). However, comparison of specific features indicates substantial differences in shape between large and small "arctometatarsalian" forms.

All examined tyrannosaurid specimens have a deep and inclined flexor insertion just proximal to the ginglymus of MT III (Figures 2.1 and 2.2). This characteristic does not occur in other theropod third metatarsals that are proximally pinched, or in theropod third metatarsals that are more robust proximally (Figures 2.1-2.4), regardless of size. I therefore interpret this feature as autapomorphic for tyrannosaurids, and not associated with allometry.

The proximal re-expansion of MT III, in particular, differs greatly between tyrannosaurids and other relatively gracile forms. In the tyrannosaurid MT III, the regions of proximal articulation with MT II and MT IV are hooked in transverse cross section (Figures 2.7 and 2.8). A small MT III at UCMP also displays this morphology. This specimen has been interpreted as a jurenile tyrannosaurid on the basis of a deep, inclined flexor insertion and asymmetry of the distal shaft (Hutchinson et al. 1997: UCMP V72085-112003). In contrast, ornithomimid, troodontid, and elmisaurid third metatarsals, even when absolutely longer than the UCMP specimen, are not hooked in proximal cross section. This evidence suggests that a proximally hooked MT III is not simply an artifact of positive allometry in arctometatarsalians.

In addition, a hook like proximal articular region occurs in the third metatarsals of non-arctometatarsalian forms that are much smaller than adult tyrannosaurids, such as *Ornitholestes hermani* or even a relatively small specimen of *Allosaurus fragilis* (MOR 693). Paul (1988) considered this feature a synapomorphy of *Ornitholestes*, carnosaurs, and tyrannosaurids. However, the preponderance of character evidence ensconces tyrannosaurids within advanced coelurosaurs (Holtz 1994b, Sereno 1999), and suggests that a hooked MT III is homoplasic for tyrannosaurids, carnosaurs, and *Ornitholestes*. In any case, the hypothesis that a hook like third metatarsal is an allometric phenomenon may be provisionally rejected. Possible functional implications of this morphology are explored below.

The second major hypothesis tested:

Hb: Metatarsi classified as arctometatarsalian (Holtz 1994a,b) have a significantly greater degree of proximal MT III constriction than do those of other theropods, relies on both statistical and descriptive data. Unfortunately the sample size of available complete or reliably figured saurischian third metatarsals is low. The concomitantly low number of specimens in specific clusters negates the possibility of statistically significant measures of close aggregation, such as the test of centroid distance or reduced major axis analysis. Nevertheless, the preliminary data show a striking pattern of separation along PC2. I predict, provisionally, that a larger sample would not significantly alter the topology of clustering.

As noted above, PC2 in this analysis can be soundly interpreted as an index of proximal gracility. Tyrannosaurids, the ornithomimid, and *Troodon formosus* all have PC2 values above 0.22, substantially higher than those of theropods identified as non-arctometatarsalian (Holtz 1994a,b). The hypothesis is therefore strongly corroborated for these taxa.

However, the PC2 value for *Elmisaurus* (0.13) is intermediate between that of the ornithomimid (0.22) and *Rinchenia* (0.02). If PC2 values were the only criteria for shape clustering, the *Elmisaurus* MT III would be revealed at gradationally transitional between the new oviraptorid and other proximally pinched forms. The hypothesis would therefore be falsified for *Elmisaurus*. Closer examination of both quantitative and descriptive data is necessary to further assess Hypothesis b.

Correlation of PCA with qualitative description

Qualitative and quantitative data accord quite well for the examined third metatarsals; variable loadings and clustering by PCA reflect observable variation in the specimens. I now discuss convergence and discordance between the data for the groupings indicated in Figure 1.

Theropods with PC2 values greater than 0.22 are visually identifiable as arctometatarsalian. The relatively low value for *Elmisaurus* correlates with a wider MT III proximally than in the other specimens, which might not be revealed under casual inspection. The tyrannosaurids have generally higher values for PC2 than the ornithomimid. Close examination of the PCA data shows that this is attributable to the proximal re-expansion of the tyrannosaurid MT III, a consequence of the element's hook shaped inflection evident upon visual inspection. The *Troodon* MT III is strikingly narrow proximally. PCA shows that

both physical narrowing and elongation of the constricted spline contribute to this impression.

Among small non-arctometatarsalian coelurosaurs (to the lower left in Figure 2.17), only the MT III of *Rinchenia* subjectively appears to approach the arctometatarsalian condition in proximal gracility. Its position along PC2 corroborates this observation. The *Ingenia*, *Deinonychus*, and *Ornitholestes* specimens all appear more robust, and cluster low along PC2. PCA of measurements in anterior view, however, does not reveal the unusual MT II articulation surface of *Deinonychus*.

Similarly, PCA does not indicate the extensive distal MT II articulation of MT III in the carnosaur *Sinraptor*. PC2 does reveal it to be slightly more gracile than the *Allosaurus fragilis* specimens. The MT III of *Allosaurus (Saurophaganax) maximus* appears to be relatively massive. Its PC1 value of 1.07 exceeds that of the longer *Tyrannosaurus rex* specimens, indicating a high summation of length and transverse dimensions. The carnosaur metatarsals are generally more robust than those of the smaller coelurosaurs, scoring lower along PC2.

The MT III of *Herrerasaurus* has a PC2 value similar to that of the carnosaurs. Subjectively, it does not appear notably robust. It reaches its narrowest point at a relatively distal position, which may account, in part, for its low PC2 loading. If *Herrerasaurus* represents the primitive condition for theropods (Sereno and Novas 1992), as suggested by its Carnian age and suite of characters primitive for Saurischia (Brinkman and Sues 1987), a more robust metatarsus than in derived theropods is perhaps not surprising. However, the quantitative and

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qualitative metatarsal data for *Herrerasaurus* are more difficult to reconcile than for the other taxa in this study.

Less problematic are *Segnosaurus* and *Plateosaurus*. The third metatarsal of each massive herbivore appears qualitatively quite robust, more so in *Plateosaurus* than in *Segnosaurus*. Their PC2 values, as shown dramatically in Figures 2.17 and 2.19, are the lowest of the sample. Varcomp2 for *Plateosaurus* (Table 2.5) shows that 97.8% of its variance is explained by PC2. The anomalously robust shape of MT III in *Plateosaurus*, quite striking in qualitative assessments, explains nearly all of the variance of the element. The statistical data alone, however, do not reveal other unusual aspects of morphology in the third metatarsals of either *Plateosaurus* or *Segnosaurus*, as described above.

Conversely, *Elaphrosaurus* presents a case in which quantitative data are more revealing than observations. The *Elaphrosaurus* MT III is not qualitatively remarkable, and its measurements do not stand out as noteworthy. However, PCA reveals a very low standard deviation of variance for *Elaphrosaurus*, placing it close to the morphological median for the sample in size and shape. While *Elaphrosaurus* has hind limb element proportions that approach those of arctometatarsalians, its MT III is only average in graciliy.

The high degree of morphological variation for the entire sample suggests differences of biomechanical, constructional, or functional significance. Only thorough analysis of variation will elicit hypotheses that differentiate between these factors.

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Is the MT III shape segregation functionally informative?

There is a strong tendency to infer function from structure in fossil organisms. Morphological clustering can imply but not demonstrate similarity of function, an inference fraught with complications even in studies of modern organisms (Lauder 1995). Particularities of skeletal and soft tissue anatomy, and unforseeable pleiotropic roles for an organ, will reduce the reliability of functional inference in fossils. This caveat applies to fossil structures with putatively analogous function in modern homologues, but especially impedes generalized inferences in the case of structurally diverse organs.

A fruitful approach, therefore, is to focus on novelties or strong aggregations in morphology. Ideally these morphologies will suggest hypotheses amenable to consilient biomechanical testing. Strong clustering on the basis of metatarsal shape (with similar values for PC2) indicates the possibility of similar function. Striking aspects of qualitative morphology can also suggest hypotheses of function, which might be missed if morphometric clustering is relied on exclusively.

MT III morphology suggests tentative hypotheses of function in

arctometatarsalians

The morphometric and observational resolutions of this study uncover possible variances in the function of theropod metatarsi, but the following hypotheses must be considered tentative in the absence of detailed biomechanical analysis. Most of these hypotheses, however, hold substantial promise for more extensive treatment. Chapters 3 and 4 explore more specific and detailed hypotheses for the tyrannosaurid metatarsus, as an exemplar of the potential of such a research program. I begin with the third metatarsal of tyrannosaurids and other arctometatarsalians.

The dorsally extensive ginglymus in tyrannosaurids indicates a wide range of motion for the proximal phalanx. While this morphology stands out statistically, its functional significance is beyond the immediate scope of this study

Generally, proximal and plantar constriction, and relative gracility, mark the arctometatarsalian MT III apart from those of other theropods. The wedge and buttress morphology noted by Holtz (1994a,b) occurs in all arctometatarsalian forms (in the phylogenetic sense: Holtz 1994b), and is consistent with vertical transference of ground-reaction forces to the outer metatarsals (Holtz 1994a). It is unclear how the length of the laterally constricted portion of the metatarsal (quite short in *Elmisaurus*, and long in *Troodon*) would affect the energy transference model (Holtz 1994a). However, other differences in morphological detail may indicate diversity of function in arctometatarsalians.

Specifically, the degree of plantar constriction and the form of proximal intermetatarsal articulations suggest differences in function. The fused proximal tarsometatarsus of adult elmisaurids would have prevented rotation of the proximal shaft of MT III (Wilson and Currie 1985), extensive pistoning motion (Coombs 1978), or energy transference to the outer metatarsals via ligaments (Wilson and Currie 1985). Stresses were presumably transmitted directly to the bone at the proximal ankylosis. Additionally, the MT III of *Elmisaurus* does not display marked distal plantar constriction, while the others do. The

tyrannosaurids, ornithomimid, and troodontid presumably relied upon ligaments to prevent the distal, triangular portion of the third metatarsal from being dislodged anteriorly during acutely angled footfalls. Distal ligaments, or proximal "snap" ligaments that mediated rotation (Wilson and Currie 1985), may have served this purpose in *Troodon* or the ornithomimid. In contrast, the hook shaped proximal articulations in tyrannosaurids would have constrained movement, preventing posterior rotation of the proximal part of the third metatarsal. A strong role for distal ligaments in the tyrannosaurid metatarsus appears to be a reasonable possibility.

From this comparative analysis of arctometatarsus morphologies, I derive a tentative hypothesis of tyrannosaurid pedal function. Specifically, the evidence suggests that the tyrannosaurid arctometatarsus was free to move distally about a proximal pivot point, and that proximal and distal ligaments constrained and facilitated such movement. The validity of this hypothesis rests upon more detailed examination of the tyrannosaurid arctometatarsus, which is the goal of Chapters 3 and 4 below.

CONCLUDING COMMENTS

As noted above, the relatively small sample size precludes statistically definitive segregation of MT III morphologies based on the PCA plots alone. However, the PCA results are clearly interpretable in light of the observed proximal robustness of the specimens. The following conclusions may be drawn from statistical and qualitative analysis of theropod third metatarsals: a) There is no substitute for morphological description. Principal Components Analysis can reveal variance and covariance of an arbitrarily large number of measurements. However, subtle or retrospectively obvious details of morphology may be missed when one is initially choosing landmarks. Accounting for all informative landmarks is time consuming in terms of experimental design and measurement, while qualitative inspection of a specimen often quickly reveals morphological novelty. Examples in this study include the shape of the mesotarsal articular surface of MT III in *Plateosaurus*, and the distal MT II articulation of the third metatarsal of *Deinonychus*.

b) PCA can uncover not only patterns of morphological clustering, but also the importance of qualitatively unremarkable specimens. Carnosaurian and tyrannosaurid third metatarsals aggregate strongly in this study, and *Troodon* and the putatively herbivorous forms are outliers at opposite ends of the robustness scale. Clear patterns do not emerge among smaller non-arctometatarsalian coelurosaurs in third metatarsal morphology. The MT III of *Elaphrosaurus* approximates the average morphology in terms of size and shape.

c) Proximal constriction distinguishes the arctometatarsalian MT III from other morphologies, but this element is variable in taxa that possess it. Third metatarsals traditionally recognized as arctometatarsalian occur above 0.22 along PC2, which is an index of proximal gracility (Figure 2.15). No non-derived morphologies cluster with them. Specimens of tyrannosaurids and the omithomimid have very similar values for PC2. *Troodon* displays an extremity of

proximal constriction, while *Elmisaurus* has a shorter narrow proximal portion of the metatarsal. The *Elmisaurus* MT III lacks the marked plantar constriction of other arctometatarsalian forms. The MT III of tyrannosaurids is unusual in its crescentic proximal expansion, which was not revealed by PCA in this study.

This variation in metatarsal morphology obviates generalized functional inferences about the arctometatarsus, beyond the energy transference hypothesis (Wilson and Currie 1985, Holtz 1994a) in forms with unfused metatarsals. The homogeneity of the tyrannosaurid specimens promises applicability of targeted hypotheses relevant to all members of that clade. Testing hypotheses of pedal function in tyrannosaurids will provide rigorous methodological and theoretical context for revisiting other morphologies (Chapter 5). I now examine the functional morphology of the tyrannosaurid arctometatarsus, and compare its structure with that of possible extant analogs (Chapter 3).

Figure 2.1. Specimens from figures in the literature employed in description and Principal Components Analysis. Figures were deemed sufficiently clear for measurement. Specimens are pictured in the order they are mentioned in the text. Scale bar=10cm.

- a. Tarbosaurus bataar (left; after Maleev 1974).
- b. Gorgosaurus libratus (right; after Holtz 1994a).
- c. Ornitholestes hermani (left; after Paul 1988).
- d. Segnosaurus ghalbinensis (right; after Perle 1979).
- e. Allosaurus (Saurophaganax) maximus (left; after Chure 1993).
- f. *Elaphrosaurus bambergi* (left; after Janench 1925, Barsbold and Osmolska 1990).
- g. Herrerasaurus ischigualastensis (right; after Reig 1963).
- h. Plateosaurus engelhardti (left; after Heune 1907-1908).



Figure 2.2. Tyrannosaurid, troodontid, and ornithomimid third metatarsals employed in description and Principal Components Analysis. Specimens are pictured in the order they are mentioned in the text. Scale bar=10 cm.

- a. Tyrannosaurus rex (left; LACM7244/23844).
- b. Tyrannosaurus rex (right; MOR 555).
- c. Albertosaurus sarcophagus (right pes; TMP 81.10.1).
- d. Albertosaurus sarcophagus (left pes; TMP 86.64.1).
- e. Troodon formosus (left pes; MOR).
- f. cf. Ornithomimidae. (left; TMP 87.54.1).



Figure 2.3. Oviraptorosaur specimens described and measured for Principal Components Analysis. Specimens are pictured in the order they are mentioned in the text.

- a. Elmisaurus sp. (left; TMP PJC collections).
- b. Rinchenia mongoliensis (right; GI 100/42, PJC photo)
- c. Ingenia yanshini (right; GI 100/34).
- d. Ingenia yanshini (left; GI 100/32).



а





b



d

Figure 2.4. Dromaeosaurid and carnosaur specimens described and measured for Principal Components Analysis. Specimens are pictured in the order they are mentioned in the text. Scale bar=10 cm.

- a. Deinonychus antirrhopus (right; MOR 793).
- b. Allosaurus fragilis (left pes; UUVP 6000, TMP cast).
- c. Allosaurus fragilis (right pes; UUVP 6000, TMP cast).
- d. Allosaurus fragilis (left; MOR 693).
- e. Sinraptor dongi (left pes; IVPP 10600, TMP cast).





d



e

Figure 2.5. Relative directional and positional conventions used for text descriptions, showing the left metatarsus of *Elmisaurus* sp. in anterior and posterior views. The animal is considered to be in a standing position, with the long axis of the metatarsus oriented vertically. Proximal is towards the ankle, and distal is towards the toes.



Figure 2.6. Template for PCA measurements, superimposed upon left MT III of *Tyrannosaurus rex* (LACM 7244/23844). Landmarks are shown on the left diagram (a), and linear distances between landmarks are numbered on the right diagram (b). The numbered measurements for PCA (b) are as follows:

1. LTOTAL	a to b.	This is measured down the central axis of the metatarsal, and is not necessarily its greatest overall length
2. WPROX	d to e	Width of the most proximal surface of the metatarsal
3. W75%TU-DE	h to i	Width 75% of the distance from width t-u
4. W50%TU-DE	l to m	Width 50% of the distance from width t-u to width d-e
5. W25%TU-DE	p to q	Width 25% of the distance from width t-u to width d-e
6. WDIST	t to u	Greatest distal width.
7. HGINGL	b to c	Height of ginglymus as measured in anterior view.





Figure 2.7. Left MT III of *Tyrannosaurus rex* (LACM 7244/23844), in anterior view. Features notable in this view include: the high proximal edge of the ginglymus; deep and inclined flexor insertion; a medial deflection marking the distal attachment with MT II; attenuation of the shaft; and a complex re-expansion of the metatarsal where it articulates proximally with MT II and MT IV. In this specimen, part of the distal articular facet for MT IV is visible in anterior view. The inset shows the region of proximal articulations in proximal view, revealing the hooked or crescentic morphology of this part of the bone.



Figure 2.8. Left MT III of Gorgosaurus libratus (MOR 657) in posterior view. Notable features evident in this view include: triangular posterior extension of ginglimus surface; extensive distal articular surfaces for MT II and MT IV; plantar constriction; and posterior and lateral projections of the metatarsal that form a hook shape in the region of proximal articulations.


Figure 2.9. Left MT III of an ornithomimid (TMP 87.54.1). Note overall similarity with the tyrannosaurid MT III (Figure 2.7). Notable traits include: a: shallow and uninclined flexor insertion; a proximal re-expansion that is symmetrical about the midsagittal plane, and which therefore lacks the deflections that give rise to a hooked shape in tyrannosaurids.



Figure 2.10. Left metatarsus of *Troodon formosus* (MOR). Notable features of MT III include: tall symmetrical ginglymus; shallow flexor insertion; straight distal contact with MT II and medially inclined contact with MT IV (opposite from the condition in tyrannosaurids, ornithomimids, and elmisaurids); extreme narrowing of MT III proximally.



