# Evolution and Mechanics of Unguligrady in Artiodactyls 

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A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the Department of Ecology and Evolutionary Biology
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## Preface

This dissertation is an anatomical and experimental foray into one of the most celebrated examples of functional specialization in mammals. Hoofed mammals hold a special place in the daily lives of people, and they have certainly served a fundamental role for millennia. People have relied on hoofed mammals for food, transportation, clothing, even companionship. This seemingly symbiotic relationship persists despite, or perhaps because of, a mechanical fascination with the construction of the seemingly graceful, elongate limbs in hoofed mammals. Technicians and lay people alike evoke the language of mechanical engineering when describing the form and function of ungulate limbs. Within a single veterinary text, dramatic mechanical analogies between features of ungulate limbs and engineered structures or mechanical tools can be found: the bowstring bridge supported by columns, the supportive pectoral sling, angled levers within the limbs, a framesaw mechanism anchoring a limb in place, the motors and springs driving limb motion, the plumb-line of support in the forelimb, a stay apparatus in forefeet, a catapult system in hindlimbs (Nickel et al., 1986: 444-450). One wonders if this is Tennyson's "Nature, red in tooth and claw" or something much more mechanical and honed. It is this seemingly-engineered morphology that is the subject of the following chapters.

Scores of researchers over at least two hundred years have addressed the anatomy and function of ungulate limbs. Their research has been synthesized several times into texts that invariably cite ungulates as models of extreme locomotor specialization. The specialized limbs of ungulates are then, literally, textbook examples of supposed extreme performance. Such eminent and well respected texts as Hildebrand \& Goslow's Analysis of Vertebrate Structure, Alexander's Principles of Animal Locomotion, Biewener's Animal Locomotion, Liem et al.'s Functional Anatomy of the Vertebrates, and Vogel's Comparative Biomechanics all relate ungulate
limbs as either manifestations of nature's most extreme engineering of fast running or the most efficient and spring-like elastic structures in large terrestrial animals.

The focus of the present studies is on the most remote outpost of these storied limbs, the manus, (autopodium, forefoot) in artiodactyls, or even-toed hoofed mammals. There are many reasons for restricting the present analysis to this seemingly small subset of such an exquisite suite of interesting morphology. The feet are, in a mechanical sense, where the rubber meets the road. They are the crucial end-effector of all the up-limb actions that these animals carry out and the first structures to deal with an often imposing ground reaction force. The following sections of this work outline mechanical and evolutionary reasons for focusing on artiodactyl forefeet. Briefly, they have a wider anatomical variation in the taxonomic order, are located closer (really - more cranial, or anterior) to the center-ofmass, and have a more weight-bearing role biomechanically than do hindlimbs. Simply stated, telling the story of the evolution of unguligrade foot posture and the accompanying mechanical changes is easier in forefeet than in hindfeet.

In some ways, this story is told backward by beginning in the present time. It is in the very specialized morphology of the present of living artiodactyls that we must begin, and this is where modern biomechanical texts confine their story. The anatomy of well-known and domesticated artiodactyls, such as goats and cattle, is thoroughly described in a number of excellent veterinary anatomy texts. The author has relied primarily on Nickel et al.'s The Anatomy of the Domestic Animals: Volume I: The Locomotor System of the Domestic Mammals. This compendium is noteworthy not only for its anatomical superiority and completeness over other veterinary anatomy texts but also for its emphasis on the functional implications of the anatomy of the locomotor system.

Nickel et al. describe a limb anatomy that is entirely amuscular from the wrist to the hoof. The hoof (or, hooves since we are focusing on even-toed artiodactyls) is the point of support for the limb. It is a keratinous nail-like structure surrounding the last bone of a toe-unguligrady is akin to a ballerina standing en pointe. The remaining bones of the forefoot-middle phalanges, proximal phalanges, metacarpals, carpals-are held off the ground by the muscular, tendinous, and ligamentous soft-tissue structures of the foot. The main structures crossing the wrist into the forefoot are the tendons belonging to the superficial and deep digit flexor muscles and the digit extensor muscles. These tendons (for the muscle fibers have ended proximal to the wrist) pass on either side of a fused metacarpal called a cannon bone (which is actually the fusion of two metacarpals, those of digits III and IV). The side facing cranially for a standing ungulate is the dorsal face of the forefoot, and it is this surface of the metacarpal across which the extensor tendons pass to insert on the distal (ungual-hence 'ungulate') phalanx, deep to the hoof. The opposite surface of the metacarpal is the volar region of the forefoot. In other mammals, such as humans, this surface is called palmar for the hand (i.e., forefoot) and plantar for the foot (i.e., hindfoot). The superficial and deep digit flexor muscle tendons pass through the volar region of the forefoot to insert on the middle and ungual phalanx, respectively.

The structures between the tendons of the digit flexor muscles and the metacarpals in the volar region of the forefoot are the chief focus of the following chapters. There is a set of stiffened muscles that attach proximally on the metacarpals, near where the metacarpals meet the carpal bones. More appropriately called ligaments, these stiffened structures extend parallel to the metacarpals to attach on the proximal part of the proximal phalanges. Interrupting this course, each digit possesses a pair of sesamoid bones on the volar surface of the joint connecting metacarpal bones to the proximal phalanges, the
metacarpo-phalangeal joint. These sesamoid bones act as miniature patellae, not only gliding along the distal articulation of the metacarpal but also dividing the stiffened muscles into a proximal part properly called interosseus ligaments (because they are derived from interosseus muscles) and a distal part called sesamoidean ligaments (because they connect sesamoid bones to proximal phalanges). The sesamoid bones, the sesamoidean ligaments, and some tough but smooth tissue between the sesamoid bones and the digit flexor muscle tendons are collectively called the sesamoidean plate. The interosseus ligaments are variably called suspensory ligaments and spring ligaments in horses and ruminants, presumably from inference of their function of maintaining an elevated foot posture or the hope that they serve as mechanical springs, since they are ligaments. There are specific anatomical differences between the homologous ligaments of horses and artiodactyls, and this dissertation will spend very little time discussing the specifics of the forefeet of horses. Instead, this dissertation attempts to ascribe a functional significance to the interosseus ligaments in artiodactyls by describing its morphology through time in the clade, measuring the motion foot bones undergo during locomotion, and detailing the mechanical contribution of the ligament during the stance phase of locomotion.

From this starting point of a startlingly mechanical morphology in many living eventoed ungulates, the first chapter attempts to describe the transitions in anatomy of forefeet in extinct groups of artiodactyls. Not surprisingly, and fortunately for this study, the origins of even-toed hoofed mammals begins with animals very different from the kinds that exist today. Because these animals are so different, we must look for an analogous kind of animal with which to compare these primitive hoofed mammals, which turn out to be not yet unguligrade or even even-toed in the first place. The analogy that fits best is, ironically, the kind of animal more likely to eat an ungulate than to give rise to one-modern cats and
dogs. Aside from the obvious presence of claws instead of hooves, the anatomy of dogs is an adequate analog for the most primitive and oldest ungulates. Once this anatomical starting point of ungulate evolution can be pinpointed, the next step is to determine when unguligrady first appeared. As with most lengthy answers to straightforward questions, unguligrady evolved through a series of subtle differences in the feet of animals that were previously thought to be rather similar to each other. That is, as far as a cursory examination of fossils had previously told us, the first unguligrade ungulates resembled very closely the last digitigrade ungulates.

The second and third chapters return to the morphology of present-day even-toed ungulates to describe the particulars of locomotion in an unguligrade foot. Minipigs are an extremely tractable research model, and they are the owners of a foot anatomy very similar to the first unguligrade artiodactyls-no foot bones are fused, only the pollex is lost, other intrinsic muscles of the foot remain despite the presence of interosseus ligaments, \&c. This fortuitous similarity hopefully sheds light on the mechanical significance of unguligrady to the first unguligrade artiodactyls, before other specializations that we see in artiodactyls like deer and antelopes and camels evolved. The experiments carried out in the studies described in the second and third chapters utilized a novel data collection system developed at Brown University.

Broadly speaking, the X-ray Reconstruction of Moving Morphology (XROMM) methodology seeks to describe the motion of skeletal elements through time and during specific behaviors. Bones are the common currency between extinct animals represented by fossil remains and the seeming limitless anatomy we encounter in living animals. This makes XROMM a powerful tool for testing inferences of motion at joints made in fossils.

Inference of hinge-like motion has certainly been a hallmark of studies in artiodactyls, both
living and extinct, and the second chapter attempts to test this inference using the extremely detailed measurements of bone motion made possible through XROMM.

The second chapter tests the hypothesis that the metacarpo-phalangeal joint functions like a hinge and explores the difference in foot motion in footfalls made on level ground versus footfalls made down a step. In the level footfalls, the range of angular positions that the foot bones use during the portion of steps when the foot is in contact with the ground turn out to be fairly small. The motion at the metacarpo-phalangeal joint turns out to be very hinge-like, even though the bulk of the motion of the foot takes place in joints of the digit. The step-down footfalls begin in positions different from footfalls used during level walking, which might not be surprising, but the end positions used are strikingly similar.

The third chapter also uses the XROMM methodology but seeks to address the function of the interosseus ligaments themselves. A combined analysis of the motion of the bones on either side of the metacarpo-phalangeal joint in pigs combined with the forces the feet experience during locomotion permits an analysis of the mechanics of the joint. Again, this joint in particular is important because it is the only joint crossed by the interosseus ligaments. If these ligaments are important for maintaining the en pointe foot posture of ungulates, then it should be responsible for much of the force production at the metacarpophalangeal joint. The specific amounts of force produced by the ligament versus the digit flexor muscles can be determined by replicating the motion pigs undergo during steps with just the interosseus ligament present and measuring the force those ligaments resist for a given motion. Thus, by comparing two data sets-one measuring the motion and forces used during locomotion in living pigs to another measuring the motion and forces in reduced (dissected) feet-we can establish the mechanical contribution of the interosseus ligament to the metacarpo-phalangeal joint. Moreover, we can assess the relative importance
of this ligament in various kinds of steps. These various steps use different forces and shed light on whether or not this ligament acts as a spring. The experiments carried out here demonstrate a significant functional importance of the interosseus ligaments at the metacarpo-phalangeal joint in some (but not all) circumstances, but there remain some interesting differences between the results found here in minipigs and the results found elsewhere in other unguligrade ungulates.