Figure 2.11. Left MT III of *Elmisaurus* sp. (TMP:PJC).

a) Anterior view. Distinguishing characteristics include: reniform ginglymus; subtriangular flexor insertion; and tall unpinched portion of metatarsal shaft

b) Posterior view. Notable morphological traits include:midsagittaly inclined ridges on posterior extension of ginglymus; wide proximal expansion of metatarsal; proximal osteological fusion of MT III with MT II.

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Figure 2.12. Right MT III of *Deinonyhcus antirrhopus* (MOR 793). Notable morphological characteristics include: spool-shaped and proximomedially inclined ginglymus; shallow flexor insertion; distally extensive articular facet for MT II; anteropsoteriorly extensive expansion for proximal articulations with MT II and MT IV.



Figure 2.13. Left MT III of *Allosaurus fragilis* (MOR 693). Notable features include: a relatively taller ginglymus in anterior view than in *Sinraptor*, ginglymus bilobed, with taller medial poriton; shallow flexor insertion; slight medial curvature to shaft; proximal articular facet for MT II more distally extensive than that for MT IV; posterior and lateral projections of the metatarsal form a hook shape in the region of proximal articulations. The lateral projection is visible in this figure. MOR 693 has an exostosic pathology on its lateral surface.



Figure 2.14. Left metatarsus of *Sinraptor dongi* in anterior view (IVPP10600; RTMP cast). Notable features of MT III include: distally restricted ginglymus with low height in anterior view; shallow subtriangular flexor insertion; slight medial curvature to shaft; distally extensive articular facet for MT II; in proximal articular region, anterior surface of metatarsal is deflected laterally relative to posterior surface.



Figure 2.15. Plots of MT III specimens against first two principal component axes. Component scores for PC1are plotted along the x axis (Component I Score), and values for PC2 are plotted along the y axis (Component II Score). PC1 is a size-related component, and PC2 is proportional to proximal gracility of MT III (see text). The dashed line at **PC2=0.22** represents the threshold PC2 value for MT III of Arctometatarsalia (*sensu* Holtz 1996).

Specimens are arrayed according to the following legend:

LEGEND:

- ty Tyrannosauridae
- bu Bullatosauria (Omithomimidae, Troodontidae)
- o Oviraptorosaurs, Ornitholestes
- se Segnosaurus
- de Deinonychus
- c Carnosauria
- el Elaphrosaurus
- he Herrerasaurus
- pl Plateosaurus



Figure 2.16. Plot of third metatarsal specimens along PC1 and PC2 axes, highlighting the positions of representatives of the Tyrannosauridae, Ornithomimidae, Troodontidae, and Elmisauridae. Symbols conform to the legend in Figure 2.15. Tyrannosaurids and the ornithomimid cluster strongly along PC2, indicating similar proximal gracility. The *Elmisaurus* MT III has a lower value for PC2, implying that it is more robust proximally than the other specimens. *Troodon* plots very high along PC2, which reflects an extreme degree of proximal narrowing of MT III.



Figure 2.17. Plot of third metatarsal specimens along PC1 and PC2 axes, highlighting the positions of representatives of the Oviraptorosauria, *Deinonychus*, and *Ornitholestes*. Symbols conform to the legend in Figure 2.15. Elmisaurid and oviraptorid oviraptorosaurs are spread out along along PC2, indicating diversity in morphology. *Deinonychus* and *Ornitholestes* plot among the oviraptorosaurs.



Figure 2.18. Plot of third metatarsal specimens along PC1 and PC2 axes, highlighting the Carnosauria and the therizinosaurid *Segnosaurus*. Symbols conform to the legend in Figure 2.15. PC1 and PC2 increase concurrently for the carnosaurian third metatarsals, indicating a possible positive correlation between size and proximal gracility.



Figure 2.19. Plot of third metatarsal specimens along PC1 and PC2 axes, highlighting the positions of *Elaphrosaurus*, *Herrerasaurus* and *Plateosaurus*. Symbols conform to the legend in Figure 2.15. The extremely low PC2 value for *Plateosaurus* indicates that is is the most robust metatarsal in the sample.



CHAPTER 3: Tensile keystone model of functional arthrology in the

tyrannosaurid arctometatarsus

As noted in the Introduction to this thesis, integrative studies of the musculoskeletal system provide a promising approach for revealing locomotor dynamics in extinct vertebrates. The immediately preceding section (Chapter 2) describes the osteological characteristics of the tyrannosaurid arctometatarsus. Osteology alone is of limited utility in interpreting biomechanics when considered in isolation from muscles, tendons, and ligaments (Alexander 1977, Maloiy et al.1979). The current chapter explores hypothesized interactions between tyrannosaurid metatarsals and the ligaments that bound them together.

A number of studies have explicated the locomotor role of foot ligaments and tendons and their interactions with associated bones. Elastic fore and hind foot connective elements store, return, and distribute footfall energies and forces; the plantar aponeurosis and intermetatarsal ligaments of humans (Kerr et al. 1987; Alexander 1988) and intercarpal ligaments of horses (Rubeli 1925) are noteworthy examples.

A shock-absorbing function of ligaments obtains under specific physical conditions. Ligaments paradoxically display greater strength and resiliency when subject to high magnitude, sudden loadings, such as those incurred during rapid locomotion (Frank and Shrive 1994). In animals of large body size the extensibility of ligaments increases, because their cross sectional area is lower relative to mass than ligaments of smaller animals (Pollock 1991). The ligaments of large animals store and return more elastic strain energy, which increases

locomotor efficiency and decreases strain energy transmitted to bones (Pollock 1991). Adult tyrannosaurids were notably large, ranging from 2 to perhaps 8 tonnes (Paul 1988; cross scaling of measurements from fragmentary metatarsals: UCMP V91181).

Extrapolating from research on living animals, it is reasonable to expect that certain characteristics of the limbs of large extinct animals will be suggestive of agility and high relative speed. In addition to a musculoskeletal configuration that promotes high out velocity at joints (Hildebrand 1988), it can also be predicted that the morphology of ligaments and bones will interact to promote effective dissipation and distribution of footfall forces. Because the arctometatarsus is proportionally long compared with primitive theropod metapodia, it would be fruitful to compare other aspects of its morphology with extant systems that promote rapid progression.

The imbricacy of the arctometatarsus in distal cross section (Holtz 1994a; this study) resembles the interdigitating wedge arrangement of horse carpals (Deane and Davies 1995). This suggests that interelement dynamics may be analogous in these phylogenetically disparate structures. Ligaments that connect horse carpals store and return elastic strain energy (Figure 3.1), which may reduce the potential for injury to the wrist when the animal is running (Deane and Davies 1995). By comparing the results of detailed analysis of intermetatarsal movement in tyrannosaurids with documented intercarpal kinematics of horse wrists, I tested the following hypothesis: Tyrannosaurid metatarsals and their ligaments

dynamically transmitted locomotor forces in a manner similar to that seen in the equine carpus.

Inference from comparative anatomy enables testing of the main assumption of this comparison, that ligaments similar in composition and properties to those of modern animals were present between theropod metatarsals. Ligaments connect bones at syndesmotic joints in living vertebrates (Hildebrand 1988), and relevant articular surfaces on the metatarsals of large theropods should display the rugose scarring or discrete facets indicative of ligaments in living animals. However, the presence of ligaments cannot be declaimed *a priori*; ligament attachments may be confused with tendinous insertions, and articular cartilage may cover closely articulating joint surfaces and result in sculpturing of the bone surface. I therefore refer to potential soft tissue attachment sites on bone as **osteological correlates**, or simply **correlates**.

There are three major correlates of arthrological soft tissue. Surfaces associated with articular cartilage are usually smooth, slightly raised, and often occur at weight bearing hinge joints, bathed in synovial fluid within a joint capsule (Hidebrand 1988). Ligament or tendon fixation sites may be recognized on metatarsals by two primary correlates. Rugosity marks the location of Sharpey's fibers, subperiosteal mineralized collagen fibers continuous with fibers of the attaching ligament (Woo et al. 1987). Ligaments and tendons may also attach to bone by so-called direct insertions, through a gradient of ligament, fibrocartilage, mineralized fibrocartilage, and bone. Direct insertions are indicated on a bone

surface that is smooth and slightly concave (Doglo-Saburoff 1929), and form corresponding facets on adjacent elements.

Using these criteria I sought to identify osteological correlates along intermetatarsal articular surfaces. Results of the type and extent of correlates, and the apparent range of motion between metatarsals, reciprocally contributed to an overall understanding of arctometatarsus functional arthrology.

MATERIALS AND METHODS

In order to explore interelement dynamics in the arctometatarsus and in other theropod metapodia, I took a comparative approach removed from absolute statements about performance, but which promised insight into functional variation in the pes of large theropods. For comparison, specimens of large and small arctometatarsalian forms were examined at UCMP, MOR, and RTMP. Metatarsal specimens of *Allosaurus fragilis* (MOR 693), and others at MOR and RTMP, provided control representatives of the primitive condition for theropods. The specimens (Table 3.1) were sufficiently complete and well preserved for evaluation of ligament scar position, and/or to resolve possible intermetatarsal movement.

Assessment of metapodial dynamics in tyrannosaurids themselves entailed three related lines of inquiry: 1) To ascertain the probable range of motion between elements in physical specimens, I manipulated casts of *Tyrannosaurus rex* metatarsals. 2) To evaluate intermetatarsal freedom of movement in other tyrannosaurids, I examined computed tomographic (CT) images of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* metatarsals. 3) Investigation of Table 3.1. Metatarsi examined in the assessment of variation in theropod pedal arthrology. Arctometatarsalian forms are designated with an asterisk, and precede non-arctometatarsalians. The table reveals which specimens are highresolution casts; specimens not so designated are original material. Taxon (arctometatarsus*)

Specimen number

Albertosaurus sarcophagus*	MOR 657
Albertosaurus sarcophagus*	TMP 81.10.1
Albertosaurus sarcophagus*	TMP 86.64.1
Daspletosaurus torosus*	MOR 590
Gorgosaurus libratus*	MOR 657
Gorgosaurus libratus*	TMP 94.12.602
Tyrannosaurus rex*	LACM 7244/23844 (cast TMP 82.50.7)
Tyrannosaurus rex*	MOR 555
Tyrannosaurus rex*	UCMP V80094-137539
Ornithomimidae*	TMP 87.54.1
Troodon formosus*	MOR
Elmisaurus sp.*	TMP 82.16.6
Chirostenotes pergracilis*	NMC 2367 (cast TMP 90.4.5)
Deinonychys antirhopus	MOR 693
Saurornitholestes langstoni	TMP 80.121.39
Allosaurus fragilis	MOR 693
Allosaurus fragilis	UUVP 6000 right (TMP casts)
Allosaurus fragilis	UUVP 6000 left (TMP casts)
Sinraptor dongi	IVPP 10600 right (TMP casts)
Sinraptor dongi	IVPP 10600 left (TMP casts)

intermetatarsal dynamics in these tyrannosaurids required evaluation of soft tissues in the arctometatarsus, and the comparative context of a nonarctometatarsalian taxon. In order to assess distribution and extent of possible intermetatarsal ligaments in tyrannosaurids and in the primitive form *Allosaurus*, I identified and measured osteological correlates of soft tissues. The details of all three methodologies are described below.

Materials and methods for physical manipulation of Tyrannosaurus rex casts

Casts of *Tyrannosaurus rex* metatarsals from the left pes of LACM 7244/23844 (TMP casts: 82.50.7) were positioned in proper articulation, and wrapped with elastic bands. 0.75 meter rubber and polyester fiber bungy cords of low stiffness were stretched and wound twice around the casts at their proximal and distal ends, tight enough for the ends to be secured together by their plastic hooks. Figure 3.2a diagrams the experimental setup, with larger cords shown for clarity.

The casts were positioned and manipulated several ways in order to investigate proximal and distal freedom of intermetatarsal movement. Method 1, described below, facilitated assessment of possible movement of the proximal part of MT III. Methods 2-4 revealed the range of motion of the distal parts of the metatarsals relative to each other.

 The distal part of the metatarsus was placed on a laboratory bench, cushioned on a thin foam packing sheet. The posterior (plantar) ginglymous surfaces of all three elements were positioned face down, and I supported the proximal end. This was repeated with the proximal anterior surface face down.

- 2. I placed the proximal portion of the metatarsus on the bench with the anterior surface down (again resting on a foam packing sheet), and supported the distal end first by the third metatarsal and then by both outer metatarsals. I manipulated the metatarsals slightly to evaluate constraints and freedom of movement.
- 3. The proximal end of the metatarsus was placed on the bench and cushioning sheet, with the posterior surface down, and I supported the specimen by the third metatarsal. Rotating the metatarsus about its fixed proximal end revealed the passive displacement of MT II and MT IV relative to MT III, with the metatarsus in various positions, ranging from 0 to –90 degrees from the horizontal. (Some of these positions are shown in the silhouettes in Figure 3.9.)
- 4. The entire metatarsus was set on the bench and packing sheet. Taking care not to apply medial or lateral pressure, I pushed down on the dorsal surfaces of MT II and MT IV about 70% from their proximal end. I then lifted the distalmost portion of MT III. This showed the behaviour of the outer metatarsals when a greater dorsally directed torque was applied to the distal part of MT III than to the distal ends of the other metatarsals.

Materials and methods for CT scanning of tyrannosaurid metatarsals The methods described above apply to overall intermetatarsal movements. The topographical and likely functional complexity of the arctometatarsus compelled analysis of movement evident in cross sections at multiple transverse and longitudinal transects. As in clinical practice, the most common nondestructive technique for macroscopic palaeontological sectioning is computed tomographic (CT) scanning.

Proper CT reconstruction of fossils offers a wealth of visual data for hypothesis testing. For instance, imaged cross sections through theropod metatarsals allow analysis of potential intermetatarsal movement in hundreds of sampled transverse planes. When a skilled CT technician has reconstructed the elements in three dimensions, the entire metatarsus may be viewed in arbitrary oblique, sagittal and frontal sections as well. Sections in any plane are viewable in rich anatomical context. Part of the specimen reconstruction can be removed, and the remainder of the specimen beyond the visible plane of section will remain restored in 3D, with the correct orientation for a given viewing angle. Overall, CT scanning provides a wide range of options for analysis and visualization of the arctometatarsus.

In order to maximize the information from CT scanning and post-processing visualization techniques, particular care was taken in specimen choice and preparation. TMP 94.12.602 is a partial skeleton of *Gorgosaurus libratus* from the Dinosaur Park Formation (Late Campanian) of Dinosaur Provincial Park, Alberta. The specimen has a complete right metatarsus that has not been disarticulated through taphonomy or preparation. This specimen is undistorted, has the distal tarsals in place, and is intermediate in length and robustness between metatarsi of subadult *Albertosaurus sarcophagus* and adult *Tyrannosaurus rex* (as

revealed through observation and measurements for Principal Components Analysis). For these reasons TMP 94.12.602 was deemed a suitable compromise for functional extrapolation to other tyrannosaurids.

CT scanning of an ideal specimen may still be undone by deficiencies in technique. Proper 3D reconstruction, and interpretation of cancellous bone trabeculae and large scale compact bone vascularization, is often hindered in CT studies by X-ray diffraction and scattering artifacts. The problem can arise from interjection of dense, X-ray opaque material, but more often from the high density gradient of the air-bone interface. Immersion of bones in water (problematic with fossils, but inevitable with humans), or encasement in clay, will alleviate this phenomenon (Glenn Daleo, pers. comm).

With these contingencies in mind, specimen preparation for CT commenced following transport from RTMP to the Radiology Department, Children's Hospital and Health Center of San Diego, California. Plasticine lent by Calgary, Alberta sculptor Brian Cooley, and purchaced at Aaron Brothers Art Mart (Temecula, California), was applied to the entire surface of the specimen to a depth of 2.5-4 cm. The metatarsus had to be carefully lifted from its foam cradle to envelop it in clay on all sides. For future orientation of slice images in a computer aided design program (if necessary), three parallel balsa wood dowels (70 cm) were incorporated into the clay to act as fiduciary markers. Height of the dowels was equilibrated at either end to within +/- 0.5 mm by measuring with a ruler positioned perpendicular to a level surface. The dowels did not interfere with CT or subsequent imaging.

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Once prepared, TMP 94.12.602 and its foam cradle were placed on a General Electric CT scanner. The combination of the breadth of the x-ray impulse normal to the long axis of the metatarsus, the distance the specimen moved between scans, and overlap of breadth of successive impulses, contrived to sample 297 continuous slices. The samples had a thickness of 2 mm with slice intervals of 1 mm, and the overlap ensured that there were effectively no interslice gaps. Scanner output was configured to 140 kVp and 170 mA, the technique settings that produce the best readings from dense bone. Density readings were sent to a G.E. CEMAX medical imaging console, and slice image files were output onto hard copy transparency and DAT tape.

With the data in hand, Mr. Daleo reconstructed the metatarsal voxel data into three dimensions using density detection and stacking algorithms. These reconstructions were further manipulated, viewed, and printed in various orientations for study.

Additional CT scans of an *Albertosaurus sarcophagus* metatarsus (TMP 81.10.1) were performed at the radiology department of Foothills Hospital in Calgary, Alberta, on a Toshiba CT scanner. This specimen had been drilled along its plantar surface in preparation for display, and affixed to a metal frame. The disparity of densities between bone and metal made 3D reconstruction problematic, but scout image scans (at 120 kVp and 40 mA) revealed that articulation surfaces were undistorted. Scanning proceeded at 120 kVp and 120 mA; a total of 273 sections were imaged, effectively at 2mm thickness with no interslice gaps. The images were output onto transparencies.

The metal frame caused diffraction artifacts, which manifested as radiating streaks on the image. To surmount this problem, the transparency printouts were digitized for image processing. I scanned them on a long-bed Relisys Avec Color Office 2400 scanner into Adobe Photoshop 3.0 for Macintosh, using transmitted light from an inverted Wolf X-Ray Corp. light table placed on the scanner bed. Adjustment of contrast in Photoshop minimized the artifacts to a satisfactory extent. From the cleared images I could easily evaluate the shape of intermetatarsal articulation surfaces, and possible relative movement, in a given plane of section.