The fourth chapter attempts to place the evolution of unguligrade foot posture into context in the life-history of artiodactyls. As often happens, the data presented here, as well as experimental data collected by others, suggest that our first explanations of the mechanically elegant limbs of such graceful animals as leaping gazelles may have been slightly off-the-mark. There may be advantages to restricting motion at joints to a single axis and reducing muscle mass in limbs, but those advantages may not be related to fast running, as was the textbook 'party line.' There is a complex interplay between the selective advantage of all possible morphologies and the restricted set of anatomical substrates that an animal inherits from its ancestors, and the evolution of unguligrady is yet another example of how mechanical and developmental constraints may be overcome by assigning novel functions (or performances) to structures that differ from the functions (or performances) they carried out in ancestors. Finally, it is apparent that unguligrady fundamentally alters the mechanics of a limb, and although we will never be able to observe and measure the specifics of the evolution of unguligrady in the extinct artiodactyls that carried it out, we can attempt to explain the evolution of a suite of extreme limb modifications in the context of organismal and environmental changes.

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This dissertation was the product of significant collaboration with the members of my committee, and I owe them the greatest thanks. First, Steve Gatesy, my primary advisor, was instrumental in helping me formulate and carry out projects in an extremely rigorous way. It is often a challenge to transition between the sometimes made-up research world of modern paleontologists and the more rigorous, but often extant-only, research world of modern functional morphologists. I owe Steve a world of thanks for helping me cross the bridge between those worlds, even if I was sometimes reluctant. Second, Christine Janis was an essential source of advice and expertise in artiodactyls, both living and extinct. Her encyclopædic knowledge of the order was an incredible resource. Finally, Beth Brainerd and Tom Roberts were fantastic additions to my committee. They were incredibly generous with their time, their equipment, their funding, and their vast expertise in experimental functional morphology. To say that I couldn't have done this work without my committee is an immense understatement, and I am indebted to them for all their hard work in this research.

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Next, I owe a debt of gratitude to the curators and collections managers at several museums who were gracious enough to allow me access to their impressive and aweinspiring collections. Like many paleontologists and functional morphologists, I have been inspired ever since my first visit to a natural history museum; having the opportunity to
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CMPL/LLEN. Color indicates digit number according to Figs. $1 \& 2$.
Posture: U—unguligrade; $\mathrm{U}^{*}$-secondarily digitigrade; D -digitigrade; D*_'subunguligrade' or 'superdigitigrade.' Abbreviations: AMNHAmerican Museum of Natural History; F:AM—Frick Collection of the American Museum of Natural History; MCZ—Museum of Comparative Zoology at Harvard University; YPM—Yale Peabody Museum.

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Figure 2.1. Experimental set-up for in vivo steps. Top-down view (left) showing abbreviated trackway (brown) on top of forceplate (grey) with a window for the plexiglass block contacting the forceplate (aqua). Colored cones represent scope of X-ray beams to the image intensifiers. Right image shows oblique view with images from both cameras. 3-D models of metacarpal, proximal phalanx, and ungual phalanx are shown with reconstructed GRF (red) calculated from forceplate data. All objects to scale.

Figure 2.2. Marker placement relative to 3-D models generated from CT data. Neutral anatomical position shown at left and representative stance pose shown at right. X-axes (red) project laterally parallel to the plane of curvature of joint surfaces. Z-axes (blue) are parallel to long axes of each bony element. Y-axes (green) are orthogonal to both of these. Rotation in the x -axis represents antero-posterior rotation (APR); rotation in the y -axis represents medio-lateral rotation (MLR); rotation in the z -axis represents long-axis rotation (LAR).

Figure 2.3. World-space lateral (left column) and frontal views (right column) of representative positions of metacarpal models. A) Metacarpal model shown in neutral position (i.e., $0^{\circ}$ for each axis of rotation). B) Position of metacarpal model after $+45^{\circ}$ APR, $+45^{\circ}$ MLR, and $+30^{\circ}$ LAR. C) Position of metacarpal model after further $+90^{\circ}$ APR from position in B. D) Position of metacarpal model after $+90^{\circ}$ APR, $-15^{\circ}$ MLR and $-60^{\circ}$ LAR from B. See text for details.

Figure 2.4. Angle distribution plots demonstrating anatomical movements. A)
APR angles from lateral view with models superimposed to show representative positions. B) MLR angles from frontal view. C) LAR angles from top-down view. Positive values for each axis to the left and negative values to the right.

Figure 2.5. Superimposed poses of foot bones during stance in a representative level walk. A) Lateral view of poses every $10 \%$ of stance. B) elevated caudal view. Scaffold trackway shown for perspective. Poses at $0 \%$ and $10 \%$ of stance nearly overlap and are labeled in B to illustrate motion early in stance.

Figure 2.6. Angle distribution plots for level walking steps. A) APR (x-axis) toe-on angular positions (left) and toe-off angular positions (right). Bars represent excursion in the APR axis, with end bars representing $\pm$ s.d. B) MLR ( y -axis) toe-on angular positions (circles) and toe-off angular positions (triangles). C) LAR (z-axis) toe-on angular positions (circles) and toe-off angular positions (triangles). Center point represents total mean across individuals, and outside points represent $\pm$ s.d. Top set of points are for metacarpal, middle set are for proximal phalanx, bottom set are for ungual phalanx.

Figure 2.7. Angular excursion graphs for level walking steps. A) Angular positions in the APR axis for metacarpal (solid line), proximal phalanx (dotted line) and ungual phalanx (dashed line). B) LAR angular positions for metacarpal (solid line), proximal phalanx (dotted line) and ungual phalanx (dashed line). C) MLR axis angular positions for metacarpal. D) MLR axis angular positions for proximal phalanx. E) MLR axis angular positions for ungual phalanx. Curves represent means across individuals and grey distributions are $\pm$ s.d.

Figure 2.8. Angle distribution plots for downhill steps. A) APR (x-axis) toe-on angular positions (left) and toe-off angular positions (right) for 10 cm step. Bars represent excursion in the APR axis, with end bars representing $\pm$ s.d. B) MLR ( $y$-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 10 cm step. Center point represents total mean across individuals, and outside points indicate $\pm \mathrm{s} . \mathrm{d}$. C) LAR ( z -axis) toeon angular positions (circles) and toe-off angular positions (triangles) for 10 cm step. D) APR (x-axis) toe-on angular positions (left) and toe-off angular positions (right) for 15 cm step. E) MLR ( $y$-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 15 cm step. F) LAR (z-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 15 cm step. Top set of points in each graph are for metacarpal, middle set are for proximal phalanx, bottom set are for ungual phalanx.

Figure 2.9. Angular excursion graphs for downhill steps. A) Angular position in the APR axis in 10 cm step. B) Angular position in LAR axis in 10 cm step. C) MLR axis angular positions for metacarpal in 10 cm step. D) MLR axis angular positions for proximal phalanx in 10 cm step. E) MLR axis angular positions for ungual phalanx in 10 cm step. F) Angular position in the APR axis in 15 cm step. G) Angular position in LAR axis in 15 cm step. H) MLR axis angular positions for metacarpal in 15 cm step. I) MLR axis angular positions for proximal phalanx in 15 cm step. For $\mathrm{A}, \mathrm{B}, \mathrm{F}, \& \mathrm{G}$, solid line is for metacarpal, dotted line for proximal phalanx, and dashed line for ungual phalanx. Curves represent means across individuals and grey distributions are $\pm$ s.d.

Figure 2.10. Metacarpophalangeal joint angle for global rotations (solid line) representing 2-D view and anatomically-based rotations (dashed line) representing anatomical joint angles. $\pm$ s.d. shown for anatomically-based (light gray) and world-based (dark gray) angles. A) Level steps. B) 10 cm downhill steps. C) 15 cm downhill steps.

Figure 2.11. Solid model representing toe-on positions of representative walk with shadows of foot bone positions at $5 \%, 25 \%$, and $50 \%$ of stance. Note the collapse (extension) at metacarpophalangeal joint that occurs very (at $5 \%$ ) early in stance.

Figure 2.12. Caudal views of foot bone positions during stance. Toe-on and mid-stance positions shown in A and poses at each $10 \%$ of stance shown in B to illustrate extent of MLR during stance in a typical walk sequence.

Figure 2.13. MLR axis angular positions of metacarpal (solid line) and proximal phalanx (dotted line). A) Level walking steps. B) 10 cm downhill steps. C) 15 cm downhill steps. Vertical dotted lines demonstrate $\%$ stance values where MLR axis angular position of proximal phalanx becomes greater than that for metacarpal.

Figure 3.1. Data flow for in vivo trials (A-D) and ex vivo trials (E-F). See text for details.

Figure 3.2. Ex vivo curve fits from experimental data. Grand average of all ex vivo trials (A) and individual averages (B). Colors correspond to individuals (green - sus03; blue - sus04; red - sus05; orange - sus06), and upper and lower thin curves indicate $\pm$ s.d.

Figure 3.3. Individual torque $v$ s. angle curves. Each graph represents all experimental trials from each individual. Colors are as follows: black -ex vivo curve for each individual $\pm$ s.d.; red - level steps; blue -10 cm steps; green -15 cm steps. sus03 in $A$, sus04 in B, sus05 in C, sus06 in D.

Figure 3.4. Total MCP joint torque showin in dark gray, + s.d. in light gray. Proportion of total MCP joint torque taken up by interosseus ligament (red) + s.d. (orange) overlain. Values for level steps (A), 10 cm step (B), and 15 cm step (C) at point where maximum torque was reached. Values for level steps (D), 10 cm step (E), and 15 cm step ( F ) at point where maximum angle is reached.

Figure 4.1. Torque vs. angle graphs for four individuals. Each graph shows the torque vs. angle loops used in the fastest (blue) and slowest (red) level walking trials. Graph labels indicate the speed which produced that loop and the \%torque provided by the interosseus ligament (upper range taken at peak angle, lower range taken at peak torque). Ex vivo fit curves (see Ch. 3) for each individual shown in black. A - sus03; B - sus04; C - sus05; D - sus06.

Figure 4.2. Cost of walking gaits (W), trotting gaits (T), and gallops (G) (black bars, left axis) showing increased relative cost of running gaits in horses. Top bars \& right axis shows increased use of pendular mechanics in horses. Taken from Reilly et al. (2007).

Figure 4.3. Mid-stance poses of digitigrade and unguligrade mammals. Digitigrade mammals in top row, from left to right: dog, dog, lion. Unguligrade artiodactyls in bottom row, from left to right: eland, goat, guanaco, pig. Red arrows indicate position of the wrist. Note how the wrist is extended past vertical in digitigrade mammals while it is held straight in unguligrade mammals. From Muybridge (1957).

Figure 4.4. Mass-specific metabolic cost of locomotion in similarly-sized carnivorans and artiodactyls. Taken from Taylor et al. (1982). Values in parentheses are normalized for speed and size $\left(\mathrm{mL} \mathrm{O}_{2}\right.$ per meter per kilogram).

## CHAPTER 1: THE EVOLUTION OF THE UNGULIGRADE MANUS IN ARTIODACTYLS


#### Abstract

Artiodactyls show a step-wise morphological transition from groups with a primitive and pentadactyl limb configuration to groups with more derived and didactyl limb configurations. An analysis of proportions of the forelimb segments indicates that artiodactyls separate based on digit number in the manus along a morphometrical axis indicating relatively longer manus segments. The three digit configurations in artiodactyls (pentadactyl, tetradactyl, didactyl) are identified and the relevant bony characteristics of each configuration are described. Among tetradactyl groups, there are two grades of anatomy in the manus. In the more derived tetradactyl groups (tayassuids, tragulids, and early camelids), the proximal volar metacarpal process reduces and joints of the digit become more ginglymal in comparison with the less derived tetradactyl groups (ticholeptine and merychyine oreodonts, leptomerycid traguloids, primitive cainotheres, oromerycids and protoceratids). The foot posture of members of the pentadactyl groups is interpreted as digitigrade. The evolution of unguligrady took place between the morphological condition of the primitive type of tetradactyl manus and the derived type of tetradactyl manus. This transition to unguligrady occurred at least 3 times and was facilitated each time by the formation of ginglymal joints of the digit and the transition to interosseus ligaments from muscular precursors.


## INTRODUCTION

Mammals possess three categories of foot posture. The primitive foot posture, and the one retained by most small quadrupedal mammals, is termed plantigrade. In this foot posture, the entire autopodium (manus or pes) rests on the ground during standing. Either the ankle (for the pes) or the wrist (for the manus) lies along the ground along with the metapodials and phalanges. A system of cutaneous fibrofatty pads forms the volar (or palmar or plantar) contact surface. A more derived condition where the ankle or wrist is elevated from ground contact during standing is termed digitigrade. In this posture, the metapodial-phalangeal (MPP) joint is the most proximal joint lying along the ground. Extant cats and dogs are good examples of species with digitigrade foot posture, and elevating the wrist off the ground accompanies a degree of cursoriality. Again, fibrofatty cutaneous pads under the MPP joints and the ends of the phalanges form the contact surface. The foot pads make the characteristic 'paw prints,' and the volar pads that do not contact the ground are variably lost.

A type of digitigrade foot posture in ungulates (herbivorous mammals with a hoofed distal, or ungual, phalanx) is often termed 'subunguligrade' (Thomason, 1986; Carrano, 1999). In this foot posture, the MPP joints again contact the ground through a fibrofatty pad, but the digits are aligned more vertically than in a simple digitigrade posture. Because this is still a technically digitigrade posture, the term 'superdigitigrade' is more appropriate than 'subunguligrade'. The most derived foot posture in mammals, termed unguligrady, is one in which the ungual phalanx is the only skeletal element contacting the ground through a fibrofatty digital pad, which is now bounded on at least two sides by a keratinous hoof. The volar pads not associated with the digit (i.e., in the palm or sole) are usually lost and, when
present, do not contact the ground in unguligrade taxa, and ungual hooves and digit pads provide much of the contact surface during standing.

Unguligrade mammals, those that stand on the hoofed distalmost phalanx, represent one of the classic examples of locomotor specialization. The elongate, gracile limbs of camels, antelopes, deer, and horses make these mammals paragons of fast, efficient terrestrial locomotion (Howell, 1944). That said, not all unguligrade taxa are long-limbed. Unguligrady has evolved several times, within the orders Cetartiodactyla, Perissodactyla, Notoungulata, and Litopterna (Howell, 1944). Cetartiodactyls, or 'even-toed' ungulates are an ideal group for studying the evolution of unguligrady and its effect on locomotor performance. The diversity of extant terrestrial cetartiodactyl species (hereafter artiodactyls, Fig. 1.1) combined with the immense fossil record of the clade indicates a complex pattern of parallelisms in the evolution of unguligrade foot posture. This paper describes the convergence or parallel evolution of the bony features indicative of an unguligrade stance and in the relevant soft-tissues that facilitate the maintenance of unguligrade posture.

The history of locomotor morphology in artiodactyls has been seen either as a stepwise 'arms race' with pursuit predators (Simpson, 1944) or as a linear progression toward a mechanically efficient, fast-moving limb (Hildebrand \& Goslow, 2001). For the former hypothesis, the crux of the argument is a simple selectionist paradigm: the fastest lion must outrun the slowest antelope, so both populations pass on increasingly cursorial traits-i.e., the classical notion of an 'arms race.' Janis \& Wilhelm (1993) showed that carnivores and ungulates did not coevolve with respect to limb anatomy, and that long-limbed and presumed cursorial herbivores first appear in the late Oligocene while similarly-proportioned predators are a Pliocene phenomenon. This arms race scenario has also overshadowed a fundamental difference between the locomotor apparatus of extant artiodactyls and their


Figure 1.1. Phylogenetic relationships of the major clades examined in this study. Topology taken from Geisler et al. (2005). Color code of branches indicates digit number: 5 digits (pentadactyl) in red; 4 digits (tetradactyl) in orange; 2 digits (didactyl) in green.
carnivoran predators: the prey have a highly derived unguligrade stance while the predators are digitigrade. If there is an arms race between these two groups, and if they had similar running speeds (as they do today), then why are the limbs so anatomically different?

Additionally, the supposed cursorial features of herbivores-namely elongated limbs and unguligrade posture—evolved around 20 Ma prior to the evolution of predators with limb proportions like those of extant pursuit predators in the Pliocene, meaning these features must have been evolved for more than predator avoidance. Because the arms race hypothesis was proffered without regard to the actual anatomy and biomechanics of the animals involved, its rejection by researchers examining anatomical features of the limb should not seem surprising. Moreover, unguligrady is unexplained by the arms race hypothesis, since the prey evolve much more derived limbs than the predators. Finally,
explaining the morphological features in the limbs of cursorial ungulates post-hoc ignores the selective pressures and evolutionary history of the species in question and says nothing about the impact these derived features have on organismal mechanics and energetics during locomotion.

The highly derived limbs of ruminants such as antilocaprids or antilopine bovids are literally textbook examples of limbs specialized for: 1) reducing distal mass of the limb, thus making the limb cheaper to swing (Howell, 1944); 2) optimizing elastic energy recovery by shortening muscle bellies and distally lengthening tendons (Alexander et al., 1982); and 3) shortening muscle moment arms by using a straighter leg posture which optimizes speed at the expense of power (Maynard-Smith \& Savage, 1955). Larger terrestrial animals stand with a more erect limb posture (Biewener, 1989) and are 'superdigitigrade' in the largest herbivores, such as rhinos and elephants (Carrano, 1999). Unguligrade limbs are also more straight-legged and erect than digitigrade ones in most cases, complicating the relationship between body size and unguligrady.

What then are the anatomical and functional differences between unguligrady and digitigrady? How many times has unguligrady evolved in artiodactyls? Where are the transitions to unguligrady within artiodactyl phylogeny? Identifying these instances of the transitions to unguligrady is a critical first step in understanding the selective pressures and performance advantage(s) leading to this extreme foot posture. The locomotor capabilities of extinct animals can be determined by linking known performance parameters found in extant species with inferred crucial soft-tissue structures in extinct species, among close relatives (e.g. Thomason, 1986). This study seeks to determine the anatomical and postural transitions in artiodactyl forefeet in order to understand the evolutionary history of one of the clade's most distinctive characteristics.

The specialized features in the limbs of artiodactyls impact locomotor biomechanics in several ways. Gregory (1912) noted that in the limbs of derived ungulates, distal segments (such as metapodials) are elongated, lateral toes are reduced or lost, and remaining digit elements are at least partially fused, thus making the limbs lighter and also permitting total limb lengthening. Howell (1944) expanded this idea, arguing that a lighter limb will require smaller swing forces, thereby reducing energy output during fast locomotion. Initially, experiments seemed to show that the cost of producing force during stance is relatively large enough to neglect costs in limb swing (Taylor et al., 1980); however, other more recent data demonstrate that swing phase muscles incur a significant metabolic cost (Marsh et al., 2004). Secondly, distal limb elongation results in a leg with longer digital tendons, such as those of the superficial and deep digital flexors, which serve as a site of elastic energy storage (Alexander et al., 1982). Also, longer legs result in longer steps, which in turn lead to faster locomotion if stride frequency is kept constant. If a lighter leg is longer and easier to move, then faster locomotion seems a natural result (Hildebrand \& Goslow, 2001).

Next, elongated and erect limbs in ungulates permit muscle attachment sites that are closer to limb joints (or, joint centers of rotation), facilitating faster motion through a wider arc for a given amount of muscle shortening due to smaller moment arms (Smith \& Savage, 1956). Finally, increased induced speed of the limb is also facilitated through erect foot posture in digitigrade and unguligrade (as opposed to plantigrade) animals by allowing 'extra' distal joints to rotate in the plane of motion. Limbs themselves are able to recycle faster, permitting a higher step frequency, which will contribute to increased speed. Joints such as the metacarpophalangeal joint (for unguligrade stance) and the wrist (for digitigrade and unguligrade stance) are now held off the ground and support some fraction of the body weight, as opposed to lying along the ground as in a plantigrade stance. Cursorial limbs are
largely restricted to pure flexion/extension motion in the parasagittal plane by trochleated or strongly ginglymal joints (Hildebrand \& Goslow, 2001). Many of these hypotheses linking morphology with locomotor performance adequately describe the performance advantages of these highly derived limbs, and considerable experimental support justifies several of these (reviewed in Biewener, 2003). However, they do not explain the reason for the evolution of these derived limbs or their ecological impacts.

The center-of-mass for quadrupeds (except primates) lies closer to the forelimb than the hindlimb. This is especially true for ungulates, due to their long necks and/or heavy heads. Forelimbs produce a net braking force during the stance phase of locomotion, since they are in front of the center of mass (Biewener, 2003). Hindlimbs, in contrast, produce a net accelerating force. For this reason, one might expect to find fundamental differences in anatomical structure between forelimbs and hindlimbs. Indeed, ungulate mammals, both living and extinct, have anatomical and postural differences between fore- and hindlimbs (Fischer, 1999). For the most part, the forelimb shows similar morphological changes as the hindlimb, but the forelimbs often tend to evolve certain features after hindlimbs do. For example, forefeet tend to retain more digits, more primitive proportions, and more primitive foot posture (Romer \& Parsons, 1977). There are extant animals, such as viverrids, procyonids and hyraxes that have a plantigrade posture in forelimbs and a digitigrade posture in hindlimbs. Because there is a wider range of anatomical variation in forelimbs than hindlimbs in ungulates, forelimbs are more amenable to studying the anatomical and postural transition from digitigrady to unguligrady than are hindlimbs.