Materials and methods for assessment of osteological correlates

In order to ascertain the distribution and extent of osteological correlates on theropod metatarsals, I assessed the presence of relevant attachment sites and measured the probable area of each attachment. I measured the area of the correlates only when their extent could be precisely determined. Likely tendon or ligament correlates were identified on specimens in a satisfactory state of preservation, using the criteria of rugosity and delineated faceting outlined above. Surfaces had to be continuous with cortical bone that had not been diagenetically eroded; otherwise the surface of infilled spongy bone might be mistaken for rugosity. This consideration curtailed the sample size, but vagaries of preservation warranted caution. Problematic taphonomic degeneration was not present on the metatarsals ultimately chosen for area measurement.

Surface areas of osteological correlates were measured on specimens of Albertosaurus sarcophagus (MOR 657), Allosaurus fragilis (MOR 693),

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Daspletosaurus torosus (MOR 590), and Tyrannosaurus rex (MOR 555). The bones were wrapped in plastic cling wrap, and attachment surface areas traced with a water-based marking pen. This facilitated area measurement of complexly contoured surfaces. The cling wrap was removed from the bone, pulled gently taut, and smoothed with a ruler. The markings were then retraced onto white paper, and scanned in greyscale at 150 dpi on a Relisys Avec Color Office 2400 digitizer into Adobe Photoshop 3.0 for Macintosh. The outlines were filled to a uniform grey with Photoshop's color picker, paintbucket fill, and magic wand color selection tools, to facilitate area measurement. To maintain proper scaling for measuring areas, the physical size of the images (in pixel and corresponding physical height and width) was never altered before measurement. The scans were saved at their original size in TIFF format with Macintosh byte order.

From these scans, I determined the areas of the representations in cm², using NIH Object-Image for Macintosh software from the United States National Institutes of Health. After importing the image, I chose Threshold under the Options menu to render a 2-bit image, set the scale to cm (Set Scale, under the Analyze menu), and activated the Measure option under the Analyze menu to measure the area.

The average of apparent attachment areas on adjacent bones was used to approximate the cross sectional area of intervening soft tissues. A disarticulated MT IV was not present in MOR 555. To estimate the areas on that bone, first the smaller ratio was found between MT IV and MT III in the other tyrannosaurids. This ratio was then multiplied by the corresponding MT III area in MOR 555.

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RESULTS

Intermetatarsal movement

1. Physical manipulation of *Tyrannosaurus rex* casts.

Proximally, movement is greatly constrained by the hooked cross section of MT III (Figure 2.7), and its articulation with anterolateral and posteromedial projections of MT II and MT IV, respectively. Movement is less restricted distally. Figure 3.2:b shows the potential movement determined with the *T.rex* casts. The results for each manipulation method are described presently.

The distal portion of the third metatarsal is free to move anteriorly. When the anterior face of the metatarsus is parallel with the ground, only the elastic bands prevent this portion of MT III from pivoting towards the floor, with its center of rotation at the anterior clasped articulation.

When the posterior surface of the metatarsus faces the ground and the distal and proximal parts of MT III are fixed in position, the distal portions of MT II and MT IV slide ventrally and towards the centerline of MT III. MT II slides in a straight line along its articular surface with MT III; MT IV slides in more of an arc along its corresponding surface.

When the posterior surface of the metatarsus again faces down, as just described, but with MT II and MT IV fixed proximally and distally, the same medial sliding motion occurs when the distal part of MT III is forced upwards and the bands stretch. As force is released on MT III, the bands recoil and the metatarsals return to their original articulation positions.
2. Freedom of movement inferred from *Gorgosaurus libratus* and *Albertosaurus* sarcophagus CT scans.

These results show no gross variation in potential movement among the three metatarsi. The CT scanned specimens show the same proximal interlocking morphology as that described for *T. rex.* Figure 3.3 shows this articulation in *G. libratus* (TMP 94.12.602). Cross sections along the metatarsus reveal that the distal articulation between MT II and MT III always slants ventromedially at the same angle. This indicates that displacement along this articulation will be in one plane, a motion identical to that possible in the physical model (see results for the cast manipulations above). By contrast, the MT IV-MT III articulations in the cross sections are not always in a straight line, and the overall angle of the articulation varies with cross section. This corroborates the inference that motion along this articulation would transcribe an arc in the metatarsi of all three tyrannosaurids (Figure 3.4).

Osteological correlate reconstruction

The following intermetatarsal osteological correlates for soft tissues were identified. Rugosity indicating Sharpey's fibers occurs at proximal articular surfaces in specimens of tyrannosaurids (Figures 3.5-3.8), and in *Allosaurus* (Figure 3.9). Smooth articular facets extend the MT III-MT II articulation somewhat in *Allosaurus* (Figure 3.9). Indications of Sharpey's fibers are most striking along the distal articular surfaces of MT III and MT II in large

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tyrannosaurids (Figure 3.5), but are not present at this locations in *Allosaurus* (Figure 3.9). A faceted distal MT III-MT IV articulation occurs in tyrannosaurids (Figures 3.6-3.8), but is entirely absent in *Allosaurus*, in which MT IV shows pronounced lateral angulation (Figure 3.9).

Figures 3.6-3.9 display the shape of all identified scars, in reconstructions of the initial tracings. Proximal scars are subtriangular in all assessed theropods, but in *Allosaurus* are long proximodistally relative to the length of the metatarsus. In all three tyrannosaurids, distal articulations are long and taper proximally. The average areas of adjacent distal scars are quite extensive in the tyrannosaurids (Table 3.2). The average distal scar area exceeds the average proximal area by 1.5728 in the *Daspletosaurus* specimen (MOR 590), 1.4029 in *Albertosaurus* (MOR 657), and by a factor of 1.4666 in the *Tyrannosaurus* metatarsus (MOR 555). Table 3.2 presents individual and average areas of intermetatarsal soft tissue correlates in all specimens.

DISCUSSION

Implications of articulation anatomy

The results indicate correlates of soft tissues present on large theropod metatarsals. However, the hypothesis that these are ligament attachment sites must first be tested. Apparent ligament sites must be differentiated from tendon attachments through phylogenetic inference (Bryant and Russell 1992, Bryant and Seymour 1990, Witmer 1995) and mechanical considerations. The metatarsus is fused in modern theropods (Gauthier 1986), which obviates extant Table 3.2. Surface areas of intermetatarsal osteological correlates in large theropods. Osteological correlate areas in *Allosaurus fragilis* (MOR 693), *Albertosaurus sarcophagus* (MOR 657), *Daspletosaurus torosus* (MOR 590), and *Tyrannosaurus rex* (MOR 555). Areas are in cm². Areas of proximal correlates are designated as "Prox.," and distal correlates as "Distal." The last row shows the ratios of distal to proximal areas. The convention for naming the metatarsals and their respective correlate areas is as follows:

MT III-II:II = articulation between Metatarsals III and II; surface of Metatarsal II MT III-II:III = articulation between Metatarsals III and II; surface of Metatarsal III MT III-IV:IV = articulation between Metatarsals III and IV; surface of Metatarsal IV MT III-IV:III = articulation between Metatarsals III and IV; surface of Metatarsal III

Area in cm ²	A fragilis MOR 693	Ditorosus MOR 590	A sarcophagus MOR 657	Tire+ MOR 555
Prox.: MT III-II:II	31.52	60.33	76.28	139.15
Prox.: MT III-II:III	72	56.49	61.47	116.01
Prox.: MT III- II:ave.	52.11	58.41	68.875	127.58
Prox: MT III-IV:IV	17.19	64.03	99.56	166.36
Prox.: MT III- IV:III	20.39	50.85	67.8	132.12
Prox: MT III- IV:ave.	18.79	57.44	83.68	149.24
Distal: MT III-II:II		99.91	114.15	220.48
Distal: MT III-II:III		93.76	107.09	168.46
Distal: MT III- II:ave.		96.835	110.62	194.47
Distal: MT III- IV:IV		85.1	99.66	203.87
Distal: MT III- IV:III		85.64	107.14	219.17
Distal: MT III- IV:ave.		85.37	103.4	211.52
Ratio of average correlate areas: distal/proximal	0 (no distal correlates)	1.5728	1.4029	1.4666

Specimen

phylogenetic bracketing (Witmer 1995) as a means of inferring intermetatarsal ligaments in extinct forms. Inference of soft tissues is still possible with broader phylogenetic comparison and extrapolatory inference (Bryant and Russell 1992), as discussed in Chapter 1.

Ligaments connect metatarsals generally in tetrapods, but muscles and tendons do not normally occur between weight bearing metatarsals. Close conformity of articular surfaces in theropods argues against the neomorphic presence of muscles; negligible fiber lengths would prevent the muscles from performing positive work. In contrast to the rarity of muscles and tendons, proximal ligaments are common between metatarsals (Kerr et al. 1987; McGregor 2000). Amongst reptiles, ligaments with oblique distolateral angulation are present in the metacarpus and metatarsus of lizards (Landsmeer 1981; McGregor 2000). The presence of oblique deep ligaments in lizards does not allow bracketing for homologous ligaments within the theropod metatarsus. However, it does show that ligaments of similar angulation to that hypothesized for the arctometatarsus are mechanically feasible. Overall it may be concluded that bony correlates for intermetatarsal articulating elements indicate ligaments, and not tendons.

The interpretation of osteological correlates as ligament scars circumscribes hypotheses of arthrological dynamics within the arctometatarsus. Soft tissue anatomy, coupled with results for range and direction of movement described above, suggests the following model for intermetatarsal kinematics.

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Kinematic model of the tyrannosaurid arctometatarsus

Results from the manipulation of computer and physical models of metatarsi of *Gorgosaurus libratus* and *Tyrannosaurus rex* reveal the likely general pattern of movement through the ground contact (stance) phase of the step cycle (Figures 3.10, 3.11a-e, 3.12).

- 1) The foot pads ventral to the phalanges would contact the substrate initially. Ground-reaction forces would transfer to the metatarsals first across the metatarso-phalangeal joints and then the portions of the foot pad ventral to the respective metatarsals. (This sequence has been corroborated through observations of domestic chickens and ostriches, in Rainbow, California.)
- 2) Because metatarsal III (MT III) is longest, the ground-reaction force would act upon the longest moment arm from the mesotarsal to the phalangeal joints. This torque differential would displace MT III anterodorsally relative to metatarsals II and IV (MT II and MT IV). Fore-aft rotation of the proximal portion of MT III, as suggested for the small arctometatarsalian *Troodon inequalis* (Wilson and Currie 1985), was not possible in tyrannosaurids (Figure 3.3). Instead, the clasped proximal articulation between metatarsals would serve as a pivot point for distal rotation of MT III.
- 3) Crucially, forces from this differential loading and displacement pattern would stretch distal intermetatarsal ligaments. The angulation of metatarsals, and orientation of ligaments, would draw the distal portion of the lateral metatarsals together ventrally, and towards the midsagittal plane of the third metatarsal (Figure 3.12).

4) Forces from anterior displacement of MT III, which stretched intermetatarsal ligaments in the manner described above, would decrease as the metatarsus became vertical and parallel with the ground-reaction force. In this position, ground-reaction loadings on MT III would be transferred laterally via MT II and MT IV to the condyles of the astragalus (Wilson and Currie 1985, Holtz 1994a). Tensional loading on intermetatarsal ligaments would mediate the energy transfer, as shown in Figure 3.13.

This pattern of movement has several implications. The distal arctometatarsus would become more unitary under high initial footfall loadings (Figure 3.12). In effect the metatarsals would "splay" laterally and medially only as forces lessened, returning to their unloaded configuration.

Upon strongly oblique or torsional footfalls, ligaments and the imbricate distal cross section of the metatarsals (Figure 3.14) would strongly arrest interelement shear. Potentially damaging torsion of the metatarsus would be induced during abrupt turns in which torque was insufficient to overcome friction between the foot pad and the ground. The plantar angulation between metatarsals would ensure that torsional loadings were transferred from one metatarsal to the next (Figure 3.14a), and would obviate anteroposterior shear. The large cross sectional area and consequent stiffness of distal intermetatarsal ligaments (Figures 3.5-3.9; Figure 3.14b) would check lateral shearing components introduced by torsion.

I propose the appellation of **tensile** (or tensional) **keystone model** for these kinematics. Although the loading regimes are inverted, one can think of the distal

part of MT III and its ligaments as analogous to the keystone of a Roman arch, in which the central element imparts stability to the entire structure.

Comparison with the equine wrist

Several aspects of the tensional keystone model, and Holtz's complementary hypothesis of energy transference (Holtz 1994a), conform remarkably with the functional morphology of the advanced equine carpus. For example, the horse carpus attains high aggregate interelement surface area, with the development of wedge-like amphiarthroses and a full complement of elements (Figure 3.15). High surface area decreases pressure impinging on any one carpal surface and pressure transmitted to the radius (Bourdelle and Bressou 1972). In the arctometatarsus distal ligaments and the distal plantar angulation of elements increased total articulation surface area and ligament cross section (Figure 3.5-3.9; Table 3.2), which probably conferred a similar benefit.

Rubeli (1925) demonstrated an additional advantage to the wedge-andligament morphology of the horse carpus. The horse carpus has dorsal ligaments on the anterior surface and deep interosseous ligaments between carpals (Figure 3.15b and c). Interosseous ligaments transduce sudden compressive loadings into a collectively longer period of elastic loadings, reducing the rate of strain. Ligaments in the arctometatarsus may have mediated the transfer of compressive forces to the astragalar condyles (Holtz 1994a) in a similar manner (Figure 3.13). Horse interosseous carpal ligaments stretch and rebound under high momentary loadings (Figure 3.16a and b; Rubeli 1925), and the same would be expected for tyrannosaurid intermetatarsal ligaments (Figures 3.12 and 3.16c; Frank and Shrive 1994).

The shear- and torsion-resisting aspects of the tensional keystone model also find analogs in the equine wrist. Wedge-like articulations generally resist shear between horse carpals (Boening 1981). A triangular sagittal projection of the distal radius (Figure 3.15b) buffers ad- or abductional torsion (Poplewski 1936). Faces of this projection act as stop facets (Yalden 1971) against dorsomedial or dorsolateral rotation of the radial and intermediate carpals. Tyrannosaurid metatarsals and metapodial ligaments would function analogously by arresting torsional forces. Unlike the horse morphology, however, these elements would primarily buffer torsion about a midsagittal axis (Figure 3.14a).

A more fundamental distinction between horse intercarpal and tyrannosaurid intermetatarsal ligament function lies in the initial loading regime upon footfall. The horse third metacarpal, the single weight bearing element of the anterior metapodium, transfers compressive forces directly to the carpus (Figure 3.16a; Rubeli 1925). The carpus acts as a shock absorber for the compressive ground-reaction force. Under the tensional keystone model, dorsally directed components of the ground-reaction force load the three tyrannosaurid metatarsals unevenly (Figures 3.12 and 3.16c). The third metatarsal is displaced anteriorly relative to MT II and MT IV; differential forces stretch intermetatarsal ligaments, which rebound elastically to draw the distal portions of the outer metatarsals together. This resulting distal unification does not have a counterpart in the horse carpus.

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Tensional keystone dynamics may explain the benefit of retention of multiple elements in the tyrannosaurid arctometatarsus, which contrasts with fused metapodia in ratites and in horses, bovids, cervids, camelids, giraffids, and other ungulates. A system of three bones and elastic ligaments may have imparted resilience and enhanced collective strength, properties diminished in a single metapodial element. The retention of multiple metapodial elements as a stay against torsion may be paralleled the Patagonian cavy, an agile cursorial rodent whose mesaxonic metapodia subtend an arch (personal observation). However, the metatarsals of the cavy lack the extremity of plantar angulation seen in the arctometatarsus, so the analogy is superficial and remains to be tested biomechanically.

A dynamically robust metatarsus is perhaps selectively logical in tyrannosaurids, which are much larger than most classically cursorial ratites and ungulates. Giraffes are potentially problematic to this view, because they are closer in mass to tyrannosaurids and have fused metapodia. As quadrupeds, giraffes have the advantage of lower loadings on the metapodia when trotting because the load is shared by two limbs, although forces on each metapodium when galloping would be higher because the duty factor is low (Alexander et al. 1977). Giraffes are also not as fast as might be expected from the extreme elongation of their limbs. The energy-absorbing metapodium of adult tyrannosaurids conceivably enabled them to outmatch giraffes in certain maneuvers or in linear speed, but such speculative transtemporal comparisons are unproductive. The preceding discussion derives from an adaptationist perspective. In contrast, phylogenetic and developmental contingency, rather than selective canalization, can also explain the persistence of separate elements in the tyrannosaurid metatarsus. Giraffids, including the modern giraffe and okapi, inherited their metatarsal morphology from less specialized artiodactyls. Ratite birds inherited fused metapodial elements from their avian ancestors, and selective pressures for cursoriality need not be invoked to explain their ankylosed morphology. With this caveat in mind, I now explore arctometatarsus function in the context of performance and phylogeny.

Comparative phylogenetic and functional implications

The tensional keystone model differs from kinematics likely evident in the foot of *Allosaurus* or other theropods with three largely autonomous metatarsals. As with humans (Kerr et al. 1987), footfall loadings would cause their outer metatarsals to splay beyond their resting orientation, essentially spreading the foot apart. During deviations from linear locomotion, metatarsals would experience increased bending loads individually, rather than as part of a single structure as predicted for the arctometatarsus (Figure 3.12). Results from Chapter 2 show that broad-footed theropods are not uniform in metatarsus morphology. None of these animals, however, displays plantar constriction of MT III consistent with distal unification of the metatarsals, which would occur in the arctometatarsalian pes under the tensional keystone model. Chapter 2 also outlines metatarsus diversity in arctometatarsalian coelurosaurs. The probable multiple origin of the arctometatarsus (Holtz 1994b, 1996; even more homoplasy is postulated by Sereno 1999) suggests it was not a legacy morphology, which was simply retained with no contemporary utility. Instead it may have conferred a selective or performance benefit. Developmental and immediate functional advantages are not mutually exclusive. The correlation between a constricted third metatarsal and proportionally long metapodium (Holtz 1994a) suggests a developmental correspondence. Unfortunately developmental hypotheses of this type will be tenuously *ad hoc*. Perhaps the ontogenetic program for lengthened separate metatarsals reciprocally invoked proximal and plantar constriction of MT III in coelurosaurs. Yet tensional keystone dynamics evince more for the tyrannosaurid arctometatarsus than simply a developmental contribution to the lengthened pes.