## Materials \& Methods

Table 1.1 lists the families of artiodactyls and other mammals studied and museums visited for this study. Segment lengths were measured in 69 different species of mammal for which complete forelimbs were available. For these species, interarticular measurements were taken for the humerus (zeugopodium), radius (stylopodium), and carpus + metcarpals + phalanx of digit IV (autopodium). In monodactyl taxa (i.e., equids), digit III was used instead. Table 2 lists the individuals measured and the specific values for each specimen. In order to compare segment proportions within a limb, these data were used to plot a ternary diagram of intramembranal proportions (cf. Gatesy \& Middleton, 1997). Although the scapula forms a freely-moving segment of the forelimb (Fischer et al., 2002), especially in terrestrial artiodactyls, this segment was omitted from the analysis because the extent of the suprascapular cartilage could not be accurately estimated, even in extant specimens. Species differ greatly in the amount of suprascapular cartilage, to which the subscapularis, supraspinatus, infraspinatus, and serratus anterior muscles attach (Nickel et al., 1986); there are no reliable osteological correlates for estimating the size of the suprascapular cartilage.

Additionally, forefeet from 10 pigs (6 Sinclair minipigs, Charles River; 4 grocery store specimens, Stop-N-Shop, Providence) were dissected to describe the soft-tissue anatomy of the foot. Veterinary texts (e.g., Nickel et al., 1986; Evans, 1993) were used to verify findings for cattle and goat and to establish homologies for soft-tissues between pigs and dogs. Standard gross techniques were used to provide detail of the interosseus structures in pigs, since other domestic species are well-described.

Artiodactyla

| Antilocapridae | SPECIMEN | LLEN | HUML | RADULL | CMPL | H\% | RU\% | CMP\% | posture |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :---: | :---: |
| 1. Antilocapra americana | MCZ 1776 | 710.0 | 176.0 | 205.0 | 329.0 | 0.248 | 0.289 | 0.463 | U |
| 2. Antilocapra americana | Brown U | 690.0 | 162.0 | 197.0 | 331.0 | 0.235 | 0.286 | 0.480 | U |


| Bovidae |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 3 Aepycerus melampus | MCZ 57521 | 684.0 | 150.0 | 207.0 | 327.0 | 0.219 | 0.303 | 0.478 | U |
| 4 Ammotragus lervia | AMNH 35456 | 587.5 | 168.0 | 182.0 | 237.5 | 0.286 | 0.310 | 0.404 | U |
| 5 Bison bison | AMNH 3458 | 1012.0 | 316.0 | 304.0 | 392.0 | 0.312 | 0.300 | 0.387 | U |
| 6 Bison bison | AMNH 19380 | 942.5 | 277.0 | 286.0 | 379.5 | 0.294 | 0.303 | 0.403 | U |
| 7 Bos taurus | MCZ 54380 | 857.0 | 294.0 | 310.0 | 253.0 | 0.343 | 0.362 | 0.295 | U |
| 8 Capra ibex siberica | AMNH 54908 | 735.0 | 203.0 | 226.0 | 306.0 | 0.276 | 0.307 | 0.416 | U |
| 9 Cephalophus silvicultor | MCZ 58312 | 614.0 | 176.0 | 173.0 | 265.0 | 0.287 | 0.282 | 0.432 | U |
| 10 Hemitragus jemlaticus | AMNH 90085 | 706.0 | 211.0 | 223.0 | 272.0 | 0.299 | 0.316 | 0.385 | U |
| 11 Litocranias walleri | MCZ 8734 | 757.5 | 148.0 | 209.0 | 400.5 | 0.195 | 0.276 | 0.529 | U |
| 12 Oreotragus oreotragus | MCZ 14555 | 384.5 | 116.0 | 107.0 | 161.5 | 0.302 | 0.278 | 0.420 | U |
| 13 Ovis canadensis | MCZ 123 | 746.0 | 191.0 | 216.0 | 339.0 | 0.256 | 0.290 | 0.454 | U |
| 14 Redunca redunca bobor | MCZ 14917 | 653.0 | 151.0 | 186.0 | 316.0 | 0.231 | 0.285 | 0.484 | U |
| 15 Saiga tatarica | Brown U | 563.5 | 139.0 | 167.0 | 257.5 | 0.247 | 0.296 | 0.457 | U |


| Camelidae |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 16 Camelus bactrianus | AMNH 14113 | 1477.0 | 384.0 | 498.0 | 595.0 | 0.260 | 0.337 | 0.403 | U* |
| 17 Camelus dromodarius | AMNH 14112 | 1302.0 | 341.0 | 434.0 | 527.0 | 0.262 | 0.333 | 0.405 | U* |
| 18 Lama buanachus | MCZ 1881 | 782.5 | 198.0 | 245.0 | 339.5 | 0.253 | 0.313 | 0.434 | $\mathrm{U}^{*}$ |
| 19 Lama buanachus | Brown U | 868.5 | 223.0 | 264.0 | 381.5 | 0.257 | 0.304 | 0.439 | U* |
| 20 Merychenia sp. ${ }^{+}$ | AMNH 24073 | 855.0 | 57.0 | 41.0 | 354.0 | 0.256 | 0.330 | 0.414 | U* |
| 21 Poebrotberium sternbergi ${ }^{\dagger}$ | AMNH 7910 | 644.0 | 57.0 | 41.0 | 264.0 | 0.261 | 0.329 | 0.410 | U |
| 22 Protolabis coartatus ${ }^{\dagger}$ | AMNH 38692 | 990.0 | 57.0 | 41.0 | 390.0 | 0.270 | 0.336 | 0.394 | U |
| 23 Stenomylus bitchcocki ${ }^{+}$ | AMNH 43569 | 594.0 | 57.0 | 41.0 | 251.0 | 0.247 | 0.330 | 0.423 | U |


| Cervidae |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 24 Alces alces | Brown U | 1304.5 | 354.0 | 397.0 | 553.5 | 0.271 | 0.304 | 0.424 | U |
| 25 Cervalces americana $^{+}$ | AMNH 107678 | 1517.5 | 404.0 | 453.0 | 660.5 | 0.266 | 0.299 | 0.435 | U |
| 26 Cervus elaphus | MCZ 133 | 1150.0 | 311.0 | 327.0 | 512.0 | 0.270 | 0.284 | 0.445 | U |
| 27 Dama dama | MCZ 59125 | 616.0 | 153.0 | 174.0 | 289.0 | 0.248 | 0.282 | 0.469 | U |
| 28 Mazama americana | MCZ 58306 | 431.0 | 129.0 | 120.0 | 182.0 | 0.299 | 0.278 | 0.422 | U |
| 29 Odocoilens sp. (?) | Brown U | 710.0 | 208.0 | 201.0 | 301.0 | 0.293 | 0.283 | 0.424 | U |
| 30 Rangifer tarandus | MCZ 1657 | 968.0 | 258.0 | 303.0 | 407.0 | 0.267 | 0.313 | 0.420 | U |
| Dromomerycidae ${ }^{\dagger}$ |  |  |  |  |  |  |  |  |  |
| 31 Aletomerox gracilis' | FAM 53226 | 455.0 | 123.0 | 156.0 | 176.0 | 0.270 | 0.343 | 0.387 | U |
| Hippopotamidae |  |  |  |  |  |  |  |  |  |
| 32 Choeropsis liberiensis | AMNH 148452 | 581.0 | 212.0 | 155.0 | 214.0 | 0.365 | 0.267 | 0.368 | D* |
| 33 Hippopotamus aquaticus | AMNH 99637 | 1011.0 | 387.0 | 264.0 | 360.0 | 0.383 | 0.261 | 0.356 | D* |

Entelodontidae ${ }^{\dagger}$

| 34 Archaeotherium mortoni ${ }^{+}$ | AM 1483 | 656.5 | 201.0 | 208.0 | 247.5 | 0.306 | 0.317 | 0.377 | U* |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 35 Davodon sp. ${ }^{\dagger}$ | AM 7380 | 1288.5 | 419.0 | 437.0 | 432.5 | 0.325 | 0.339 | 0.336 | U* |
| Giraffidae |  |  |  |  |  |  |  |  |  |
| 36 Giraffa camelopardalis | MCZ 14564 | 2019.0 | 407.0 | 662.0 | 950.0 | 0.202 | 0.328 | 0.471 | U |
| 37 Okapia johnsoni | MCZ 38015 | 1063.0 | 274.0 | 319.0 | 470.0 | 0.258 | 0.300 | 0.442 | U |

## $\underline{\text { Leptomerycidae }{ }^{\dagger}}$

| 38 Lepromerox sp.' | AMNH 38910 | 230.0 | 79.0 | 74.0 | 77.0 | 0.343 | 0.322 | 0.335 | D* |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Merycoidodontidae ${ }^{\dagger}$ |  |  |  |  |  |  |  |  |  |
| 39 Megoreodon grandis ${ }^{\dagger}$ | F:AM 42320 | 553.0 | 204.0 | 169.0 | 180.0 | 0.369 | 0.306 | 0.325 | D |
| 40 Bragurus swectuvaternsis ${ }^{+}$ | F:AM 33494 | 433.0 | 161.0 | 128.0 | 144.0 | 0.372 | 0.296 | 0.333 | D* |


| 41 Merycoidodon culbertsoni ${ }^{+}$ | AM 72286 | 391.0 | 146.0 | 120.0 | 125.0 | 0.373 | 0.307 | 0.320 | D |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 42 Merychyus arenarum ${ }^{+}$ | F:AM 43279 | 381.0 | 140.0 | 121.0 | 120.0 | 0.367 | 0.318 | 0.315 | D* |
| 43 Stenopsochoerus douglasensis ${ }^{\dagger}$ | F:AM 45492 | 314.0 | 118.0 | 90.0 | 106.0 | 0.376 | 0.287 | 0.338 | D |
| 44 Psendogrlopidens lullianus ${ }^{\dagger}$ | AM 57090 | 296.0 | 114.0 | 85.0 | 97.0 | 0.385 | 0.287 | 0.328 | D |

$\underline{\text { Protoceratidae }}{ }^{\dagger}$

| 45 Protocensus ctar' | F:AM 1227 | 440.0 | 57.0 | 41.0 | 158.0 | 0.318 | 0.323 | 0.359 | D |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Suidae |  |  |  |  |  |  |  |  |  |
| 46 Hylochoerus meinlertzhageni | MCZ 27851 | 604.5 | 232.0 | 169.0 | 203.5 | 0.384 | 0.280 | 0.337 | U |
| 47 Pbacochoerns acthiopticus | MCZ 51083 | 513.0 | 182.0 | 158.0 | 173.0 | 0.355 | 0.308 | 0.337 | U |
| 48 Sus scrmfa | MCZ 6246 | 630.0 | 223.0 | 191.0 | 216.0 | 0.354 | 0.303 | 0.343 | U |