Another possibility is that the tensional keystone morphology conferred heightened agility for a given body mass. As such, the arctometatarsus may have been broadly analogous to the stiffened tails of dromaeosaurid coelurosaurs (Ostrom 1969), which have been suggested as dynamic stabilizers. Because there was no anteriorly propulsive component to the elastic rebound of ligaments, third metatarsal constriction did not directly avail increased speeds. Instead, the unifying and shear-resisting properties of the arctometatarsus may have absorbed forces involved in linear deceleration, lateral acceleration, and torsion more effectively than the feet of other theropods. These forces are limiting factors to combat performance in humans (personal observation in open hand and weapons sparring), and the arctometatarsus may have imparted momentarily excessive construction (Gans 1974) for selectively crucial behaviors, such as predation or escape.

However, while the potential may have been present, the employment and utility of increased agility in tyrannosaurids is no more directly testable than ontogenetic hypotheses. As with the connection between cursoriality and predation in theropods (Carrano 1998), alternate hypotheses must be explored. In addition, the tensional keystone model cannot be taken to indicate that tyrannosaurids behaved more dynamically than *Allosaurus*. Whether tyrannosaurids used the potential for higher maneuverability during prey capture, and how close these animals operated to safety limits, are untestable by observation. Consequently definitive statements about comparative agility in theropods are premature. However, the tensional keystone model demonstrates, in one aspect of hind limb function, potential benefits to agility in large arctometatarsalians. I explore the selective implications of increased agility below (see Chapter 5).

CONCLUDING COMMENTS

Although the sample size of large, rare fossil organisms is archetypically small (Kemp 1999), the morphological evidence outlined above suggests significant dynamic differences between the metatarsi of tyrannosaurids and allosauroid carnosaurs. The tensional keystone model proposes that orientation and extent of ligaments in the arctometatarus increased resistance to dissociation over that of other theropods, and yet allowed resiliency otherwise diminished in metapodia reduced to a single element, as in horses. Further calculations are necessary to test these hypotheses. In the following chapter, I subject the metatarsus of the tyrannosaurid *Gorgosaurus libratus* (TMP 94.12.602) to a finite element analysis, which quantifies stress distribution and metatarsal displacement suggested by the tensional keystone model.

Figure 3.1. Schematic representation of several elements of the left equine mesocarpal joint. Compression (yellow arrows) on the radius (R) and third carpal (C3) causes the wedge-like dorsal surface of C3 to laterally displace the radial and intermediate carpals (Cr and Ci). A portion of the compressive force is translated into tensile loading (green arrows) on the interosseous ligament between Cr and Ci.



Figure 3.2. Freedom of intermetatarsal movement determined in cast left metatarsus of *Tyrannosaurus rex* (LACM 7244/23844: cast TMP 82.50.7).

a. Diagram of experimental setup. The metatarsus was wrapped in bungy cords to simulate a mechanism of elastic articulation.

b. Arrows show general type of motion. MT II (left) slides in one plane, while MT IV (right) translates along an arc. MT IV was incorrectly restored proximally, but this has no effect on the interpretation of distal movement.



b

a



Figure 3.3. CT reconstruction of right *Gorgosaurus libratus* arctormetatarsus (TMP 94.12.602) in proximal view near ankle. Proximal expansion of MT III at the exposed cross section is outlined in white. Anterior and posterior projections of the outer metatarsals constrained this portion of MT III from fore-aft rotation. This partially clasped morphology functioned as a pivot point, enabling ligamentdamped displacement of the distal third metatarsal.



Figure 3.4. Freedom of intermetatarsal movement, as revealed by CT scans of a right metatarsus of the tyrannosaurid *Gorgosaurus libratus* (94.12.602). Arrows show a sliding motion evident between MT II and MT III, and a slight rotational motion between MT IV and MT III.



Figure 3.5. MT II (left element) and MT III (right element), from a left metatarsus of *Tyrannosaurus rex* (LACM 7244/23844: cast TMP 82.50.7). Green indicates ligament scars, on MT II below and MT III above, sloping away from the plane of the figure. The portion of either bone that lies anterior to the other in a given region is rendered transparent.



Figure 3.6. Osteological correlates on the left arctometatarsus of the tyrannosaurid *Albertosaurus sarcophagus* (MOR 657). For clarity these are mapped onto an articulated right metatarsus of *Albertosaurus sarcophagus* (TMP 81.10.1) with MT III recessed to show distal correlates on outer metatarsals. These and proximal scar locations are shown in green. Grey-filled tracings show the shape and size of correlates, and red arrows and metatarsal numbers (II, III, and IV) indicate the corresponding metatarsal for each scar.



Figure 3.7. Osteological correlates on the right arctometatarsus of *Daspletosaurus torosus* (MOR 590). For clarity scars are mapped onto an articulated arctometatarsus of *Albertosaurus sarcophagus* (TMP 81.10.1) with MT III recessed to show distal correlates on outer metatarsals. These and proximal scar locations are shown in green. Grey-filled tracings show the shape and size of correlates, and red arrows and metatarsal numbers (II, III, and IV) indicate the corresponding metatarsal for each scar.



Figure 3.8. Osteological correlates on the right arctometatarsus of the tyrannosaurid *Tyrannosaurus rex* (MOR 555), with the articulated left metatarsus shown for clarity. Locations of scars are identical to those on preceding tyrannosaurid figures. Grey-filled tracings show the shape and size of correlates, and red arrows and metatarsal numbers (II, III, and IV) indicate the corresponding metatarsal for each scar.



Figure 3.9. Osteological correlates on the left metatarsus of *Allosaurus fragilis* (MOR 693). For clarity these are mapped onto an articulated left metatarsus (UUVP 6000). Locations of scars are shown in green. Grey-filled tracings of the scars show the shape and size of correlates, and red arrows and metatarsal numbers (II, III, and IV) indicate the corresponding metatarsal for each scar. Note the distally divergent MT IV (right) and MT II (left) metatarsals. Footfalls of great lateral or medial offset, respectively, would disproportionately load these elements



- Figure 3.10. Step sequence of *Gorgosaurus libratus* metatarsus in lateral view, showing forces acting upon bones and ligaments during linear locomotion. Metatarsal images are not free body diagrams, because forces are not in equilibrium. Silhouettes depict the tyrannosaurid at appropriate locomotory stages. Green=tensile forces on ligaments. Yellow=External force resultants on bone. Red=muscle forces.
 - a: prior to footfall, ligaments suspend metatarsus and toes; flexor muscles draw toes forward.
 - b-e: Differential forces on Metatarsal III and outer metatarsals stretch intermetatarsal ligaments, which return elastic strain energy. For clarity, displacement of MT III is exaggerated, and articulating bones and bending components are omitted.



Figure 3.11a-e. The metatarsal reconstructions and force vector arrows shown and described in Figure 3.10 are displayed on successive pages. Note that displacements are exaggerated for clarity. By flipping through these pages from a to e, the reader can view the hypothesized tyrannosaurid footfall kinematics as an animation sequence.



a








Figure 3.12. CT reconstructions of right Gorgosaurus libratus arctometatarsus, showing tensional keystone model of stance phase kinematics. Letters correspond with the step cycle positions in Figure 1.

- a. Resting configuration prior to footfall.
- b. When the foot pads beneath the metatarsals come into full contact with the substrate, the longer central Metatarsal III (MT III) is displaced dorsally (white arrow) by ground-reaction forces greater than those on MT II and MT IV (yellow arrows). This force differential imposes tension on intermetatarsal ligaments (green arrows).
- c. Ligaments draw outer metatarsals towards each other (white arrows), as elastic strain energy stored in the ligaments is returned.



а

þ



Figure 3.13. Ligament contribution to vertical energy transference by the tyrannosaurid MT III (Holtz 1994a; left *Tyrannosaurus rex* metatarsus LACM 7244/23844: cast TMP 82.50.7). Yellow arrows indicate resultants of compressive force; the green arrow indicates tension on ligaments. Compressive loading on MT III stretches stiff ligament fibers oriented along the long axis of the metatarsus. The ligaments transmit this force to MT II, which is pulled dorsomedially. MT II thus transmits its own compressive loadings, and those of MT III, across the mesotarsal joint. MT IV also transfers loadings from MT III, but is omitted here for clarity.



Figure 3.14. Torsional loading transfer within the *Gorgosaurus libratus* arctometatarsus (right: TMP 94.12.602).Yellow arrows indicate torsion.

- a: Torsion translated into compression impinging on adjacent metatarsal.
- b: Anterior components (white) offset from compressional translation would cause anterolaterally directed tension on intermetatarsal ligaments (green).





Figure 3.15. Anatomy of the equid carpus (all images after Sisson and Grossman 1953).

- a. Lateral view of left horse carpus, with pisiform (accessory carpal) to the right. This view shows the striking interlocking wedge arrangement of the proximal intermediate carpal (Ci) and the distal third and fourth carpals (C3 and C4).
- b. Anterior view of left horse carpus, showing wedge like articulations between carpals and dorsal ligaments connecting them.
- c. Frontal section in anterior view of right horse carpus. Interosseous ligaments are present between the radial, intermediate, and ulnar carpals (Cr, Ci, and Cu)



Figure 3.16. Comparison of loading regimes on bones and ligaments of the equid carpus and tyrannosaurid arctometatarsus. Tyrannosaurid intermetatarsal ligaments are analogous in position and function with the interosseous ligaments of the horse carpus.

- a. A sudden compressive load (yellow arrows) is applied to the equid carpus. Modified from Sisson and Grossman (1953).
- b. This loading causes movement of carpals along their wedgelike articular surfaces, imposing tensile stresses (green arrows) on interosseous ligaments (shown), and on dorsal ligaments. Modified from Sisson and Grossman (1953).
- c. A plurality of ground-reaction loadings (yellow arrows) are imposed upon the tyrannosaurid MT III, the central element in this diagram. Loading differentials between MT III and MT II and MT IV, respectively, cause tensile stresses on intermetatarsal ligaments.



a

b

C



CHAPTER 4: Finite element model of locomotor stress in the metatarsus of Gorgosaurus libratus (Tyrannosauridae)

INTRODUCTION

The third metatarsal (MT III) of tyrannosaurids is triangular in distal cross section. The tensile keystone hypothesis (Chapter 3) proposes that under high impulse loadings, with the metatarsus acutely angled to the substrate, the distal portion of MT III is displaced anterodorsally. Ligaments arrest this displacement, and draw metatarsals II and IV towards the plantar centerline of MT III. These loadings therefore unify the structure distally. The metatarsals are less subject individually to torsion and shear, and their collective strength is thereby increased.

A prerequisite to the tensile keystone hypothesis is the structural integrity of the proximal splint of MT III. Using beam theory equations, Holtz (1994a) found that the splint could not support body weight in large tyrannosaurids, but did not investigate the combined effects of locomotory stresses on the splint and the rest of the metatarsus. This chapter incorporates morphology, biological material properties, and loading environments of the metatarsals into a finite element stress analysis. Finite element analysis (FEA) elucidates stress and strain within constitutive bones of the arctometatarsus, and reveals the potential role of ligaments on intermetatarsal kinematics.

Finite element modeling: background and applicability to biological questions Finite element analysis determines stresses and strains within a structure by subdividing it into a finite number of shapes (elements) connected at points (nodes), and solving stress/strain equations for each node and element. The equations can be considered analogs of Hooke's Law:

(1) F=kx,

in which F is force, x is displacement, and k is a spring constant. This relationship is applied to all nodes in a finite element model by matrix equations incorporating these variables for all nodes:

(2) $\{\sigma\}=[k] \{\epsilon\}.$

In these equations { σ } is the stress matrix. Each number in the matrix reflects the force vector acting upon an element, incorporating vector sums of forces impinging on its nodes from other nodes in the system. The matrix { ϵ } represents the displacement of nodes. [k] is the stiffness matrix for an element, and includes the following material properties:

 A) Elastic (Young's) modulus: Stress σ (force/area) divided by strain ε (change in length/initial length) parallel to the imposed force.

(3) $E=\sigma/\epsilon$ Units: N/m², in pascals or gigapascals (GPa)

B) Poisson's ratio: Lateral strain divided by axial or longitudinal strain.

(4) $v = \varepsilon_{lateral} / \varepsilon_{axial}$ Units: dimensionless

Because bone is an orthotropic material, elastic modulus and Poisson's ratio vary according to the direction of loading. Non-linear finite element models, such as that presented in this chapter, incorporate all necessary values for E and v.

Forces acting upon a structure are determined for the finite element model. These forces depend on the static or kinematic hypotheses to be tested. The forces are applied to nodes on the surface of the model. Boundary conditions, which are constraints on the movement of elements and the displacement of nodes, are also applied. Some nodes, typically at one end or side of a model, are set to a boundary condition of zero displacement, as though the model is fixed to an immobile surface. Otherwise, little strain would occur at internal nodes unless tremendous energies were applied, and forces would cause the entire structure to accelerate.

Boundary conditions, forces, and material properties are entered into a finite element computer program. The program then solves the resulting systems of linear equations, typically by Gaussian elimination. While this algorithm is tenable for the solution of simple matrix equations by hand, the huge number of nodes in a finite element model necessitates intensive use of computer resources.

Finite element stress modeling has a number of practical and scientific applications. FEA is a common procedure for investigating material stresses and strains in engineering (Chandrupalta and Belegundu 1997). In modeling 3D solids, a sufficiently large number of elements approximates the continuity of the original object. The finite element method is therefore able to accurately simulate and predict stress-strain relationships in physical structures, if the correct values for material properties are supplied. FEA provides crucially accurate predictions for airframe and automotive design (Belytschko et al. 1975), and biomedical engineering (Taylor et al. 1998). The accuracy of the method thus has immediate benefits for vehicle and building safety, as well as for the development of medical prostheses.

The practicality of the finite element method has also been demonstrated for testing biomechanical hypotheses (Beaupre and Carter 1992). FEA has been successfully applied to studies of diving stresses on the shells of ammonoids (Daniel et al. 1997), stress distribution in the skulls of rodents, humans, and shoebill storks (Moss 1985, Moss 1988, Richtsmeier and Cheverud 1986, Guillet et al. 1985), and to extensive research on adaptive bone remodeling (Carter et al. 1987, Fischer et al. 1993). Simple finite element models accurately simulate experimentally measured strains, even in bones of complex shape. Using a model that incorporated a relatively small number of elements, Gupta et al. (1999) found congruence between predicted strains on the human scapula and deflections measured physically with strain gauges.

Despite its predictive power, applications of FEA have been rare in vertebrate palaeontology. Carter et al. (1992) investigated flight stresses in the humerus of the giant pterosaur *Quetzalcoatlus northropi*. Rensberger (1995) used FEA to investigate stresses on the teeth of the early horse *Hyracotherium* and the modern hyena. Jenkins (1997) employed FEA in consideration of biting stresses in gorgonopsian skulls, and Rayfield (1999) modeled biting stresses in the jaws of *Allosaurus fragilis*, incorporating estimates of muscular forces.

The complex dynamics of the arctometatarsus are an appropriate subject for finite element modeling, because the method simultaneously tests hypotheses, reveals patterns of stress distribution, and suggests further hypotheses based upon revealed stresses and strains. Finite element analysis of any structure requires consideration of material properties and loading conditions.

Material and loading regimes of the tyrannosaurid arctometatarsus

Chapters 2 and 3 describe bone and probable ligament morphologies of the metatarsus of tyrannosaurids. The right metatarsus of a relatively complete and well preserved specimen of *Gorgosaurus libratus* was CT scanned. These scans revealed the structure of the medullary cavity and distribution of compact and trabecular bone. This metatarsus was therefore chosen for finite element modeling, because its morphology can be assessed at several scales.

Material properties are best examined at the histological level. Bone and ligament tissues are broadly consistent in their respective material properties, composition, and development. Ligament consists of fibroblasts, collagen and elastin fibers, and glycoprotein ground substance, while in mature bone osteoclasts and osteoblasts remodel and secrete a matrix of hydroxyapatite within a framework of mineralized collagen fibers (Hildebrand 1988). However, specific tissue properties vary with the loading, adaptive, and ontogenetic regimes of each animal (Martin et al. 1998).

The strength of bone, for example, varies greatly according to the type of load, macrostructural properties, and histology. The cortical bone of a bovine femur is extremely strong in resisting bending and compression, with ultimate (breaking) stresses of 228.3 and 237 MPa, respectively (Cowin 1989), normalized to the long axis of the bone. In contrast, the ultimate shear stress of cortical bone is only 73 MPa. For cancellous (spongy) bone in load-bearing elements, compressive ultimate stress ranges from 2.52-17.8 MPa depending on the age and activity level of the animal, and the structure, orientation, and

collective density of trabeculae (Kuhn et al. 1989, Vahey et al. 1987). Haversian bone is somewhat weaker than primary bone, and on the microstructural level different types of osteons vary in material properties (Martin et al. 1998).

These considerations of material and functional properties must be regarded concurrently with possible loadings on the metatarsals of *Gorgosaurus libratus*. Fusion of the neural arches to the centra in the specimen TMP 94.12.602 (*G. libratus*) indicates that the animal was at or near a fully adult age when it died (pers. obs.). For the purposes of modeling, the tissue properties of the metatarsus can be considered those of a healthy, active adult animal.

Because estimated loading regimes are inextricable from force inputs for biomechanical modeling, specific locomotor conditions are addressed in the Materials and Methods section. Putative loading regimes on the arctometatarsus derive from the energy transference model (Holtz 1994a), and from the tensile keystone model (Chapter 3). These models lead to the following kinematic hypotheses, which are testable with the finite element method:

H(a): The energy transference hypothesis (Holtz 1994a): When the metatarsus was perpendicular to the substrate, stresses on ligaments would cause a transfer of loading from MT III to MTs II and IV.

H(b): The tensile keystone hypothesis: Ligament stresses within the arctometatarsus when the metapodium is at an acute angle to the substrate would cause MT II and MT IV to move posteromedially relative to the long axis of MT III.

Two analyses were run in order to test these hypotheses, using the finite element method. The first investigation assumed loading regimes with the metatarsus normal to the substrate. The pattern of resulting strain energy would serve to identify areas where energy transference by ligaments would be most felicitous, and where the maintenance of safety factors would be most critical. This analysis, therefore, tested whether the position of ligaments postulated in Chapter 3 correlates with regions of high strain within the metatarsus, and aimed to reveal regions of osteological weakness that would potentially benefit from elastic energy transfer.

With ligament position tested under the first finite element run, the second analysis incorporated a loading regime with the plantar surface of the metatarsus inclined at 50 degrees to the substrate. The model of MT III was subjected to bending loads. This analysis was designed to determine if and where in MT III bending strains were likely to be damaging. If MT III was in danger of breaking under these loads, resistance of ligaments to anterodorsal displacement of MT III, as postulated under the tensional keystone model, would serve to prevent this damage.

MATERIALS AND METHODS

As with other finite element analyses, this investigation requires four steps: assessment of the physical environment of the *G. libratus* metatarsus just after footfall; creation of a finite element model and mesh; solution of stiffness matrix equations to determine stresses and strains; and postprocessing for visualization and evaluation of results.

A. FORCE INPUTS AND MATERIAL PROPERTIES

1. Force and torque inputs

Determination of the locomotor loading regime for the metatarsus of *Gorgosaurus libratus* requires estimates or measurements of several quantities. These variables include mass, moment arms, areas across which forces are transmitted, duty factors, acceleration, and the angle of the metatarsus relative to the substrate. The rationale and methods behind these estimates are now described.

a. Mass and duty factor estimates:

The mass of this *G. libratus* individual (TMP 94.12.602) was the constant parameter that determined instantaneous forces acting upon the metatarsus. Cross scaling revealed a rough estimate of the animal's mass. Femoral lengths of closely related animals are a common comparative benchmark for estimating masses (Paul 1988, 1997; Holtz 1994, Christiansen 1999). Paul (1988) volumetrically estimated the mass *G. libratus* specimen TMP 81.10.1 at 2000 kg. The femur length (l_1) of this specimen is 88 cm, while that of TMP 94.12.602 (l_2) is 91 cm. Mass (m) is proportional to the cube of ratios of linear size (l_2/l_1):

(5) $m_2 = (l_2/l_1)^3 \times m_1$

The mass of *Gorgosaurus libratus* TMP 94.12.602 is therefore estimated at 2212 kg. This estimate may be slightly low, because many of its elements appear more robust than those of TMP 81.10.1 (Donna Sloan, pers. comm.1999). The femora of the two animals appear to be comparable in robustness, however, so the estimate is likely to be a reasonable starting point (Anderson et al. 1985).

During linear progression when an animal is moving at a constant speed, forces acting on the foot during stance phase are directly proportional to body weight (mg: mass x gravitational acceleration), and inversely proportional to duty factor (β), the fraction of time the foot spends contacting the ground (Alexander 1979):

(6) $F=\pi mg/4\beta$.

Quantities for m (2212 kg, neglecting the mass of the phalanges) and g (9.81 meters/second²) are estimated or known. The value for duty factor (β) depends upon the gait of the animal.

Because animals utilize varying gains, a specific duty factor must be estimated to determine forces germane to the problem at hand. For example, at the walk-trot transition, the minimal value for β is 0.5, because each foot is on the ground half the time. When walking, animals employ a double stance phase, and the duty factor is above 0.5. This study examines the potential effects of high stresses on the *G. libratus* metatarsus; therefore faster gaits are considered.

Running gaits, such as trotting or galloping, incorporate a ballistic suspended phase in which both feet are off the ground. The duty factor during running decreases to below 0.5. As a biped, *Gorgosaurus libratus* could not gallop, but could trot if forces and moments did not exceed safety factors for the limb bones. *Gorgosaurus libratus* probably employed gaits similar to those of bipedal modern ratites, such as ostriches (although limb proportions more closely match those of cursorial mammals: Carrano 1998). For a male ostrich running at high speed, Alexander et al. (1979) recorded a duty factor β =0.29 at a stride frequency of 2.3 Hz.

Such a low duty factor seems unrealistic for *G. libratus*, a much larger biped than the ostrich. With legs roughly twice as long as those of an ostrich, the tyrannosaurid could conceivably reach fairly high absolute speeds without recourse to a long ballistic suspended phase. Carrano (1998) and Christiansen (1999) hypothesized that large theropods were unlikely to have employed long suspended phases. These would require the inducement of high potential energies, leading to high (and potentially damaging) bending force about secondary moments when the foot returned to the ground.

These authors did not consider how energy storage by elastic tissues would decrease the rate of strain on bone and distribute footfall energies (see Discussion below). Nevertheless, the high number of unknown factors introduced by tendon elasticity, as well as consideration of bone strength (Christiansen 1999), signal caution in ascribing long ballistic periods to large theropods. A conservatively high duty factor, β =0.45, is therefore estimated for a running *Gorgosaurus libratus*.

b. Forces with the metatarsus normal to the substrate:

Substituting these quantities into equation (6): m=2212 kg, g=9.81 meters/sec², β =0.45, gives the resulting ground-reaction force F_G:

(7) F_G=37873 N

This quantity approximates the vertical ground-reaction force acting upon the foot during fast linear locomotion, when the metatarsus is perpendicular to the ground (Figure 4.1).

With the metatarsus at 90 degrees to the substrate, most of the groundreaction force would be channeled vertically through the proximal phalanges and metatarsals. The proportion of F_G channeled through a given metatarsal is directly proportional to the area of ground underneath the element.

To determine relative areas, the metatarsus of TMP 94.12.602 was inverted, and the distal surface of each metatarsal was photographed from above. A plumb bob, hanging from the camera to the visual center of each distal surface, ensured that the three elements were photographed from the same distance. The photographs were scanned, and the relative areas determined by Object-Image for Macintosh software, from the United States National Institutes of Health.

Metatarsal III accounted for 0.4 of the total area; MT II and MT IV accounted for 0.3 each. These quantities and F_G from equation 7 were substituted into the following equation:

(8) $F_{GMTx} = (F_G) (MTx\%),$

4.1 diagrams the resulting axial forces on each metatarsal:

 F_{GMTII} =(37873 N)(0.3)=11362 N F_{GMTIII} =(37873 N)(0.4)=15149 N F_{GMTIV} =(37873 N)(0.3)=11362 N. The preceding loading regime entails forces acting upon the metatarsus during locomotion that was rapid, but perhaps not strenuous enough to approach compressional safety factors of the bones. Animals impose extreme loading on their limbs during highly vigorous activities, such as decelerating rapidly with a leg fully extended, or dropping quickly onto one foot. While rare, these behaviours may have direly immediate selective consequences as the limb elements may maintain integrity or fail (Gans 1974).

In order to examine possible axial strains on the *Gorgosaurus libratus* metatarsus during such activities, a load of four times body weight (21700 N \times 4) was simulated for the model. This approximates the highest loadings that normally impinge upon the limbs of modern animals (Hildebrand 1988). Under this loading regime, equation 8 gives these force estimates for each metatarsal:

F_{GMTII}=(86800 N)(0.3)=26040 N

F_{GMTIII}=(86800 N)(0.4)=34720 N

 F_{GMTIV} =(86800 N)(0.3)=26040 N.

c. Forces and moments with the metatarsus at 50 degrees to the substrate:

During accelerations postulated under the tensile keystone hypothesis (Chapter 3), forces are likely to be higher than those during normal, rapid linear locomotion. The tyrannosaurid would experience these forces as it imparted sudden lateral and linear accelerations to its body, such as when dodging aside or pulling up short.

To simplify the model, somewhat lower forces are estimated here. Under the modeled kinematic regime, the *G. libratus* individual is quickly shifting its weight

to its right foot to prepare for a change in direction. The force on the metatarsus is therefore higher than if the leg was extended to the same angle during linear locomotion, but lower than if the animal was stopping up short or propelling itself from a standstill.

The magnitude of the force can be set to that just before the animals uses muscular forces to decelerate from a linear speed or to change direction. For simplicity the same duty factor may be assumed as for the linear progression above, but the angle will be less than 90 degrees. In walking humans, the forces of the phalanges on the metatarsals are a small percentage of the vertical ground force on these elements (Stokes et al. 1979). The stance modeled here for *Gorgosaurus libratus* entails the metatarsus at 50 degrees to the substrate, with the toes flat on the ground. This approximates the condition in humans near the push-off phase of the step. Therefore, horizontal forces of the phalanges on the metatarsals are neglected under this loading regime, although they are conceivably very important if the animal was decelerating.

Figure 4.2 is a diagram of forces on MT III experienced during this loading regime. When the metatarsus is at an angle of 50 degrees to the horizontal, all three metatarsals are in contact with the substrate through their footpads. Footpad area would be a better approximation of the proportion of mass each metatarsal bore. Probable Campanian tyrannosaurid tracks are known from the St Mary's River region of Alberta, but unfortunately were not accessible in time for this analysis. Therefore the area of ground underneath each metatarsal was

determined by using the photographic method described above, with the metatarsals held at a 50 degree angle.

Area proportions are 0.406 for MT III, and 0.297 for MT II and MT IV. Using equation (8), the resulting forces on the metatarsals at 50 degrees are therefore:

F_{GMTII}=(37873 N)(0.297)=11248 N

F_{GMTIII}=(37873 N)(0.406)=15376 N

F_{GMTIV}=(37873 N)(0.297)=11248 N.

The force on the distal end of MT III, with it inclined at 50 degrees, is the important value for this analysis. The vector components of this force (Figure 4.2) were calculated; these components were input along the z and y ordinate axes in the finite element program. It was assumed that the proximal end of MT III was held rigid by its articulations with MT II and MT IV. With boundary conditions set to zero displacement or rotation at the proximal end of the MT III, the finite element program calculated bending moments acting on the metatarsal, in order to arrive at the resulting strains.

2. Material properties

Finite element modeling can incorporate material properties of objects with non-homogeneous internal structure, such as bones with cortical and trabecular constituents, as well as structurally homogeneous objects such as ligaments. CT scans revealed that dense cortical bone is predominant in the *G. libratus* metatarsus. Cancellous bone is restricted to narrow bands near the phalangeal and mesotarsal articular surfaces, and to small regions near the proximal and distal extremities of the medulary cavities. Unfortunately, the size and shape of

elements in the finite element mesh precluded precise regional distinctions between cortical and cancellous bone. Therefore material properties for cortical bone were applied to the entire model. Values for elastic modulus and Poisson's ratio were taken from the literature (Table 4.1).

B. PREPROCESSING FOR FEA: MODELING AND MESH GENERATION

Preprocessing of data for finite element study involved constructing a 3D model from CT data, and creating a finite element continuum mesh within that model. Creation of the model entailed the use of several software packages at the University of Calgary Visualization Center, with corresponding iterations of data manipulation. The sequence of methodologies involved data transfer and preparation, curve identification and stacking, and mesh generation.

1. Data transfer

Raw data from CT scans of *Gorgosaurus libratus* (see Chapter 3) were extracted from DAT tape at the Alpha Cluster Supercomputing Center at the University of Calgary. These were transferred via FTP to Apple Power Macintosh G4 and IBM UNIX computers in the Visualization Center. The headers of the image files (including specimen and CT technique setting information) were excised. The resulting 300 images measured 512x512 pixels each, and showed cross sections through the metatarsus in transverse planes. These images were saved in uncompressed TIF format with Macintosh byte order, and were written to a CD-ROM.

2. Preparation of data for contour identification

In order to prepare metatarsal cross sectional shapes for curve detection software, the outlines of each metatarsal were selected and filled with color. Every fifth slice was sampled initially, to evaluate the potential of this sampling frequency for accurate 3D reconstruction. Object-Image for Macintosh software facilitated selection. With a standard ADB mouse, I used the point-connect lasso tool for larger curves, decreasing the spacing between points for lower-radius curves. The continuous lasso tool served for selecting very small curves, such as those subtending the medullary cavity. Holding down the shift or control keys during selection allowed additions or subtractions to selected curves. This enabled selection of the medullary cavity outline within the larger outer bone contour, and also allowed for the correction of errors and refinement of selection shape.

Because contour detection software searches for pixels of uniform color value, each metatarsal was assigned a different fill color. The Graphic Interchange Format (GIF) color palette provides only 256 colors. The limited GIF color space ensured that precise colors were applied to respective metatarsals in each image. The Object-Image's Fill command applied chosen colors to spaces bound by selected curves. The second metatarsal was assigned red, the third metatarsal green, and the fourth metatarsal was filled with blue. The red-greenblue color values were checked using the eyedropper tool from Adobe

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Table 4.1. Material properties of bone in *Gorgosaurus libratus*, estimated from tissue properties of modern vertebrates. Values for elastic modulus and Poisson's ratio of bone are from Cowin (1989).

	BONE	
	Corticai	Cancellous
Elastic modulus		
(GPa)		
Ex	11.7	0.491
Εy	11.7	0.491
Ez	20.4	0.491
Poisson's ratio Vzx,y	0.36	
V _{xy,z}	0.42	

Photoshop 3 for Macintosh, to ensure that the same hue was applied to each respective metatarsal cross section.

The results were 57 images, saved as GIF format, with metatarsal cross sectional outlines filled with color. MT II, MT III, and MT IV were selected out of each image, and pasted into respective files. The new files had the same pixel dimensions as the originals, and the respective metatarsal images remained in the same position as in the original image. This meant the cross sections of the metatarsals would remain in the same relative position when the images were stacked for 3D reconstruction, and would maintain the same spatial relationships as the original bones. Images of individual metatarsal cross sections were also saved in GIF format.

Sets of individual images for each metatarsal were then concatenated into three large files, containing data for all image slices of each respective metatarsal. These were saved as raw data format files, with names containing as much information as possible, to facilitate input for subsequent processing. For instance, the file containing red-filled outlines of the second metatarsal was called red_512x512x57.raw2, signifying that there were 57 images each measuring 512 pixels square.

3. Slice spacing calculations and curve detection

Once these collective image files were created, they required preparation for curve detection and stacking software. A program written by Dr. Doug Phillips, volume_to_nuages, performed the necessary calculations and format

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conversion. Volume_to_nuages facilitates spacing of images on the z-axis, with the units being the number of pixels. Z-axis dimensions can be fractions of a pixel, to ensure maximum fidelity to the proportions of the modeled object. The program asks for the size of each image in the x and y dimensions (in this case 512 pixels each), and then asks for the z dimension between slices.

From the length of the original specimen (TMP 94.12.602), scale bars on the CT images, and the x and y pixel dimensions, I calculated the necessary z-axis spacing between images. The physical width of MT II is 7 cm at a position corresponding to slice 131. The length of the metatarsal is 49.9 cm, or 7.13 times 7 cm, over the distance covered by 54 slices. On slice 131, the width of the image of MT II is 115.45 pixels. Therefore, to calculate the length L of the 3D model in pixels:

(9) L_{model}= W_{image} x 7.13=823 pixels

To calculate the z-axis spacing (z_{spacing}) between the slices:

(10) z_{spacing} = L_{model}/ slices(=54) =15.24 pixels

The result of 15.24 pixels between slices of each metatarsal ensured that the 3D model matched the proportions of the fossil.

With the dimension variables entered into volume_to_nuages, I specified output file for the NUAGES edge detection and modeling software. An initial NUAGES file requires the .cnt suffix (specifying contour or edge data for the file). The resulting .cnt files for each metatarsal were then subject to processing by this program. NUAGES typically found one curve per image or two if a medulary cavity was present in a given region of the metatarsal.

4. 3D modeling and finite element mesh generation

To create a 3D model from image slices stacked along the z-axis, NUAGES formulates connectivity between curves according to user-supplied commands. These commands also facilitate mesh creation. For example, the –tri command generates a triangular surface mesh, and –tetra creates a tetrahedral volumetric mesh. For finite element analysis, a volumetric mesh with tetrahedral elements was chosen as the reconstructed 3D model.

Other commands entered into NUAGES ensured that the number of tetrahedra within the mesh was sufficiently high for informative stress analysis, but low enough for efficient processing by MARC finite element software. These commands were entered as preprocessing options into NUAGES (-popt in the NUAGES command line, followed by the appropriate commands and arguments).

For example, the command –approx reduces the number of elements by deleting vertices (points in space). If three points form an angle that is less than a specified number of degrees, one of those points is deleted. The result is a straight line between two vertices; the line becomes one side of a larger tetrahedral element. Large-scale contours are retained whenever three points subtend an angle greater than the specified amount. Therefore, if a small angle is chosen, extraneous vertices are deleted, but fidelity to the original shape is maintained. An angle of 2 degrees proved adequate for authentic surface contours with a minimum number of elements.

The resulting meshes (Figure 4.3) consisted of 3237 tetrahedral elements for MT II, 2226 for MT III, and 3101 for MT IV. These were converted to AVS and xgobi visualization formats and MARC input format by the program extract_tetra, written by Dr. Phillips. MARC/MENTAT is a set of finite element processing and user interface software, held under license by the University of Calgary Human Performance Lab (HPL). The MARC format files were transferred via FTP to the server at the HPL. Calculated forces, material properties, and boundary conditions were applied in MENTAT, and MARC carried out the construction and solution of finite element equations.

RESULTS

I. The metatarsus normal to the substrate

Figures 4.5 and 4.6 show the pattern of compressive strain energy in the *G*. *libratus* metatarsus model. Figure 4.4 is a contour plot of compressive strain. The simplest visualization option, showing contour lines of strain along element sides, proved to be the most informative. Two salient patterns emerge from the results: 1) Artifacts of the tetrahedral meshing technique are easily differentiable from informative results; 2) Regions of high strain correlate with proposed distal ligament positions and the proximal gracile portion of MT III. These points are now examined in turn.
1) Informative strain results versus mesh artifacts. Figure 4.4 overlies strain results from the first analysis on the surface of the finite element model. The faded gray lines are edges of visible element faces, and the purple lines represent concentrations of compressive (z-axis) strain. Near the proximal and distal ends of the bone, several purple lines show strain at particularly long element edges that are perpendicular to the compressive stress (one is pinpointed by the green line in the figure). Because these edges are long and have a subhorizontal orientation, they act as long moment arms for the compressive loading. This results in artifactual strain on the elements.