Tayassuidae

| 49 Platgeonus compressus ${ }^{+}$ | AMNH 45751 | 510.5 | 163.0 | 148.0 | 199.5 | 0.319 | 0.290 | 0.391 | U |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 50 Prosthenops niobrarensis ${ }^{+}$ | F:AM 42886 | 458.0 | 141.0 | 130.0 | 187.0 | 0.308 | 0.284 | 0.408 | U |
| 51 Tagassu pecari albirostris | AMNH 23538 | 372.5 | 57.0 | 41.0 | 138.5 | 0.352 | 0.277 | 0.372 | U |
| 52 Tayassu tajach tajacu | AMNH 215157 | 330.5 | 57.0 | 41.0 | 124.5 | 0.348 | 0.275 | 0.377 | U |
| 53 Tagassus tajach | MCZ 1915 | 337.0 | 123.0 | 90.0 | 124.0 | 0.365 | 0.267 | 0.368 | U |

Tragulidae

| 54 Hemoschus aquaticus aquatious | MCZ 1109 | 251.0 | 91.0 | 71.0 | 89.0 | 0.363 | 0.283 | 0.355 | U |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 55 Trugulus jaramious | MCZ 3828 | 191.0 | 64.0 | 59.0 | 68.0 | 0.335 | 0.309 | 0.356 | U |

## Perissodactyla

Equidae

| 56 Equus caballus | Brown U | 1238.0 | 348.0 | 378.0 | 512.0 | 0.281 | 0.305 | 0.414 | U |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 57 Pliohippus pervix ${ }^{\dagger}$ | YPM 13007 | 775.0 | 206.0 | 238.0 | 331.0 | 0.266 | 0.307 | 0.427 | U |
| Rhinoceratidae |  |  |  |  |  |  |  |  |  |
| 58 Ceratotherium simum | MCZ 24917 | 1106.0 | 385.0 | 367.0 | 354.0 | 0.348 | 0.332 | 0.320 | D* |
| 59 Diceros bicornis | MCZ 15695 | 1075.0 | 388.0 | 355.0 | 332.0 | 0.361 | 0.330 | 0.309 | D* |
| Tapiridae |  |  |  |  |  |  |  |  |  |
| 60 Tapirus bairdi | MCZ 63107 | 726.0 | 247.0 | 217.0 | 262.0 | 0.340 | 0.299 | 0.361 | D* |

Carnivora
Canidae

| 61 Canis latrans | MCZ 57485 | 474.0 | 160.0 | 167.0 | 147.0 | 0.338 | 0.352 | 0.310 | D |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 62 Cbrysoçon brachyurus | AMNH 133941 | 718.0 | 248.0 | 272.0 | 198.0 | 0.345 | 0.379 | 0.276 | D |
| 63 Cuon alpinus javamicus | AMNH 102083 | 359.0 | 128.0 | 113.0 | 118.0 | 0.357 | 0.315 | 0.329 | D |
| 64 L.jucaon pictus lupinus | AMNH 82087 | 537.0 | 184.0 | 194.0 | 159.0 | 0.343 | 0.361 | 0.296 | D |
| 65 Speothos venaticus | AMNH 167846 | 265.0 | 95.0 | 83.0 | 87.0 | 0.358 | 0.313 | 0.328 | D |
| Felidae |  |  |  |  |  |  |  |  |  |
| 66 Acinonyx jubatus | AMNH 35037 | 570.0 | 201.0 | 207.0 | 162.0 | 0.353 | 0.363 | 0.284 | D |
| 67 Felis domestica | Brown U 68-2378 | 238.0 | 89.0 | 80.0 | 69.0 | 0.374 | 0.336 | 0.290 | D |
| 68 Pantbera leo | Brown U | 739.0 | 264.0 | 241.0 | 234.0 | 0.357 | 0.326 | 0.317 | D |
| Hyaenidae |  |  |  |  |  |  |  |  |  |
| 69 Hyaena brunnea | MCZ 57136 | 587.0 | 195.0 | 208.0 | 184.0 | 0.332 | 0.354 | 0.313 | D |

Table 1.1. List of specimens and limb measures used to generate limb proportion ternary diagram.
Abbreviations: LLEN - total leg length; HUML - interarticular length of the humerus; RADULL interarticular length of the radius (or fused radius + ulna); CMPL - combined length through digit IV (or III if no IV) of the carpus, metacarpus, and phalanx; H\% - HUML/LLEN; RU\% - RADULL/LLEN; CMP \% - CMPL/LLEN. Color indicates digit number according to Figs. 1 \& 2. Posture: Uunguligrade; $\mathrm{U}^{*}$ —secondarily digitigrade; D —digitigrade; $\mathrm{D}^{*}$-subunguligrade' or 'superdigitigrade.' Abbreviations: AMNH—American Museum of Natural History; F:AM—Frick Collection of the American Museum of Natural History; MCZ—Museum of Comparative Zoology at Harvard University; YPM—Yale Peabody Museum.

## Results

## Intramembranal proportions

Intramembranal proportions, or the proportion of total limb length taken up by the proximal, middle, and distal limb segments, show an interesting trend in artiodactyls. Values for early forms, such as members of the oreodont clade, cluster tightly together and lie fairly close to carnivorans such as canids and felids (Fig. 1.2). The variation between these


Figure 1.2. Ternary plot of forelimb proportions in selected artiodactyl and terrestrial cursorial taxa. A) full plot showing the spread of data points within a possible morphospace. B) trimmed morphospace to show detail of data. Color scheme as in Fig. 1; tridactyl taxa in purple; monodactyl taxa in blue. Numerals adjacent to data points correspond to measurements for individual specimens listed in Table 1.1.
(mostly) pentadactyl groups occurs along a humerus proportion between $33 \%$ and $38 \%$. The axis of greatest variation for artiodactyls, and possibly all ungulates, lies along the manus axis, while for canids, and possibly all carnivorans, the axis of greatest variation is along the radius axis. From this intersection of extinct pentadactyl artiodactyls and extant canids, the remaining artiodactyls vary approximately along the line indicating limbs with $30 \%$ of total limb length in the radius (middle) segment. What makes this variation most interesting is that taxa are separated roughly by the number of digits they possess in the manus. The pentadactyl groups sit at the bottom of this cluster, while the slender-limbed didactyl groups sit at the top. A series of tetradactyl groups occupies the intermediate space within the cluster. Other ungulate taxa that possess a tetradactyl manus (i.e., extant tapirs) also occupy a similar region, although usually with a slightly longer radius.

The line signifying a limb that is $40 \%$ manus more-or-less separates taxa that fuse the metacarpals (above the line) from those that do not (below the line). The only tetradactyl taxon above this line, the extinct peccary Prosthennops, is a long-limbed suoid with metacarpals that are fused proximally. Didactyl taxa that fall below this line are as follows: entelodonts (Archaeotherium and Daeodon) with unfused metacarpals but otherwise unusually derived limbs (Effinger, 1998), Bison with a secondarily-shortened manus (Scott, 1985), the camelid Protolabis also with secondarily-shortened limbs (Honey, et al., 1998), the domestic Bos (which occupies an admittedly bizarre place), and Hemitragus (Himalayan taur). Crown ruminants and camelids cluster together with a manus making up at least $40 \%$ of total forelimb length. Also, among equids, both extant Equus and extinct Pliohippus also fall into this cluster of didactyl artiodactyls. Tetradactyl (tapirs) and tridactyl (rhinos) perissodactyl taxa cluster more closely to tetradactyl artiodactyls, and perissodactyls demonstrate a similar trend to that in artiodactyls-perissodactyls vary in intramembranal proportions from
tetradactyl to monodactyl taxa primarily by the proportion of the forelimb taken up by the manus. The taxa with forelimbs that have the largest forelimb proportion as manus are Giraffa, Antilocapra (pronghorn), and the medium-sized bovids Redunca (reedbuck), Aepyceros (impala), and the outlying Litocranius (gerenuk). The didactyl taxa with the highest proportion of forelimb as humerus are the small-bodied cervid Mazama (brocket deer), the small-bodied bovid Oreotragus, the caprine bovid Hemitragus, and and large-bodied bovine bovids such as Bos and Bison, in addition to the unusually-derived entelodonts.

## Pentadactyl artiodactyl manus

The ancestral manus of artiodactyls is pentadactyl, with a reduced digit I (i.e., pollex) and fairly equally-sized digits II-V (Fig. 1.3). Defining digit reduction relative to other digits is problematic, since artiodactyls enlarge the digits III and IV as the digits II and V are reduced. In this study, a digit is defined as reduced if the width of its metacarpal is less than half the width of the metacarpal of digit III or IV (since those digits are never 'reduced'), and a digit is defined as complete if all elements of the digit (metacarpal and phalanges) are complete. These definitions seem arbitrary, but they are easily measured even in incomplete specimens. Additionally, lateral digits that are half the width of central ones clearly seem to be taken out of an important role in locomotion; they are not strong enough to transmit substantial supportive forces or to withstand propulsive ones, and they likely do not significantly contact the ground during normal locomotion.

There are several important characteristics of the ancestral manus in artiodactyls, and these features are shared among families in disparately related groups. The groups examined in the present study possessing the primitive and pentadactyl manus outlined below are listed in Table 1.1 and Figure 1.1. Most of these taxa are small- and medium-sized forms from the Eocene, and the lack of well-preserved postcrania for several of these taxa and the apparent


Figure 1.3. Pentadactyl artiodactyl taxa. A) Heptacodont, an anthracothere, right manus in dorsal view. B) Hypertragulust, a basal ruminant, right manus in dorsal view. C) Merycoidodont, an oreodont, right manus in dorsal view. D) Merycoidodont, right manus in volar view. A) \& B) after Scott \& Jepsen (1940). C) \& D) from AM72286. Abbreviations: dmf - dorsal metacarpal fovea; mk - metacarpal keel; vpc - volar process of the capitate; vph - volar process of the hamate; vpm - volar process of the metacarpal. Scale bar $=$ 1 cm .
derived nature of some other basal artiodactyls (e.g., diacodexeids) complicates any description of the actual ancestral manus for the group. Diacodexeids, small early Eocene artiodactyls from North America and Eurasia, are relatively long-legged and have been compared more often to derived artiodactyl taxa like tragulids than more contemporaneous taxa like dichobunids and later Eocene oreodonts (Theodor et al., 2005). In fact, some of the most exemplary taxa showing the most primitive pattern of manus anatomy in artiodactyls are well-nested within the phylogeny and are later in time. That said, oreodonts are an exemplary group for describing the primitive manus of artiodactyls. Oreodonts are an
exclusively-North American extinct group of small and medium-sized artiodactyls from the late Eocene to the late Miocene. Bony features such as muscle and ligament scars and articular surfaces of the limbs of oreodonts (except for the more derived ticholeptines and merychyines, described later) are identical to those seen in the limbs of many primitive extinct artiodactyl groups such as homacodonts, hypertragulids, anthracotheres and dichobunids. Also, the body sizes of most oreodont taxa allow for sufficient examination of these features, which are difficult to discern in smaller and less well-preserved taxa.