In contrast, strain is also evident along element edges that are short and vertically oriented (Figure 4.4, located by red lines), providing moment arms of negligible to zero length for stresses along the z axis. The small size of elements in these regions provides high resolution for strain results. The magnitude of strain (close to 0.2 mm) is more significant when the element edges are nearly parallel with the compressive ground-reaction force, because bone is strongly resistant to such loadings. Conversely, the same apparent magnitude of strain at long, horizontal element edges indicates that in vivo strain was less extensive in these regions, and that indicated strain along subvertical edges is more biologically informative. The distribution of significant strain results is now delineated.

2. Strain distribution. Under both loading regimes with the metatarsus normal to the substrate, the regions of greatest bone strain occur along the distal articular surfaces between metatarsals, and along the proximally narrow portion

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of MT III (Figure 4.4, pinpointed by the red lines). The significance of strain in each location corresponds to the respective morphologies of these regions.

Purple element edges indicate strain along the lateral and medial surfaces of the distal third metatarsal, where the bone slants proximally towards its midsagittal plane. The location of these indicated strains is congruent with that of osteological correlates for ligaments in the tyrannosaurid metatarsus, as described in Chapter 3 (Figures 3.6-3.8).

Compressive strain is also prominent where MT III narrows to become a proximal splint (Figure 4.4). Contour plots of relative strain magnitudes on MT III (Figure 4.5) corroborate the high strain on the splint during compressive loading, in this case four times body weight. The concentration of strain energy in this region is consistent with higher stresses per unit cross section, as would be expected in particularly gracile regions of the bone.

II. The metatarsus at 50 degrees to the substrate.

Figure 4.6 depicts contour plots of strain magnitudes, assuming that MT III is angled, held rigid at the proximal end, and loaded by a ground reaction force perpendicular to the substrate. Under this loading regime, the proximal splint of MT III experiences high bending strains. In Figure 4.6, bright yellow and gray in this region show displacement along the y axis, which signifies anteriorly directed strain. Elements in this narrow region are relatively small, indicating that the results reflect potential *in vivo* strains rather than artifacts.

The numerical results output from MARC are insufficiently legible to determine if bending strain was sufficient to break the proximal splint. However, the buildup of strain energy evident in Figure 4.6 shows that the proximally constricted portion of MT III was potentially vulnerable to damage.

DISCUSSION

FEA directly supports the energy transference hypothesis

The results corroborate the hypothesis that energy was transferred from MT III to adjacent elements when the metatarsus was normal to the substrate (Holtz 1994a), and suggest a mechanism for this transfer. Figures 4.5 and 4.6 indicate that if energy transference did not take place, strain would become concentrated in the weakest part of the metatarsal, its fragile proximal splint. Strain parallel to the long axis of the metatarsus also occurred where distal ligament correlates are found on MT III (Figure 4.4). The concentration of bone strain energy at these locations implies that MT III wedged up between MT II and MT IV. The correspondence with ligament scars indicates that ligaments probably absorbed strain energy as MT III was displaced vertically. Strain results from the first analysis, therefore, suggest that ligaments facilitated the transfer of footfall energies along the long axis of the metatarsus.

FEA results complement the tensional keystone hypothesis

Results from the second analysis indicate that when the metatarsus was inclined to the substrate, ligaments would prevent damage to the splint of MT III from bending stresses. If distal ligaments were not present to damp the

anterodorsal rotation of the distal portion of MT III, bending strains concentrated in the region of the proximal splint were probably greater than the bone could withstand without breaking. As with results from the previous analysis, specific strain magnitudes are difficult to ascertain from MARC's visualized output. However, strain energy concentration shown (Figure 4.6) implies that ligaments were necessary to prevent MT III from breaking under the angled loading regime.

Taphonomic evidence strikingly demonstrates the strength of ligamentous articulation in tyrannosaurid metatarsi (Philip Currie, personal communication 2000). Despite their proximal gracility, fractured and healed arctometatarsalian MT III are unknown in the fossil record. This indicates that some strong mechanism prevented the elements from breaking. In contrast, tyrannosaurid fibulae are often found with healed breaks. This bone is more robust than the proximal splint of MT III. Logically, we would expect to find more broken tyrannosaurid third metatarsals than fibulae, unless connective tissues of the metatarsus were absorbing locomotor stress. Tyrannosaurid metatarsi are usually found intact even when the rest of the skeleton is disarticulated. The specimen from which this metatarsus was taken, TMP 94.12.602, was incomplete, with bones scattered over a wide area. Both metatarsi were found intact, indicating that intermetatarsal ligaments may have been stronger, and slower to degenerate, than other soft tissues (Philip Currie, personal communication 2000). The extent and orientation of these ligaments ties in with putative function suggested by bone strain data.

Specifically, osteological correlates of ligaments along the plantar angulation of articulating metatarsals (Chapter 3) have a great deal of surface area evident in anterior or posterior view. This suggests strong resistance to anterior displacement of MT III, which would presumably prevent breakage of the bone. The resulting damping function of ligaments augments the tensional keystone hypothesis, but does not support or contradict the distal unification of metatarsals proposed under that model. Finite element analyses that directly incorporate ligaments will be the subject of future investigation, and will corroborate or falsify the specific kinematics of the model. An example of the encompassing importance of ligament and tendon studies is now discussed, in light of their implications for the present study.

Dynamic versus static loading: are locomotor force estimates for Gorgosaurus libratus too low?

Estimates for footfall forces in *G. libratus* assumed momentarily static loading on the femur, epipodium, and metatarsus, imposing instantaneous bending loads on the elements. However, the distribution of strain energies in both bone and connective tissue must be considered. If a limb element is held rigid while torque is applied and tendons and ligaments do not deflect, the bone must absorb the full energies of the load. Storage and return of elastic strain energy becomes much more effective at large body sizes, because tendon and ligament cross sections scale proportionally lower with increasing body mass (Clark and Alexander 1975, Alexander et al. 1979, Pollock 1991). Conservation of energy predicts that if connective elements such as the tendons of extensor muscles are allowed to stretch slightly under the bending loads, stresses on the bone will decrease.

In addition, elastic deformation and recoil of tendons would decrease the rate of strain on the bone; unlike tendons and ligaments, bone is less brittle under longer periods of loading. A longer collective loading period on tyrannosaurid hind limb elements, including soft and hard tissues, may have allowed their bones to withstand torque imposed by lower duty factors than normally expected for animals of their great size.

While these relationships hold for mammals over wide range of body mass (Pollock 1991), benefits of elastic storage have yet to be quantified in tyrannosaurids. Based on regression equations from quadrupedal mammals (Pollock 1991),

(11) U=0.14m^{1.14} U=elastic strain energy storage, m=body mass, the M. gastrocnemius tendon in G. *libratus* would be expected to store and release at least 910 Joules.

Because tendons of M. flexor digitorum longus also span the mesotarsal joint, and because *G.libratus* is a biped, the maximum capacity for elastic energy storage of all tendons around the joint was almost certainly higher. The cross section of these tendons in ostriches is 1.95 times that predicted for an antelope carrying the same amount of mass on its back legs (Alexander et al. 1979), and the tendons are much longer than those of ungulates. If the same were true for *G. libratus* versus a quadrupedal mammal of its mass, its mesotarsal tendons would potentially be quite efficient at elastic storage. The tendons thus may have cushioned the metatarsals against bending force incurred after moderately long suspended phases.

CONCLUDING COMMENTS AND FUTURE DIRECTIONS

While elastic storage by tendons and ligaments may have enhanced the locomotor performance of tyrannosaurids, the preceding considerations do not support the 70 km/hr speeds postulated by Bakker (1986) and Paul (1988). These speeds would require lower duty factors or higher stride frequencies than are probably realistic for such long-legged, heavy animals (Christiansen 2000). However, the elastic properties of ligaments and tendons should be incorporated into future studies, including investigations expanding upon the finite element analyses presented in this chapter. Without consideration of elastic connective tissues, attempts to set rigorous upper and lower bounds on tyrannosaurid capabilities will be inadequate.

Figure 4.1. Initial loads and boundary conditions applied to left *Gorgosaurus libratus* metatarsus in anterior view, normal to the substrate, with a vertical ground reaction force. The arrows indicates force direction, but the lengths of arrows do not reflect relative force magnitudes. The parameters are designated as follows:

apply1 (purple arrows)	zero displacement or rotation of nodes at proximal end
mtiiiz90 (orange arrows)	15149 Newtons applied to MT III along z axis
mtiiz90 (red arrows)	11362 Newtons applied to MT II along z axis
mtivz90 (blue arrows)	11362 Newtons applied to MT IV along z axis



Figure 4.2. Initial loads and boundary conditions applied to left MT III (lateral view) of *Gorgosaurus libratus*, with the plantar surface at 50 degrees to the substrate. The direction of arrows indicates the direction of force components, but the lengths of arrows do not reflect relative force magnitudes. The parameters are designated as follows:

apply1 (purple arrows)	zero displacement or rotation of nodes at proximal end
ngl501 (orange arrows)	components of force of 15376 Newtons perpendicular to substrate, when MT III is positioned at 50 degrees to substrate



Figure 4.3. Finite element mesh of left *Gorgosaurus libratus* metatarsus, created using NUAGE modeling software. Medullary cavities are visible as oblong shapes within the interiors of the metatarsals. The coloration is the default setting of the AVS/Express visualization program. This mesh is of a somewhat higher resolution that that used in the analyses.



Figure 4.4. Simplified representation of important strain energy locations in left metatarsus of *Gorgosaurus libratus*, loaded at 90 degrees to the substrate (see text). Purple lines along element edges signify strain. The green line points to an example of artifactual strain, and the red lines point to probable important regions of *in vivo* strain.



Figure 4.5. Strain distribution in left metatarsus of *Gorgosaurus libratus* (anterior view), loaded at 90 degrees to the substrate with forces four times body weight. Red lines point to high compressive strain (signified by bright yellow) on the proximal splint of MT III, and at the position of intermetarsal ligament correlates, visible on the anterolateral edge of MT III. Artifactual strain is evident on elements with long edges perpendicular to the compressive force (see text and Figure 4.4).



Figure 4.6. Strain distribution in left MT III of *Gorgosaurus libratus* (lateral view), with the metatarsus positioned at 50 degrees to the substrate, and loaded at its distal end with a ground-reaction force perpendicular to the substrate. Red lines point to indications of high bending strain (signified by gray and yellow colors) at the proximal splint of MT III. Unless ligaments running to MT II and MT IV were present to arrest anterodorsal displacement, the metatarsal was in danger of breaking under this loading regime.



CHAPTER 5: Mechanical and evolutionary integration of the tyrannosaurid

arctometatarsus

Chapter 1 introduced the bones and ligaments of the arctometatarsus as an integrated subsystem of the tyrannosaurid phenotype, and intervening sections tested hypotheses that this unusual morphology suggests. This chapter explores the implications of putative metatarsus function for tyrannosaurids and other theropods. The first section discusses the utility of the finite element method for assessing combined functions of bones and elastic connective organs, with the loading regime of the arctometatarsus presented as a salient example. Subsequently, the chapter consolidates findings on theropod MT III variation and biomechanics, and discusses the ramifications of these hypotheses in the context of phylogenetic distribution, biological role, and selective utility of the arctometatarsus.

FINITE ELEMENT ANALYSIS AND THE FUNCTIONAL INTERPLAY OF BONES AND LIGAMENTS

Lessons for applying the finite element method to palaeontology

The finite element results (Chapter 4) point to the promise and limitations of the method for the study of kinematics of extinct animals. The rigor of any finite element analysis is proportional to the quality of the model. Uninformative results do not arise from deficiencies of the method, but rather from unrefined structural representations. Yet computer models of only moderate resolution, such as those employed in this study, can yield data useful for testing functional hypotheses when initial kinematic conditions and material properties are realistic. The analyses of the *Gorgosaurus libratus* metatarsus (Chapter 4) suggest three lessons for future palaeontological applications of the finite element method:

1. Primary data from fossils take precedence over other considerations in the execution of a realistic model and analysis. The *G. libratus* metatarsus investigated in this study was remarkably well-preserved and undistorted. This ensured that digitized and stacked cross sections from CT scans replicated the metatarsus of the living animal with a high degree of fidelity. In addition, proper density settings for the CT scans easily resolved the medullary cavities, even where they were filled in with matrix.

2. Finite element analysis can be informative using meshes of moderate resolution, but meshes with larger numbers of elements are both desirable and practical. Generally, a mesh with more elements will result in a more realistic assessment of strain distribution, because the elements are smaller. Short lengths of element edges potentially present shorter moment arms for impinging stresses. In a mesh of a 50 cm bone consisting of 2200 elements, the large size of some tetrahedral edges resulted in identifiable artifacts (see Results, Chapter 4). These undesirable results are avoidable. The processing power of modern computers allows for rapid solution of stiffness matrix equations, even with very large file sizes (represented by large numbers of elements). The construction and solution of equations for a tetrahedral mesh of the combined metatarsus, with approximately 8000 elements, took less than one minute.

3. Strain results from static analyses of bones can elucidate the function of associated ligaments. If the tyrannosaurid MT III was not suspended elastically

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by distal intermetatarsal ligaments, its proximal splint was in danger of breaking under moderate locomotory loadings.

FEA and ligament-skeletal dynamics

Successful application of bone strain analysis (Chapter 4) is encouraging for the use of finite elements in the palaeontological study of ligament function. Finite element analysis incorporating bones, ligaments, tendons, and muscles will aid in the overall investigation of kinematics in extinct animals. The complete locomotor repertoire has yet to be circumscribed for any extant animal, much less for a Mesozoic dinosaur. However, neontologically informed finite element modeling will be a useful tool for elucidating the locomotor systems of extinct animals. The next section details the importance of these investigations, by showing how the biomechanical role of the arctometatarsus influences broader questions of evolution and behaviour.

REDUCTION AND SYNTHESIS OF THE ARCTOMETATARSUS AS A BIOMECHANICAL SYSTEM

Descriptive morphology, qualitative modeling, quantitative testing

Chapters 2, 3, and 4 tentatively elucidated foot function in tyrannosaurids. The primary impediments to this and other functional studies of extinct animals are the imprecision of soft tissue reconstruction, and the dearth of performance data. The methodological scope is much greater for neontological studies, which have a wider array of available modeling and statistical approaches. Because the performance of living organisms can be measured, it is possible to compare their

individual organs with ideally efficient models, and to compare the collective performance of organs with models of compromised efficiency (Zweers 1979). It is also possible to correlate measured performance with morphometric attributes, such as clinging ability with size and zeugopodial morphology in lizards (Zani 2000). These studies can incorporate aspects of neurology (Zweers 1991) that are impossible with extinct organisms, except by broad inference (Giffin 1990, 1992; Martin et al. 1998).

Assessments of absolute or realized performance are extremely difficult with fossil animals. Therefore, hypotheses of function must be refined in focus through the accumulation of inductive data, using comparisons with other extinct and extant taxa. For example, in this study of the arctometatarsus, a broad hypothesis of difference from other forms was tested through detailed morphological description and PCA of theropod third metatarsals. The distribution of osteological correlates suggested that ligaments arrested anterior displacement of MT III in tyrannosaurids, in the manner of interosseous ligaments that bind the intercalating carpals of horses. This proposed function was refined into the tensile keystone hypothesis, and finite element analysis quantitatively tested the resulting kinematic model.

Through this progression, a hypothesis of arctometatarsus function emerged that is based on thorough morphological understanding, and that is amenable to further quantitative falsification or support. I now briefly recapitulate and synthesize these findings for tyrannosaurids, and discuss their implications for other theropods.

Probable function of the tyrannosaurid arctometatarsus

The preceding chapters offer observational and biomechanical support for the energy transference (Holtz 1994a) and tensional keystone hypotheses of tyrannosaurid metatarsus function. These may be summarized as follows:

1) When the tyrannosaurid pes contacted the substrate at an acute angle, distal intermetatarsal ligaments prevented the greater torque on MT III from displacing it anterodorsally relative to MT II and MT IV. Instead, the plantar angulation of the metatarsals and orientation of ligaments drew MT II and MT IV towards the plantar midline of MT III (Figure 3.12), although the displacement was slight. This caused the metatarsus to be loaded as a unit during the push off phase of the step cycle, and lateral and medial angulation of the metatarsus did not disproportionately load MT II or MT IV.

2) When the animal imposed torsion on its foot, the plantar angulation of metatarsals translated this force into compression on adjacent elements across their articular surfaces, and/or into modest tension on intermetatarsal ligaments (Figure 3.14).

3) When compression was channeled along the long axis of the metatarsus (either at midpoint in the linear step cycle or when the animal was decelerating), loading on MT III was transferred to the outer metatarsals (Wilson and Currie 1985, Holtz 1994a) via tension on intermetatarsal ligaments (Figure 3.13). MT II was the primary recipient of these loadings, because its articular surface with MT III has a more acute angle to the substrate than the corresponding surface of MT IV.

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These considerations of ligament morphology and kinematics in tyrannosaurids suggest hypotheses of function for other theropod metatarsi. With putative biomechanics of the tyrannosaurid arctometatarsus established as a baseline, the morphologies of other theropods are now revisited and explored from a functional standpoint.

What do bone and ligament morphology imply for metatarsus function of other theropods?

The descriptive morphology of theropod third metatarsals, outlined in Chapter 2, provides comparative data for hypotheses of pedal function. The most broadly applicable hypothesis is that tensile keystone dynamics did not occur in theropods that lacked a distal plantar angulation of metatarsals. The distal facing surfaces of their metatarsals were parasagittally oriented. If ligaments were present, they would have resisted anteroposterior shear and lateral or medial displacement of the outer metatarsals, but the bones would not be free to move towards the plantar midline as in arctometatarsalian forms. Because most of these taxa lack correlates for distal intermetatarsal ligaments, the moment arm of ligaments holding the metatarsals together was presumably shorter (Alexander: pers. comm. 1999), and the intermetatarsal articulations may not have been as strong as they were in tyrannosaurids.

Generally, taxa with an extensive anteroposterior expansion of MT III (for example tyrannosaurids, *Deinonychus*, *Ornitholestes*, and carnosaurs) probably had stronger metatarsal articulations in this region than did other taxa. A hook shaped proximal cross section of MT III (in tyrannosaurids [Figure 2.7], *Ornitholestes*, and carnosaurs) increased ligament cross section, and also prevented proximal anteroposterior displacement of this element.

Peculiarities of MT III morphology invoke more specific hypothses for several taxa. These hypotheses largely trace the succession of descriptions presented in Chapter 2. Taxa with particularly noteworthy features are discussed, in comparison with tyrannosaurids and other forms.

1) cf. Ornithomimidae and Troodon formosus.

These MT III specimens are classically arctometatarsalian. Proximally some degree of parasagittal rotation of this element may have been possible in either form (Wilson and Currie 1985), but because the animals were probably low in mass relative to the cross section of ligaments, little displacement was likely (Pollock 1991).

The distal morphology of the ornithomimid MT III (Figure 2.9) was so closely akin to that of tyrannosaurids that function in this region was probably similar to that of the larger forms, although scaling variance must be considered. The modest size of the specimen measured in this study indicates an ornithomimid of relatively low mass. Presumably this mass imposed lower elastic displacements of distal ligaments than those likely in adult tyrannosaurids (Pollock 1991). This proportionality of ligament strain probably applied to adults of both clades; adult ornithomimids were generally smaller than adult tyrannosaurids. Small ligament elastic displacements in large ornithomimids were probably paralleled in very young tyrannosaurids, whose mass, limb proportions, and presumed running performance were very similar to those of adult ornithomimids (Currie 2000). The precise scaling of metatarsal ligament cross sections between ornithomimids, tyrannosaurids, and troodontids has yet to be investigated.

The morphology of buttressing surfaces in the *Troodon* metatarsus (Figure 2.10) was the mirror image of the condition in omithomimids and tyrannosaurids, in which footfall energies were transferred from MT III to MT II. Instead, with *Troodon* long axis compressive forces on MT III would be transferred mainly to MT IV. Its buttressing surface for MT III was more acutely angled to the substrate than that of MT II, and would have been loaded by the component of the ground-reaction force parallel to the long axis of the metatarsus. In contrast, the MT II-MT III contact is in a parasagittal plane. In *Troodon*, MT II is shorter than MT IV, and bears a retractile ungual phalanx presumably held clear of the ground; it is unlikely that the second pedal digit contributed to weight bearing.

2) Oviraptorosauria: *Elmisaurus* sp.

MT III of this specimen shows proximal constriction on its anterior surface, but plantar constriction is restricted to the distal portion of the metatarsal (Figure 2.11). As in other elmisaurids (Currie and Russell 1988), the metatarsals are also fused proximally. Compressive energy would transfer from the distal third metatarsal to the proximal ankylosis of the bones, and would not be transmitted by ligaments to the astragalar condyles, as was likely in tyrannosaurids (Chapter 3, Holtz 1994a).

3) Deinonychus antirrhopus.

MT III of *Deinonychus* displays a slight plantar angulation on its medial surface, and a distally extensive articular facet for MT II (Figure 2.12). Neither

morphology matches in degree the condition in tyrannosaurids. These morphologies probably correlate with a strong MT II-MT III articulation in life. *Deinonychus* has a large, trenchant ungual phalanx on digit II. The strong intermetatarsal articulation may have resisted torsional forces when the animal employed this weapon during predation (Ostrom 1969).

4) Carnosauria: Sinraptor dongi:

Unlike in the *Allosaurus* specimens, the *Sinraptor* MT III (Figure 2.14) shows some plantar angulation along its articular surface with MT II. As with *Deinonychus*, there is also a more extensive distal articular facet with MT II. This indicates that the MT II-MT III articulation was potentially stronger in *Sinraptor* than in *Allosaurus*.

Interestingly, recent examination of MT III of a unnamed giant South American carnosaur (Carcharodontosauridae, n. gen., n. spec: Plaza Huincul specimen; TMP Ioan) reveals a discrete area of distal rugosity on the distal articular surface with MT II. MT II of this specimen is unavailable, so it cannot be determined if it bears a rugosity corresponding to that on MT III. However, if the roughened surface on MT III of this animal is a ligament scar and not a pathology, these morphologies indicate a diversity of MT II-MT III articulation mechanisms and strength among large carnosaurs.

The functional implications of this diversity are unclear. *Sinraptor* and large *Allosaurus* specimens were of similar mass (Paul 1988, 1997), while the carcharodontosaurid was much larger (Currie: pers. comm. 2000). Speculations on whether stronger articulations correlated with size or activity level are not

tenable from the available evidence. However, gracility of the MT III of *Sinraptor* (UUVP10600) may indicate immaturity (Currie: pers. comm. 2000). Theropod metatarsals scale negatively with femur length during ontogeny (Currie 2000).

An arctometatarsus occurs in coelurosaurs of a broad range of adult sizes (Figure 1.5, Chapter 1; Holtz 1994a,b), including tyrannosaurids comparable in size to giant carnosaurs. Therefore aspects of their morphology other than size must be considered in examination of the arctometatarsus' biological role. The following section explores the possible phylogenetic and selective ramifications of the arctometatarsus, with the overriding caveat that hypotheses of biological role are difficult to test adequately.

EVOLUTIONARY CONTEXT FOR THE ARCTOMETATARSUS

This thesis tests the hypothesis that the tyrannosaurid arctometatarsus imparted benefits to foot resilience and strength. These advantages have been mechanically corroborated, but their origin and utility require the contexts of phylogeny and historical aptation (traditionally adaptation). In the following section, I consider the arctometatarsus from an evolutionary perspective. The discussion begins with an explanation of aptational terminology. With this background in place, I then use recently published cladograms as baseline distributions of relevant characters and taxa. From there I proceed into more complex evolutionary hypotheses (scenarios) based upon the pertinent cladistic hypotheses and the morphological evidence presented in this thesis. This

discussion elucidates the evolution of the arctometatarsalian pes, and the implications of the morphology for tyrannosaurids and other coelurosaurs.

Aptational terminology

An adaptation is usually considered a structure or behavior with current selective utility. The concept has been subdivided into discrete and operational classifications. Herein I will largely follow the conventions Gould and Vrba (1982), with reference to historical usage. Gould and Vrba (1982) restricted the term *adaptation* to beneficial innovations that retain their original use. Adaptation is a subset of *aptation*, defined as any feature that potentially aids an organism's fitness, or the evolutionary process that molds the feature. Therefore, references to aptation or its subordinate concepts refer to either an actualized combination of form and function, or to the evolutionary origin and development of such a complex.

For the purposes of illustration, aptation is here defined in terms of functional anatomy. I have modified the definition of Gould and Vrba (1982) to incorporate Bock's energetic perspective, introduced in the context of adaptation (Bock 1965, 1989):

aptation: a form-function complex with biological and selective utility,

effective to the extent that it minimizes energy use in its current role The concept of energy efficiency may be broadly interpreted. A turbocharged 1.5 liter BMW Formula 1 engine from the early 1980s had poor fuel efficiency per distance traveled, relative to 1.5 liter passenger car engines. However, the engine approached 1000 horsepower per liter of displacement. To produce the equivalent horsepower, 15 economy car engines of the same size would collectively consume more fuel. For organisms, an aptation will reap benefits to performance so long as resources for its function are not prohibitively limiting. Particularly fortuitous aptations will maximize selective benefit for a given amount of resources and output of energy (Bock 1965).

Aptations can arise from a number of sources. One type of origin would involve acquiring a neomorphic feature that imparts a new selective benefit (an adaptation *sensu* Gould and Vrba 1982). A pre-existing structure can also be coopted for a new function. The original morphology is retrospectively identified as the precursor to the current aptation. This process of cooption integrates two concepts:

pre- (or proto-)adaptation: the original structure which is later coopted for a new role (Bock 1959, 1963, 1965; Russell 1979a);

exaptation: a new form-function complex derived from structures with a different original utility (Gould and Vrba 1982).

Adaptation and exaptation exist along a continuum of evolutionary change. Several examples set the stage for categorizing the arctometatarsus along this complex biological gradient.

A preadaptive structure need not lose its original utility when exapted for a new role. For instance, lateral extension of the basitemporal process in skimmers increased the surface area for neck muscle attachment, beneficial for controlling the head as the fishing bird's beak skims the surface of the water.

Developmentally and phylogenetically, these lateral extensions of the posterior

face of the skull met part of the medially expanding lower jaw. The bones formed a stout new joint that braces the jaw articulation when the skimmer spears a fish (Bock 1959).

The sequence of functional acquisition, determined through character analysis (Bock 1965) and ideally through fossil evidence, allows us to classify the relevant aptations. The new function of bracing the jaw is an exaptation derived from lateral extension of the basitemporal processes, which was not originally involved with a second jaw joint. The original function of increased muscle attachment is still in effect, and thus falls under the category of adaptation proper (Gould and Vrba 1982). Both functions (termed *postadaptation* by Bock 1959) are amenable to further refinement.

Epistemology and evolution of aptations

With this background of terminology, further examples illustrate the evolution of exaptive functional complexes. A simple instance involves one aspect of the origin of flight in birds. The range of motion evident in the forelimb joints of small theropod dinosaurs indicates these animals could sweep their claws down and forward; one possible utility of this action was to strike and grasp prey. Gauthier and Padian (1985) propose that the same motion was incorporated into the downward component of the flightstroke in birds, the descendants of earlier predaceous theropods. If a predation strike was the primary selective benefit of forelimb kinematics in the ancestors of birds, the avian downward flightstroke may be interpreted as an exaptation derived from an anteceding function.

Other aptations reflect multiple functions that potentially stem from a single, broad morphological innovation. African cichlid fishes have developed a second set of jaws within their pharynx, exapted from tooth bearing pharyngobranchials and ceratobranchials, and associated branchiomeric musculature and innervation (Liem 1973). These cichlids can transport and process food within their throats, and their primary jaws have been freed for wildly diverse specializations in food collection. Liem (1973) and Liem and Osse (1975) term such fortuitous structures *key innovations*, because they allow extensive exploitation of new adaptive zones.

Other key innovations enable less dramatic diversification than that of cichlids, but can still trigger elaboration and multiple functions when selective forces are brought to bear. The strength of the rostrum of synapsids increased substantially with the development of a full secondary palate (Thomason and Russell 1986). This resistance to bending and torsion enabled a diversification of mechanisms for continuous and energetic mastication in mammals (Thomason and Russell 1986). Caniniform and canine teeth in mammals and other synapsids have been expressed as saber-like modifications in the gorgonopsian *Inostrancivia*, herbivorous pantodonts, marsupial carnivores, and in saber-toothed cats and their nimravid relatives (Carroll 1990). Lateral body folds in gekkonid lizards, initially involved in fat storage, have become modified for crypsis and parachuting (Russell 1979a). These variegated functions in geckos are not mutually exclusive, and their selective expression depended upon the interplay of behavior, morphology, and environment (Russell 1979a).

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Alternately, a morphological novelty can yield convergence upon a single functional outcome by multiple modifications of the original structure. Gekkonine and diplodactyline geckos display parallelism in the occurrence and structure of subdigital adhesive pads (Russell 1979b). The specific morphology, which enables these lizards to cling to surfaces, differs in closely related clades. The common denominator in development of adhesive pads in geckos is a spinose Oberhäutchen, or outer integumentary layer with spines. Outgroup comparison indicates that the spines have independently evolved into adhesive setae in several distantly related clades of geckos. Morphologically generalized spines are retrospectively identifiable as a key innovation that facilitated the emergence of parallelism (Russell 1979b). The original shared structure has become modified for the same function several times, along multiple evolutionary pathways (Bock 1965).

The evolution of the arctometatarsus, and its emergence and/or loss in several coelurosaurian taxa, may also have proceeded along multiple pathways. Intermetatarsal ligaments, indicated by rugosity on the articular surfaces, would be a necessary precursor to distal ligament expansion involved in tensile keystone dynamics. In this way, multiple elaborations of theropod intermetatarsal ligaments may have paralleled specializations of the spinose Oberhäutchen of geckos. It is hypothesized, therefore, that these ligaments were the prerequisite key innovation common to dramatic parallelisms in foot morphology that occurred in coelurosaurs.

This and other systematically informed hypotheses are testable by mapping characters onto a well-supported phylogeny of theropods, and determining temporal polarization of characters through parsimony. The distribution of the arctometatarsus on a phylogeny, for instance, allows us to predict the occurrence of associated features, including intermetatarsal ligaments and an elongate metapodium. Additionally, phylogenetic testing can illuminate the evolution of selective utility of the arctometatarsus: What selection pressures led to the fixation of the arctometatarsus when it arose? The following discussion therefore details pathways of possible evolutionary emergence of the arctometatarsus, in the hopes of testing hypotheses of origin and utility.

Implications of phylogenetic distribution of the arctometatarsus

The presence or absence of an arctometatarsus, and intermetatarsal ligament correlates, serve as character states that can be mapped onto two competing but well-corroborated theropod phylogenies (Currie and Padian 1997 and Holtz 2000; Sereno 1999). The phylogenies summarize the relationships of taxa bearing an arctometatarsus, and reveal the distribution of intermetatarsal ligaments, the arctometatarsus, and trophic habit in coelurosaurs and their sister taxa.

The taxa in these phylogenies primarily include those investigated in the Principal Components Analysis in Chapter 2. Inclusion of a taxon in Figure 2.16 designates it as arctometatarsalian; the Cretaceous Mongolian bird *Mononychus* (Chiappe 1997), which was unavailable for examination, is also scored as such (Holtz 1994b, Sereno 1999). The sauropodomorph *Plateosaurus* serves as the

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outgroup to all theropods, and the Carnosauria (*Allosaurus fragilis*, *Allosaurus* (*Saurophaganax*) maximus, and Sinraptor) is the sister group of the Coelurosauria. The relationships of *Herrerasaurus* were unresolved by Holtz (2000), and alternate placements are shown in Figures 5.1, 5.3, and 5.5. Relationships within the Coelurosauria follow the results of Holtz (2000) in Figures 5.1, 5.3, and 5.5, and Sereno (1999) in Figures 5.2, 5.4, and 5.6. *Ingenia* and *Rinchenia* are included in the monophyletic Oviraptoridae.

In order to determine polarity for the ancestral diet of arctometatarsalians, four successive outgroups of the Theropoda are included in addition to *Plateosaurus*. These are the herbivorous dinosaurs of the clade Ornithischia, the small dinosauromoprh *Marasuchus*, the flying Pterosauria, and the Crocodylia. The systematic position of non-dinosaurian outgroups follows the phylogenies presented by Sereno and Arcucci (1994), and Gauthier (1986).

Did proximal intermetatarsal ligaments facilitate partially exaptive origination of the arctometatarsus?

The first hypothesis to be tested is that intermetatarsal ligaments were generally distributed in theropods. Deep ligaments like those proposed for the arctometatarsus often occur between carpals and tarsals in tetrapods (Sisson and Grossman 1953), but extensive deep ligaments are not normally present between metatarsals. Instead, superficial ligaments attach to the dorsal (or anterior) surfaces of the proximal metatarsal heads, and span the transverse gap between the heads (McGregor 2000). Cruciate ligaments also occur, running distolaterally from the metatarsal heads to the metatarso-phalangeal joint
(Russell 1975, McGregor 2000). Metatarsal shafts do not normally conform tightly, except in some cursorial mammals (Coombs 1978) and proximally in theropods. Ligaments on the abutting metatarsal surfaces of theropods would be a novel development, and a logical prerequisite to expansive distal ligaments of the arctometatarsus.

One overall theme of this thesis, as expounded in the introduction, is the inference of soft tissue in fossil organisms. Extrapolatory inference (Bryant and Russell 1992) indicates that ligaments are the connective tissue elements most parsimoniously concordant with soft tissue correlates on examined metatarsal articular surfaces (Chapter 3). Rugose proximal articular surfaces occur on metatarsals of tyrannosaurids, *Deinonychus*, and carnosaurs (Chapter 2; carnosaurs are equivalent to allosauroids *sensu* Sereno 1999). Discrete facets delineate rugose surfaces in these taxa, an additional indication that ligaments were present. Similar facets also occur in ornithomimids and troodontids. Figures presented by Heune (1907-8) indicate that proximal intermetatarsal articular facets were most likely present in *Plateosaurus*, a representative of the sister taxon to all theropods. The degree of rugosity on these surfaces could not be determined from the figures.

Iterative homology between fore and hind limbs provides additional, albeit circumstantial, support for the presence of intermetatarsal ligaments in carnosaurs and coelurosaurs. Ostrom (1969) reported roughened facets on the respective articular surfaces of Metacarpals II and III (MC II and MC III) in *Deinonychus antirrhopus*. Rugose MC II and MC III articular facets are less

convincingly evident in figures of *Allosaurus fragilis* elements (Madsen 1976). These metacarpals articulate tightly with one another, much like the proximal portions of theropod metatarsals.

While the manus and pes of theropods are disjunct functionally (Gatesey and Middleton 1997), developmental correspondence predicts that if osteological indications of intermetatarsal ligaments are present, correlates of intermetacarpal ligaments would not be surprising. However, identification of correlates as ligament scars on either manus or pes is uncertain. Arguments for iteratively associated intrametapodial ligaments are therefore circular, without independent evidence for ligaments in either metapodium.

By phylogenetic inference (Bryant and Russell 1992) or bracketing (Bryant and Russell 1992, Witmer 1995), we can deduce the presence of intermetatarsal ligaments in taxa intervening between carnosaurs and tyrannosaurs, and perhaps in Mesozoic theropods primitively (Figs. 5.1 and 5.2).

The distribution of osteological ligament correlates in both phylogenies indicates that coelurosaurs inherited them from the common ancestor of all saurischians, or from that of tyrannosaurs and carnosaurs (Figs. 5.1 and 5.2). The postulate emerges that proximal ligaments were a necessary step before the acquisition of distal ligaments, which would bind the metatarsals where their distal plantar angulation occurs. Osteological correlates in the arctometatarsus indicate a disjunct ontogeny for ligaments, in which strong ligaments developed proximally and distally, but not in the intermediate region. Further testing will reveal whether or not this apparent ligament ontogeny of the arctometatarsus

was the default developmental pattern for coelurosaurs, or how often it became expressed or lost in various taxa.

How often did the arctometatarsus evolve?