Each of the three major lineages of terrestrial artiodactyls (the suines, tylopods, and ruminants) has members possessing a basal pentadactyl manus, and, as a first approximation, Dollo's Law should at least presuppose that this is the ancestral condition for these clades: since pentadactyl taxa are nested within the phylogeny, it is much more likely that they retained an inherited pentadactyl manus rather than they re-developed (or 're-evolved') digits. The generalized pentadactyl manus of artiodactyls has several key features of the bones of the wrist, palm, and digits that are shared among all the pentadactyl groups and are crucial for understanding the functional morphology of these earliest and most primitive artiodactyls. It is from this manus that the great variation of manual anatomy among artiodactyls was derived.

The carpal bones of the generalized primitive artiodactyls are unremarkable in their morphology, as compared to those of other closely related terrestrial orders. There is a full and unfused set of carpals whose articular surfaces are more or less rounded. Articulations between the radius and ulna with the proximal row of carpal bones (scaphoid, lunate, and triquetrum) are strongly curved in both the volar/palmar and the mediolateral axes. The joint surfaces alone do not suggest a plane of restricted motion. The carpometacarpal articulations are similarly unspecialized. There is moderate curvature in the mediolateral
direction, yielding joints that have the greatest range of motion in the palmar/volar axis. For the most part, there is a curved surface of the proximal metacarpal articulation, which would apparently allow for considerable flexion of the wrist in addition to extension past 90 degrees (i.e., hyperextension). The capitate and hamate possess distally-projecting processes that extend onto the volar surface of the base of the metacarpal. These processes add to the curvature of the carpo-metacarpal joints, suggesting primarily flexion/extension motion along the dorsovolar axis.

The metacarpals themselves have several distinguishing characteristics that are common among many groups of primitive artiodactyls. The metacarpals are subequal in length—metacarpals of the second and fifth digit are always shorter than those of the third and fourth. When the metacarpals are held in a neutral position, the metacarpals give the manus a convex shape. Features of the first metacarpal and its associated phalanges are unremarkable, except in their reduction. Since the first digit is so obviously reduced, there are few distinguishing and common osteological features that have any functional consequences. Additionally, the reduction of the pollex apparently induces greater variation which makes comparing features of the pollex problematic. The proximal articulating surfaces of functional digits are slightly ginglymal, extending over part of both the volar and dorsal surfaces of the bones. In almost all of these primitive taxa, a large roughened process is present at the volar base of each of the four unreduced metacarpals that extends away from the metacarpals and curves slightly distally. This process is more or less continuous with the volar processes of the capitate and hamate, and it is usually largest on digits III and IV. The metacarpals become slightly wider at their distal ends than at their proximal ones, and the distal articulating surfaces are strongly spherical (compared to the condition in more derived taxa where they are more cylindrical). There is usually a conspicuous neck, or
constriction, between the shaft of the metacarpals and the distal heads containing the articular surface. The dorsalmost extent of the articulating surface ends in a small fovea or pit that is bordered on either side by a small roughened process. The head of the metacarpals contains a roughly spherical articular surface which curves more tightly in the dorsovolar plane than the mediolateral one. All artiodactyls, and probably all terrestrial quadrupedal mammals, possess at least a small, or incomplete, distal "metapodial keel" (Janis \& Scott, 1988) that extends away from the distal articular surface of the metacarpal head between the two sesamoid bones of the superficial flexor tendons. In primitive and pentadactyl taxa, this keel never extends on to the dorsal face of the articular surface.

The phalanges in primitive artiodactyl taxa are, for the most part, unremarkable except at their articular surfaces. They are thinner than the metacarpals, possess constrictions around the distal-middle of their length, and have fairly inconspicuous tuberosities only at the proximalmost volar surface. Their articular surfaces, however, are different from most extant terrestrial artiodactyl taxa. The proximal articulation is concave and more or less fits exactly with the distal head of the metacarpal. However, the volar end of the articular surface contains a strong indentation which corresponds to the incomplete keel of the metacarpal head. This indentation extends for only a quarter to a third of the length of the articulating surface. The distal articulating surface of the proximal phalanges is largely spherical (rather than hinge-like). Correspondingly, the proximal articulation of the middle phalanx is convex. The articulation between the middle and distal phalanges are hemisellar in most taxa in which this condition can be judged. The distal phalanges are usually too variable to determine if there are particular specializations unique to them.

## Tetradactyl artiodactyl manus

The next important change in artiodactyl manus anatomy is the loss of the pollex. This occurs independently several times, as shown in Fig. 1.1. For many tetradactyl taxa, simply the loss of the pollex does not alter the rest of the manus. There appears to be two anatomically-distinct tetradactyl groups: a relatively less-derived group consisting of ticholeptine and merychyine oreodonts, leptomerycids, cainotheres and protoceratids (group 1); and a more-derived group of suids, tayassuids, tragulids, and oromerycids (group 2) (Fig.
1.4). Group 1 clusters closer to pentadactyl taxa in the ternary diagram, while the members of Group 2 cluster more closely to didactyl taxa (Fig. 1.2). These groups differ in the ratio of the lengths of the central metacarpals (III and IV) to the outer ones (II and V) and some important bony features of the metacarpals, explained below.


Figure 1.4. Tetradactyl artiodactyl taxa. A) Protocerast, a protoceratid, right manus in dorsal view. B) Protocerast, right manus in volar view. C) Merychyust, an oreodont, right manus in dorsal view. D) Sus, domestic pig, right manus in dorsal view. E) Prosthennopst, a peccary, right manus in volar view with digits removed. F) Tragulus, a tragulid, right manus in volar view. A) after Scott \& Jepsen (1940). B) from F:AM1227. C) from F:AM43279. D) from MCZ6246. E) from F:AM42886. F) from MCZ3828. Abbreviations as in Fig. 3. Scale bars $=1 \mathrm{~cm}$.

The carpal bones in all tetradactyl taxa interlock more tightly than in the pentadactyl taxa. These tetradactyl forms tend to be fairly large-bodied (sheep or deer sized), except for tragulids and cainotheres, and body size alone may account for this difference in some taxa. Radiocarpal articulations become more cylindrical when viewed mediolaterally while carpometacarpal articulations become cylindrical to hemisellar. At the carpal surface of the radiocarpal articulation, there is a small shelf that corresponds to a flattened ridge on the articular surface of the radius. The carpometacarpal articulations contain a similar shelf/ridge configuration at their dorsal extent, possibly limiting extension of the manus at the carpus. Finally, the volar processes belonging to the capitate and hamate are greatly reduced, further reducing the dorso-volar curvature of the carpometacarpal joints, which are mostly hemisellar.

The metacarpals of tetradactyl taxa are the most modified bones of the manus. The most obvious change, after the loss of digit I , is the suite of changes in the metacarpals. There is some variability in the reduction of digits II and V, the size and shape of the proximal metacarpal volar process, and the shape of the metacarpophalangeal articulations. This variability can be roughly parsed between the two main groups: in group 1, side metacarpals (II and V) maintain similar relative lengths compared to the central (III and IV) metacarpals (Fig. 1.4A-C); in group 2, side metacarpals are markedly reduced compared to the central digits (Fig. 1.4D-F). In this latter assemblage, the metacarpals appear to make up a larger proportion of the length of the manus. The proximal articulating surfaces are hemisellar or more flattened, and there is a characteristic volar curvature that does not extend over to the dorsal surface. At the dorsal extent of the articular surface of the metacarpal, there is a flattened ridge that corresponds to the same on the distal articular surfaces of the carpal bones. The volar processes of the proximal metacarpals that are
continuous with the processes of the capitate and hamate in pentadactyl taxa are reduced to roughened tubercles in group 2, while in group 1 this process retains its size as the carpal processes reduce. In both groups, the distal ends of the metacarpals are much straighter, and the articular surface takes up the entire mediolateral width of the distal metacarpal head.

Topological features surrounding the articular surface in tetradactyl taxa are much less pronounced than in pentadactyl ones. The fovea at the dorsalmost extent of the articular surface is either entirely absent or much reduced. The edges of the metacarpal heads have tubercles on their abaxial sides and pits on the adaxial sides. The articular surfaces themselves are ginglymal with respect to the dorso-volar plane. Tetradactyl taxa differ in completeness of the metacarpal keel. Group 1 tetradactyl taxa (such as cainotheres and protoceratids, in addition to all tylopods, discussed later) lack a complete keel. The keel is complete in suids and tayassuids. The keel appears to be the continuation of the distal volar projection which is present in pentadactyl taxa, except that its articulations are no longer restricted to the sesamoid bones and the volar portion of the proximal phalangeal articulation. When the complete metacarpal keel is present, the arc of curvature in the metacarpal head is much greater. The increased curvature of the metacarpal heads causes their articular surfaces to extend past the plane of the metacarpals; i.e., the dorsovolar thicknesses of the articular heads of the metacarpals are thicker than the metacarpal shaft, as in pentadactyl taxa. When this is the case, there is a dorsal fovea present on the metacarpal shaft at the intersection with the articular head. The metacarpal keel (complete or not) divides the volar extent of the articular surface into slightly subequal curves, with the adaxial curve larger than the abaxial one.

Features of the phalanges are also strikingly different between tetradactyl and pentadactyl taxa. In particular, the proximal articular surface of the proximal phalanx is
larger on the abaxial side than on the adaxial side in taxa with a complete metacarpal keel, reflecting the subequal curves of the volar portion of the metacarpal head. The indentation of the proximal phalanx that accommodates to the incomplete metacarpal keel persists, and the tuberosities on either side of this indentation on the volar surface are less pronounced than in pentadactyl taxa. The phalanges of tetradactyl taxa are almost as wide as the corresponding metacarpal. The phalanges are more robust, in that their width is consistent along their proximo-distal length.

## Didactyl artiodactyl manus

The most obvious change between the didactyl manus and the ancestral tetradactyl manus is the further reduction of digits II and V such that there is an interruption in the articulating chain of carpal-metacarpal-proximal phalanx. This change is significant because it indicates the digit is no longer functional, and the break in articulation can happen in several ways. Cervids lose either the proximal part of the metacarpal (telemetacarpal condition) or the distal part (plesiometacarpal condition), while all cervids retain phalanges. Bovids all lose metacarpal elements, but they vary widely in the number of phalangeal bones they retain. Antelopine bovids lose all phalangeal bones while retaining rudimentary keratinous spurs homologous to the hooves of digits II and V, while caprine bovids retain at least one phalangeal bone (probably the distal phalanges of II and V). Other didactyl taxa, such as extant antilocaprids and extant camelids, lose all traces of digits II and V (Fig. 1.5).

Fusion of the remaining metacarpals into a cannon bone also results, although the fusion can be incomplete distally. Cameline camelids show this distal 'splaying' of the metacarpals, in association with a secondarily digitigrade foot posture, although other camelid groups, such as stenomylines and the genus Poëbrotherium, possess metacarpals that are unfused and more parallel. Since digits II and V are so greatly reduced and can be variable within a species,


Figure 1.5. Didactyl artiodactyl taxa. A) Antilocapra, a pronghorn, right manus in dorsal view. B) Lama, a cameline camelid, right manus in dorsal view. C) Pöebrotheriunt, a cameline camelid, right manus in dorsal view. D) Daeodont, an entelodont, right manus in dorsal view. A) from MCZ1776. B) from MCZ1881. C) from AMNH7910. D) from AM7380. Abbreviations as in Fig. 3. Scale bar $=5 \mathrm{~cm}$.
topological features of those digits are worthless for any cross-clade comparisons. Camelids and the various pecoran families reduce these lateral digits and fuse elements of the manus differently, as evidenced by digit reduction being a feature distinguishing subfamilies of deer, and incomplete fusion of metacarpals and/or the development of a "metatarsal gully" (Janis and Scott, 1987) being distributed variously throughout Pecora. Several of the unique features of the manus in camelids (Webb, 1972; Janis et al., 2002) and ruminants (Janis and Scott, 1987) have been sufficiently described; there are, however, features common among didactyl taxa other than digit loss that distinguish them from the tetradactyl taxa ancestral to them.

In didactyl taxa, the radiocarpal articulations are largely ginglymal, and the dorsal shelves first seen in tetradactyl taxa are usually larger. The unciform usually bears trochleated articulations at its proximal and distal ends. Carpometacarpal articulations are almost entirely flat or have very few distinct surface features. Adjacent to this flattened surface, the proximal metacarpal volar process seen in more primitive taxa persists only as a roughened tubercle that usually extends as ridges on the lateral-volar surfaces of the cannon bone. The distal ends of metacarpals are modified in pecorans similarly to (and independently from) those in suines-the distal ends are trochleated and possess a complete keel in pecorans. As in suines, the keel coincides with dorsal and volar foveae that give the articular surface a much more rounded appearance when viewed in profile. Tylopods never develop a complete metapodial keel, although the metacarpal head is highly ginglymal in all camelids, such as the basal camelid, Poëbrotherium (Fig. 1.5C). Topological features of the phalanges of digits III and IV are similar to the homologous digits in tetradactyl taxa, with the notable exception of cameline camelids (Webb, 1972; Janis et al., 2002).

Entelodonts are a fascinating exception to all other didactyl taxa, both in terms of intramembranal proportions, as described in the ternary diagram, and in specific anatomic features of the manus. These unusual artiodactyls differ from every other ungulate group in their limbs. There are no fusions of carpals or metacarpals, making them unique among didactyl artiodactyls (Fig. 1.5D). The carpals and remaining metacarpals are very similar to tetradactyl taxa that lack a complete metapodial keel in both morphology and proportions, and their phalanges resemble extant camelids, as described by Janis et al. (2002). The proximal phalanges are much longer than the middle and distal ones, and the middle phalanges show a characteristic lateral flaring, similar to most camelids.

## DISCUSSION

## Body size and intramembranal proportions

The most important variable affecting limb morphology is body size (Alexander et al., 1979). The postural changes necessary to accommodate the stresses that accompany larger size are well-characterized (Biewener, 1989), but the effects of altered anatomy (in terms of digit number) and intramembranal proportions with respect to body size are poorly understood. Many of the anatomical changes traditionally correlated with running speed also tend to occur in mammals over 200kg (Steudel \& Beattie, 1993). Frequently, the same anatomical features that correlate with speed, such as shortened muscular insertion processes on long bones, ginglymal (hinge-like) joint surfaces, and elongated distal segments (Gregory, 1912; Smith \& Savage, 1955), are the same features that accompany erect or columnar posture at large body sizes (Biewener, 1989), except in graviportal forms like hippos and elephants. Overall limb length accompanied by distal segment elongation has been argued to correlate with speed and mobility (i.e., cursoriality), because larger steps alone can increase overall speed and/or endurance (Hildebrand \& Goslow, 2001), and because longer limbs possess longer extrinsic manual tendons available for elastic energy storage (Alexander et al., 1982). Some authors have suggested that elongated distal segments and fused digital elements make a limb lighter and easier to swing (Howell, 1944; Smith \& Savage, 1956), but this assumption has never been rigorously tested. Alternatively, one could also argue that a long, light limb has the same rotational inertia as a shorter, heavier limb; the two alternatives could be identical in terms of swing cost. The key difference then is total limb length, since this increases step length and elongates elements improving locomotor efficiency, such as digital flexor muscle tendons.

The ternary analysis in this paper does not address body size as a factor in intramembranal proportions, but the observation that the taxa cluster without any apparent body size effect has a large bearing on the evolution of unguligrade and cursorial taxa (Fig. 1.2). Most estimates of body mass for wild-caught animals are inaccurate and are often based on dressed weight (Silva \& Downing, 1995), so many body mass comparisons are dubious. Within the cluster of didactyl pecoran taxa, Giraffa (body mass $\sim 850 \mathrm{~kg}$ ) lies very close to the much smaller Aepyceros (impala, $\sim 60 \mathrm{~kg}$ ). Within the cluster of tetradactyl artiodactyls, the comparatively tiny Tragulus (mouse deer, $\sim 7 \mathrm{~kg}$ ) lies near the much larger Pbacochoerus (warthog, $\sim 100 \mathrm{~kg}$ ). Clearly, then, the intramembranal proportions and the anatomy of the limbs themselves are more important factors distinguishing limb posture in the terrestrial artiodactyls than is body mass. It is also fundamental to the evolution of unguligrady that the limb segments showing the largest variation within intramembranal proportions are the most proximal and the most distal. The taxa with the shortest zeugopodia have the longest autopodia and vice-versa, which could support the observation that fast-running taxa have limb muscle mass concentrated proximally and have elongated distal segments, since the bulk of limb muscle mass lies within proximal and middle segments (Hildebrand \& Goslow, 2001). This is not to say that proximal segments vary morphologically, since the fact that they are composed of a single bony element reduces the amount of possible anatomical variation, only that they vary with respect to intramembranal proportions. Other workers (Garland \& Janis, 1993) have not found a correlation between the ratio of proximal to distal elements of hindlimbs and running speed when comparing cursorial taxa to each other, meaning that the relative shortening of proximal segments and relative elongation of distal segments may not be a design for increased locomotor speed. The sample analyzed in this ternary diagram is similar to that of Garland \& Janis (1993) in
that it is composed of mostly cursorial taxa, and all of the taxa included here are at least digitigrade. The sample included here is different from Garland \& Janis (1993) in that it analyzes forelimbs rather than hindlimbs. Forelimbs and hindlimbs have fundamentally different roles in locomotion (Griffin et al., 2004), so there might be a different pattern of distal elongation relative to proximal shortening between fore- and hindlimbs. However, there does appear to be a clear pattern of increasing distal forelimb elements of so-called cursorial artiodactyls.

In order to describe the effect of phylogeny on limb anatomy, one would first have to determine the probable body mass of a clade's ancestor. A body mass of around 30 kg (a large peccary, a small white-tailed deer, or a medium-sized gazelle) has been shown to be a threshold for optimizing relative running speed (relative to body length) with total speed (Iriarte-Diaz 2002; Garland, 1983). That is, by analyzing both total speed and (a possibly more ecologically-relevant indicator) speed normalized to body length, a body mass of 30 kg represents a body mass for maximizing both absolute and relative running speed. Other workers (Reilly et al., 2007) have shown a size threshold of 1 kg above which mammals adopt an increasingly upright posture and reduced muscle moment arms. Secondarily small artiodactyls would inherit anatomical features of limbs that served as adaptations for speed or endurance in ancestors, like digit loss and unguligrady, if those ancestors attained cursorial features at larger body sizes. Tragulids and small-bodied antelopes might be examples of this phenomenon: their highly specialized and unguligrade limbs are not shared by other herbivores of similar size, such as leptaucheniine oreodonts and cainotheres. Of course, the morphological changes in limbs necessary to support very large body masses make cursoriality not feasible and result in graviportal forms (Biewener, 1989). Graviportal groups like proboscideans and hippos might likewise affect limb proportions in descendants; dwarf
elephants and pygmy hippos might be examples. Their limbs are much more similar to their larger-bodied ancestors than to other ungulates of similar body sizes. When body size changes within a lineage, limb morphology may reflect ancestry more than specific or inferred performance selection pressures.

## Osteological correlates of foot posture in Artiodactyls

## Inference of foot posture in basal artiodactyls

One of the biggest challenges in reconstructing limb posture in many primitive artiodactyl groups is that there are few adequate extant analogs for comparison. Pentadactyl ungulates have a forelimb anatomy not shared with any living ungulate groups, with the partial exception of Hippopotamidae, which do have a rudimentary pollex. Since there are no extant artiodactyls with which to frame the basal groups (sensu Witmer, 1997), analogy to other cursorial groups must be made. The criteria for such a group would include pentadactyly combined with terrestrial cursoriality and a fairly large (ca. above 10 kg ) body size. Fortunately, extant felids and (especially) canids fit these criteria. These groups have derived their upright posture, fast running speed, and high mobility independently from ungulates and serve as adequate anatomical analogs. There are several convergent features of the bones of the manus of canids and basal artiodactyls.

The general size and shapes of bones of the manus are extremely similar between extant canids and basal artiodactyls, suggesting that many of the soft-tissue features are similar as well. Without delving into a lengthy discussion about the anatomy of the extrinsic muscles of the manus (since these are likely to be highly conserved within the manus and leave osteological correlates only on middle and ungual phalanges), the intrinsic muscles of the manus do leave conspicuous features. The manus of extant canids is functionally mesaxonic (having a weight-bearing axis passing through digit III), and this is mostly
reflected in the intrinsic musculature. The following muscle description is taken from Evans (1992) and Nickel et al. (1986), although my own dissections have verified these descriptions (Fig. 1.6). Each functional digit receives an interosseus muscle that acts as a short flexor. The proximal attachment of the interossei from digits III \& IV lie deep to a pair of adductors for digits II \& V, which, as their attachment suggests, resist splaying of the digits. The interossei attach in two locations distally: a primary attachment on the sesamoid plate between and around a digit's pair of sesamoids, and across the metacarpophalangeal joint to the extensor hood. Digits I \& V also have abductor muscles, and digit I possesses a short flexor muscle, a short adductor muscle, and an opponens muscle. The proximal volar processes of the metacarpals serve as attachment sites for the interossei and short adductors of the digits. Finally, there are a set of lumbrical muscles that extend from the superficial flexor tendons in the hand to the extensor tendons past the metacarpophalangeal joints (these muscles have no bony attachment).