The presented phylogenies conflict in regard to how often the arctometatarsus emerged, and in the distribution and inclusiveness of arctometatarsalian clades. The simplest hypothesis of character evolution usually attracts provisional acceptance, because it entails the fewest evolutionary steps (acquisitions and reversals). However, the most parsimonious scenario is not necessarily correct.

The broad distribution of the arctometatarsus in competing phylogenies suggests that the simplest and other scenarios be tested with independent character evidence. The levels of parsimony of the Sereno (1999) and Holtz (2000) phylogenies cannot be directly compared. The most economical resulting cladograms for each analysis are internally consistent with their respective data sets, and are the most parsimonious solutions given the taxa and characters included in that study. Nevertheless, if one analysis results in fewer steps for the emergence of a given character, its results may be interpreted provisionally as the simpler evolutionary explanation for that character.

The arctometatarsus is the relevant subject of character evolution here, and several patterns of loss and emergence were deduced from its occurrence on both phylogenies. These patterns divulge which phylogeny presents the simplest hypothesis of arctometatarsus evolution. Because the simplest explanation does not definitively reflect the true evolutionary pattern, at minimum the first two most

parsimonious scenarios are outlined for each phylogenetic hypothesis. By the two outgroup rule (Maddison et al. 1984), the first scenarios assume that an arctometatarsus was not present in the common ancestor of coelurosaurs more derived than *Omitholestes*, although the alternative view is subsequently explored.

In one phylogeny (Figure 5.3; Holtz 2000), the simplest pattern holds that the arctometatarsus arose once in birds (in *Mononychus*), once in the common ancestor of tyrannosaurids and bullatosaurians (ornithomimids plus troodontids), and once in elmisaurids (*Elmisaurus* in Figure 5.3). Three independent gains of the arctometatarsus, with 0 losses, is the most parsimonious scenario for its evolution that can be derived from this hypothesis (Figure 5.3).

The second most parsimonious scenario involves 4 evolutionary steps (Figure 5.3). The structure could have arisen only twice, in *Mononychus*, and in the common ancestor of tyrannosaurids and *Elmisaurus*. If this is the case, at least two losses are implied, in therizinosaurids and oviraptorids.

This phylogeny implies that the potential for arctometatarsus expression evolved initially in the common ancestor of birds and tyrannosaurids. If the morphology was present in this common ancestor, there are several patterns of possible loss and emergence. In Holtz's phylogeny (Figure 5.3; Holtz 2000), identical permutations occur in the dromaeosaurid-avian clade and the therizinosaur-oviraptorosaur clade. The oviraptorosaur *Elmisaurus* and the bird *Mononychus* are the sole arctometatarsalians in either clade. I use birds and dromaeosaurids as an example. Among dromaeosaurids and birds, the arctometatarsus could have been present in their common ancestor, retained in *Mononychus*, and lost in both Dromaeosauridae and Aves. Alternately it may have been lost in the common ancestor of the dromaeosaur-bird clade, and regained either as the primitive condition for all birds (and subsequently lost in Aves), or acquired exclusively in *Mononychus*.

Which of these scenarios constitutes the simplest explanation for the available evidence? *Mononychus* is the known only member of the dromaeosaurid-avian clade, including Mesozoic birds, known to have an arctometatarsus. A full arctometatarsus as defined by Holtz (1994a) is not expressed embryologically in extant birds (Heilmann 1926, Chiappe: pers. comm. 1994). Rheas display a distal wedge like morphology of MT III in early development. However, the proximal part of the element is robust, circular in cross section, and lies posterior to and free of MT II and MT IV. This morphology contrasts with the gracile proximal splint of MT III in Mesozoic arctometatarsalian forms, which is medially and laterally constrained by MT II and MT III. (The proximal robustness of the embryonic rhea MT III superficially recalls that of *Elmisaurus*, although *Elmisaurus* MT III is not circular in proximal cross section, and is flanked by MT II and MT IV). It is more parsimonious to conclude that an arctometatarsus was not present in the common ancestor of dromaeosaurids and birds.

In Sereno's phylogeny (Figure 5.4; Sereno 1999), the arctometatarsus emerges four times: in tyrannosaurids, *Elmisaurus*, troodontids (aligned with

dromaeosaurids), and a clade comprising ornithomimids and *Mononychus*. The potential for arctometatarsus development would have first arisen in the common ancestor of *Mononychus* and tyrannosaurids (Figure 5.6). If this was the initial condition, the structure was convergently expressed in four instances: the clade comprising *Mononychus*, ornithomimosaurs, and their common ancestor, and separately in the clades *Elmisaurus*, Troodontidae, and Tyrannosauridae.

If the arctometatarsus itself was present in the common ancestor of tyrannosaurids and *Mononychus*, and passed on to the descendents of that ancestor, the phylogeny implicates four losses. Therizinosaurs, *Nomingia*, dromaeosaurids, and Aves would have lost the structure. The association of *Mononychus* with ornithomimids minimizes the permutations involved in the occurrence of an arctometatarsus in that taxon (see the preceding discussion).

An alternative hypothesis, suggested by both phylogenies, is that the arctometatarsus is a synapomorphy of the clade comprising the common ancestor of Tyrannosauridae and Aves and all its descendents (Tyrannoraptora: Sereno 1999). Losses of the morphology would have occurred within the Eumaniraptora (dromaeosaurids and birds: Holtz 2000), and therizinosaur-oviraptorosaur (Holtz 2000) or therizinosaur-omithomimosaur (Sereno 1999) clades. This would require only one gain and four losses on one phylogeny (Sereno 1999), and minimally one gain and three losses on the other (Holtz 2000). The universal lack of an arctometatarsus in adult birds, the most speciose and accessible coelurosaurian clade, may be a spurious bias against this

hypothesis. Fossil evidence of basal tyrannoraptorans (*sensu* Sereno 1999) will potentially corroborate or falsify the proposal of a single arctometatarsus origin.

Overall, the distribution mapped onto Holtz's topology (Holtz 2000; Figure 5.3) is more parsimonious, as it requires only three gains in one scenario, or one gain and three losses, of this complex functional suite. More crucially, however, both phylogenies indicate multiple independent origins and/or losses. The implications of this convergence must be discussed in the context of selective pressures leading to fixation of the arctometatarsus once it emerged. The following section explores this selective aspect of arctometatarsus evolution

What selective factors contributed to arctometatarsus evolution?

The hypothesis tested here is that the arctometatarsus was an innovation initially involved in prey capture. The long legs of theropods have been considered adaptations enhancing predatory behavior (Gauthier 1986), and with equal validity as an adaptation associated with increases in home range size (Carrano 1998). Tensile keystone dynamics imply the capacity for increased agility in arctometatarsalians, as presented above in Chapter 3. Modern animals employ agility in order to procure prey or to escape predators, and also for intraspecific combat. Potential modern behavioral analogs suggest parallel hypotheses of biological role in theropods.

Although observational corroboration is impossible, hypotheses of the biological role of potential agility are subject to testing by falsification. We can falsify the prey capture hypothesis if herbivory was the primary habit of

arctometatarsalian forms. The converse hypothesis, that the arctometatarsus enabled these animals to escape predators, is harder to falsify. Presumably young or small adult arctometatarsalians could employ heightened agility to escape larger theropods, whether the arctometatarsalians were carnivorous or not. I initially concentrate on the prey capture hypothesis, and revisit alternate hypotheses below.

Because three outgroups to theropods are carnivorous (Figs. 5.5 and 5.6), carnivory is implicated as the primitive condition for theropods. Morphological evidence from teeth indicates carnivory in the majority of Mesozoic theropods (Currie 1997). Because so many successive outgroups of coelurosaurs, and most coelurosaurians themselves, display adaptations for carnivory, it is safe to infer carnivory in the common ancestor of forms with the potential for the arctometatarsus. A shift from a macrocarnivorous diet, indicated by toothlessness or other factors (Currie 1997), evolved three times (Figure 5.5; Holtz 2000) or twice (Figure 5.6; Sereno 1999) in theropods with an arctometatarsus, as evinced by its occurrence in Elmisaurus, ornithomimids, and Mononychus. Kobayashi et al. (1999) cite gastroliths associated with ornithomimid skeletons as evidence of herbivory, although modern crocodilians may masticate animal prey with gastroliths in a muscular gizzard (Bakker 1986, Grenard 1991). The arctometatarsus could have been exapted for the primary function of escape in edentulous theropods, but predatory utility cannot be ruled out. Elmisaurids and their oviraptorid relatives, while toothless, had raptorial hands similar to those of dromaeosaurids, with acute recurved claws and joints

suggestive of grasping ability. Neonate *Velociraptor* remains have been found in the nest of an oviraptorid. Predation is therefore a possibility in *Elmisaurus*. If so, agility imparted by the arctometatarsus may have been beneficial in acquiring prey, although the evidence is sparse and indirect.

The forgoing seems to corroborate agility associated with predation as the initial selective impetus for the arctometatarsus, especially because the common ancestor of all coelurosaurs was probably carnivorous. However, neither phylogeny has sufficient resolution to infer that the carnivorous common ancestor had an arctometatarsus. Although available data suggests otherwise, the fossil record is too depauperate to falsify with certainty whether carnivorous arctometatarsailans had herbivorous sister and outgroup clades. However, if this was the case, the arctometatarsus would be interpreted as multiply exapted for a predatory role, from preceding functions for escape or intraspecific combat among herbivores. More crucially, the hypothesis that predation was the motive selective factor rests on accepting the hypothesis of increased agility in arctometatarsalians, and upon a secondary extrapolation that carnivorous coelurosaurs were predaceous. While these suppositions are ostensibly reasonable, in concert they doubly weaken the selective link between potential agility and predation.

A PARSIMONIOUS SCENARIO FOR ARCTOMETATARSUS EVOLUTION

The preceding hypotheses suggest the following tentative conclusions and considerations:

- Proximal intermetatarsal ligaments were probably a prerequisite to the developmental cascade responsible for the arctometatarsus (including the appearance of extensive distal ligaments).
- 2. The arctometatarsus is a homoplasious (convergent) complex that evolved several times in coelurosaurs. The developmental potential for the arctometatarsus was present within coelurosaurs, but apparently not in other theropod taxa. An arctometatarsus discovered in a non-coelurosaurian theropod will falsify this conclusion.
- Finite element results suggest that distal ligaments were mechanically necessary in the arctometatarsus, to prevent breakage of the proximal splint of MT III during vigorous activity.
- If tensile keystone dynamics abetted agility, the probable selective regime under which the arctometatarsus became established was predation performance in carnivorous taxa.

These conclusions, and the mapped distribution of characters in Figures 5.1 through 5.6, suggest possible scenarios for the evolution of the arctometatarsus. The parsimonious distribution on Holtz's phylogeny (Holtz 2000) predicates the scenario outlined below. A scenario serves as an expanded evolutionary hypothesis incorporating a number of lines of evidence, and is most valid when based on simpler hypotheses of relationship (Tattersall and Eldredge 1977). While scenario building was more the rubric in evolutionary systematics, the following narrative phylogeny is falsifiable in whole or in part, and integrates the

available evidence without proprietary didacticism. Thus the scenario is presented as a tentative hypothesis of arctometatarsus evolution.

Intermetatarsal ligaments were present in early carnivorous coelurosaurs. At some point the clade acquired the phylogenetic and developmental propensity for plantar angulation of the metatarsals. When this potential was triggered (along with the development of a lengthened metapodium), the third metatarsal became constricted plantarly and proximally, and intermetatarsal ligaments developed distally on the artictular surfaces. The arctometatarsus developed convergently in the Arctometatarsalia, Elmisauridae (including *Elmisaurus*), and in the alvarezsaurid *Mononychus*.

The arctometatarsus may have imparted functional and selective benefits to predation and/or escape behavior. Within the Arctometatarsalia, predation performance was the likely selective benefit to adult tyrannosaurids and troodontids, and was possibly of benefit to ornithomimosaurs and elmisaurids as well (omnivory has been suggested for these forms and for troodontids; Currie 1997, Holtz et al. 2000; although see Ryan et al. 2000).

The scenario is consistent with the evidence presented in this thesis, but is speculative given the lack of observational data. The remoteness of fossil organisms, their temporal span, and taphonomic limitations to sample size curtail more extensive investigation into the evolution of the arctometatarsus.

However, while evolutionary scenarios are difficult to corroborate (Gee 2000), they are easy to falsify with phylogenetic evidence (Lauder et al. 1989). By this criterion, evolutionary hypotheses are as scientifically credible as hypotheses

with a surfeit of potentially supportive evidence. The limitations of paleontological data must be accepted (Bryant and Russell 1995), but should not deter investigation based on consilient methodologies and skeptical interpretation of available evidence. Figure 5.1. Phylogeny of the Theropoda, primarily after Holtz (2000). *Plateosaurus*, ornithischian dinosaurs, and other archosaurian clades serve as outgroups. Dotted lines show alternate phylogenetic positions for *Herrerasaurus* and *Troodon*. The letter A marks taxa with an arctometatarsus. The diagram designates the observed and inferred presence of extensive proximal intermetatarsal ligaments, according to the following conventions.

IL	Intermetatarsal ligaments present
IL0	Intermetatarsal ligaments not present
-IL	Secondary loss through metatarsal fusion.
IL?	Equivocal evidence
>	Presence inferred through bracketing



Figure 5.2. Phylogeny of the Theropoda, primarily after Sereno (1999), with outgroups as in Figure 5.1. The letter A marks taxa with an arctometatarsus. The diagram designates the observed and inferred presence of extensive proximal intermetatarsal ligaments, according to the following conventions.

- ILIntermetatarsal ligaments presentIL0Intermetatarsal ligaments not present-ILSecondary loss through metatarsal fusion.
- IL? Equivocal evidence
 - Presence inferred through bracketing



Figure 5.3. Phylogeny of the Theropoda, primarily after Holtz (2000), with outgroups as in Figure 5.1. Dotted lines show alternate phylogenetic positions for *Herrerasaurus* and *Troodon*. The occurrence and inferred potential for the development of an arctometatarsus are designated according to the following conventions.



Arctometatarsus

Potential inferred through bracketing

The diagram outlines the first two most parsimonious patterns of the origin and loss of the arctometatarsus derivable from the phylogeny. The following conventions are used:

Possible gain
Possible loss
MP Most parsimonious scenario
SMP Second most parsimonious scenario



Figure 5.4. Phylogeny of the Theropoda, primarily after Sereno (1999), with outgroups as in Figure 5.1. The occurrence and inferred potential for the development of an arctometatarsus are designated according to the following conventions.



Arctometatarsus

Potential inferred through bracketing

The diagram outlines the first two most parsimonious patterns of the origin and loss of the arctometatarsus derivable from the phylogeny. The following conventions are used:

+	Possible gain
-	Possible loss
MP	Most parsimonious scenario
SMP	Second most parsimonious scenario



Figure 5.5. Phylogeny of the Theropoda, primarily after Holtz (2000), with outgroups as in Figure 5.1. Dotted lines show alternate phylogenetic positions for *Herrerasaurus* and *Troodon*. The letter A marks taxa with an arctometatarsus. The diets of theropods and other taxa on the cladogram are designated according to the following conventions:

С	Carnivory
н	Herbivory
?	Equivocal diet





Figure 5.6. Phylogeny of the Theropoda, primarily after Sereno (1999), with outgroups as in Figure 5.1. The letter A marks taxa with an arctometatarsus. The diets of theropods and other taxa on the cladogram are designated according to the following conventions:

C Carnivory H Herbivory ? Equivocal diet



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APPENDIX: Principal Components Analysis

The mechanics and theory behind morphological Principal Components Analysis (PCA) are relatively simple. Dimensions between landmarks on an anatomical structure, or angles subtended by its contours, are measured for a number of specimens. These data are typically log transformed and entered into a matrix of measurements versus specimens.

The variables for these measurements represent coordinate axes in multidimensional space. Each specimen is plotted in a given position in a multidimensional cloud of points (Sokal and Rohlf 1995). PCA determines the variance and covariance of measured dimensions. Important elements of variance and covariance describe the shape of this cloud of points, much like the length and width axes that might describe the shape of an elipse. These **principal axes** that represent important aspects of variation are called **eigenvectors**, and values which denote variance along the axes are called **eigenvalues** (Sokal and Rohlf 1995).

Eigenvalues reveal the relative contribution of principal axes to overall variation. These important contributing factors of variation are called **Principal Components** (abbreviated as **PC**). Because different eigenvalues can represent either variance or covariance, they can reveal the importance size or shape. Measures of linear size might be responsible for the most variation, or a measure of shape, such as ratios of variables, might contribute more.

To reveal what kind of variation a principal component represents, we must examine the impact that individual variables have on that principal component. Different variables in a PCA will have differing contributions to a principal component axis. These contributions are described in terms of numerical **loadings**, which can be either positive or negative. The absolute value of the loading is directly proportional to the variable's contribution to the principal component. If the loadings of nearly all or all variables are positive for that principal component, the component describes size variation for the sample. If many loadings are negative, the principal component probably describes shape variation (Pimentel 1979). Careful examination of loadings can determine the type of shape variation that a given principal component reveals.

The relative importance of a variable to a principal component is determined by its **correlation** with that component. A correlation is simply the correlation coefficient between a variable and its loading on the PC. A high absolute value for a correlation indicates a strong association between the loading and the original variable. If the correlation is low, the variable is less important in explaining the variance along that PC. Regardless of the relative importance of a variable to a PC, the sign of the correlation indicates a shape or size contribution congruently with the sign of the variable's loading. For example, if a variable has both a negative correlation and a negative loading, its importance for shape variation if strongly validated.

PCA therefore determines which Principal Components are responsible for given amounts of variation (Pimentel 1979). Principal Component 1 or PC1 (the largest eigenvector), is responsible for the most variation, PC2 for the second

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highest degree, and so on. Specimens that are similar for a given kind of variation will cluster together, perpendicular to a principal component axis.

While it is difficult to visualize clustering of specimens in a multidimensional space, PCA can show where specimens reside relative to each other along whatever principal component axes we choose. The multidimensional matrix can be rotated mathematically so that PC1 and PC2 (or other combinations) become axes on a two dimensional graph. This process of informatively projecting multidimensional coordinates onto a two dimensional plot is called **ordination** (Pielou 1984). The last five figures of Chapter 2 depict examples of ordination.