Figure 1.6. Intrinsic muscles of the pentadactyl manus. A) Canis, domestic dog, left manus dissection in volar view. B) Canis, lateral view of isolated digit with corresponding metacarpal and interosseus muscle. After Evans (1999). Abbreviations: eh - extensor hood of M. interosseus; mabp - M. abductor pollicis; mabq M. abductor digiti quiniti; madp -M . adductor pollicis brevis; madq -M . adductor digiti quinti; mads -M . adductor digiti secundi; mi -M . interosseus; os - Os sesamoideum.

Bony features of the metacarpals of extant canids are almost identical to those of basal artiodactyls: both clades have large proximal volar processes, spherical metacarpal heads, and dorsal foveae immediately proximal to the articular surface of the metacarpal head. Canids adopt a digitigrade stance, where the heads of metacarpals II-V support body weight through a digitial fibrofatty pad. Intrinsic muscles of the manus are here interpreted as mechanical impediments to an unguligrade foot posture, since the small intrinsic muscles of the manus are unable to support the body weight in an unguligrade position. Their presence correlates with large volar bony processes on the proximal metacarpals. The similarity between the large volar process of the metacarpal in both extant canids and basal artiodactyls suggests that the latter also possessed muscular interossei. Additionally, the spherical metacarpal heads suggest joints unable to transmit the body weight (due to instability of a rounded joint stabilized by small intrinsic muscles) and that the proximal phalanx will rest in an extended position during stance. The relatively thin metacarpals and phalanges in extant canids also correlate with a digitigrade stance.

The pentadactyl artiodactyl taxa seem similarly unable to potentially support their body weight with a manus in an unguligrade posture, since the same muscular insufficiencies and joint instabilities as in extant canids would be present. For these reasons, all pentadactyl artiodactyl taxa are here interpreted as being obligately digitigrade and having a foot posture and soft-tissue anatomy similar to that of extant canids, despite many reconstructions of these taxa as unguligrade (e.g., Erfurt \& Metais, 2007). Interestingly then, the earliest eventoed ungulates were odd-toed and digitigrade. Further, paraxony, the original defining feature of Artiodactyla (Cuvier, 1822) appears not to have been present from the beginning of the clade (Theodor et al., 2005). The earliest and most primitively-featured artiodactyls appear to have a mesaxonic forelimb while also possessing a paraxonic forelimb (Theodor et
al., 2005). Other postcranial features, such as the double-trochleated astragulus in the ankle (Schaeffer, 1948), and dental features, such as the six cusps on the deciduous lower fourth premolar (Luckett \& Hong, 1998), are usually invoked in character-based definitions of Artiodactyla.

## Tetradactyl artiodactyl taxa and the transition to unguligrady

Unike the situation in pentadactyl artiodactyls, there are adequate extant analogs for most extinct taxa that have lost the pollex and retain digits II-V. Loss of the pollex accompanies several other bony changes: the articulating surfaces of the carpal bones become more restricted, the volar processes of the capitate and hamate reduce, the volar processes of the base of the metacarpals reduces, and the articular surfaces of the MCP joints become more ginglymal. As noted above, there are two groups of tetradactyl artiodactyls that differ in the degree of change in these characters. Loss of the pollex coincides with a relative elongation of the manus and a relative shortening of the humerus within the limb, and when this is combined with osteological changes of the manus, there appear to be significant soft-tissue and postural consequences.

Suids are the best model for inferring the intrinsic soft-tissue structures in tetradactyl taxa, thanks to their availability and relatively large body size. Unlike the situation with the description of canid manual anatomy, my interpretations of manus anatomy in Sus differ from much of the veterinary literature. The intrinsic musculature of the Sus manus consists exclusively of adductor muscles for digits II and V and poorly-developed lumbrical muscles. The adductors of digits II and $V$ attach to the volar surfaces of the capitate and hamate, acting through a dense set of carpal ligaments. The interosseus muscles present in other mammals are reduced to stiff ligamentous tissue in the pig that extends in distinct bands from the volar surface of the base of the metacarpal to a split distal attachment both on the
sesamoid plate and, by extension, then to the proximal-volar surface of the proximal phalanx and the extensor expansion (Fig. 1.7). This ligamentous tissue, converted from muscular interosseus muscles, has been studied in other artiodactyls such as cattle (Nickel et al., 1986), goats (Cuming et al., 1978), and fallow deer (Dimery et al., 1986) and in perissodactyl equids (Callegari, 1968). There is probably a developmental component to the transition from a muscular interosseus in artiodactyls, mirroring the one in equids (Callegari, 1968), so the age of an individual may have a bearing on whether there is muscular tissue to be found in the interosseus ligaments of tetradactyl artiodactyls. So, the loss of the pollex in pigs also coincides with the development of stiffened interosseus ligaments attaching to the basal volar processes of the metacarpals, which are smaller than the processes in taxa (such as canids) with muscular interossei (Fig. 1.8).


Figure 1.7. Sus, lateral view of isolated digit and corresponding metacarpal and interosseus ligament. Abbreviations: ad - M. adductor digiti (either quinti or secundi, whichever digit is adjacent); eh - extensor hood of interosseus ligament; il - interosseus ligament; os - sesamoid bone.


Figure 1.8. Lateral view of selected third metacarpals. A) Canis, after Evans (1999). B) Merycoidodont, from AM72286. C) Merychyust, from F:AM43279. D) Dyseohyust, a peccary, from F:AM73679. E) Aepyceros, an impala, from MCZ57521. Abbreviations: vmp - volar metacarpal process; vmt - volar metacarpal tubercle. Scale bar $=1 \mathrm{~cm}$.

Extant tetradactyl artiodactyl families (Suidae, Tayassuidae, and Tragulidae) are all unguligrade, so clearly the transition from digitigrady to unguligrady must have occurred somewhere in the ancestry of these lineages. The key osteological features of unguligrady found in this study are: ginglymal MCP joints, reduced (but not lost) digits II and V, and reduced volar processes on carpal bones. Didactyl artiodactyl taxa are likewise unguligrade and have reduced basal proximal volar processes on the metacarpals, making the reduced volar processes of the hamate and capitate a feature that correlates much more strongly with
overall unguligrady. Many tetradactyl taxa share features with the late Eocene equid Mesohippus, which Thomason's (1986) analysis of foot posture termed 'subunguligrade' in foot posture. This foot posture is characterized by outer (II and V in artiodactyls, II and IV in Mesohippus) digits that are almost equal in length (but not robustness) to central digit(s), permitting contact with the ground, and a proposed fibrofatty volar pad similar to that in digitigrade taxa. Ticholeptine oreodonts, leptomerycid traguloids, (at least) primitive cainotheres, oromerycids and protoceratids share these osteological features, whereas suids, tayassuids, tragulids, and early camelids do not. The former collection (i.e., Group 1) possessed longer lateral digits that probably did contact the ground during stance, whereas the latter collection (i.e., Group 2) did not. These two groups also differ in the size of the volar process of the metacarpal; a muscular interosseus is indicated in the former group with the large volar metacarpal process, while a ligamentous one is present in the second group, which does not develop a large process. Based on the osteological correlates of the interosseus ligament, the transition from muscular interosseus to ligamentous one occurred within tetradactyl taxa. This situation is analogous to Thomason's (1986), analysis in which unguligrady was attained in equids within a collection of tridactyl groups, attained by the level of Merychippus. It is likely that the loss of the pollex in tetradactyl forms indicates the initial transition to 'subunguligrady' or 'superdigitigrady' in artiodactyls, where the foot posture is more erect than in a simple digitigrade stance. Subunguligrade taxa still possess muscular interossei and a volar foot pad that is used to transmit force during stance and to support the MCP joint, and it is the later development of a ligamentous interosseus that permits an unguligrade foot posture.

The transition from digitigrady to unguligrady likely took the following path. First, the foot posture became more upright through a thicker volar pad, carpometacarpal
articulations became more stabilized, MCP joints became more ginglymal, and the pollex was lost. At the same time that the carpometacarpal articulations became more stabilized and less capable of extension past the vertical, and the MCP joint became elevated through a thickened fibrofatty volar foot pad, like the condition seen in extant rhinoceratids, who are 'subunguligrade' or 'superdigitigrade' (von Hauwald, 2001). Since the interossei likely play a part in ab/adduction of the digits, ginglymal MCP joints release a lateral stability constraint on the muscles and allow these muscles to act as pure flexors of the digit at the MCP joint. Interossei are likely present in all 'subunguligrade' or 'superdigitigrade' taxa, as they are present in extant hippos (Fisher et al., 2007). These changes permitted a functional elongation of the manus by increasing step length through the slightly elevated MCP joint. Stabilization of the joints of the digit released potential functional constraints on a manus capable of non-locomotor tasks such as grasping, and the distal compliance of the limb shifted from the wrist to the MCP joint. This first transition took place between pentadactyl and tetradactyl taxa, indicated by the loss of the pollex and slight relative elongation of the manus. Next, the interossei stiffened and the volar pad under the MCP joint was lost, and stance became unguligrade. Since the central toes in a tetradactyl foot (digits III and IV) are larger than outer digits (II and V), the central toes supported body weight during stance, permitting a further reduction of lateral digits. This second transition occurred within tetradactyl taxa, without significant distal limb segment elongation. Finally, tetradactyl and unguligrade groups gave rise to didactyl groups that lost outer digits and lengthened distal limb segments to varying degrees and further increased step length and potentially increased elastic energy storage through elongated digit flexor muscle tendons and/or interosseus ligaments.

Unguligrade foot posture evolved independently at least three times in artiodactyls. Each of the three main lineages of artiodactyls (tylopods, suiforms, and ruminants) independently evolved a nearly identical sequence of digit loss and changes in foot posture. Only suiforms lack members with an elongated, didactyl manus, although a didactyl and secondarily-digitigrade foot evolved somewhere in the lineage giving rise to entelodonts (which may not be suiforms at all). The transitions to unguligrady are most clearly understood in ruminants, where there is an identifiable morphological sequence from pentadactyl, digitigrade hypertragulids; to tetradactyl, ‘superdigitigrade’ leptomerycids; to tetradactyl, unguligrade tragulids; to unguligrade, didactyl pecorans. Transitions within suiforms and tylopods, however, are less clear. Tylopods evolved unguligrade foot posture either within potentially paraphyletic oromerycids or at the base of the camel family. Basal camelids were didactyl and unguligrade, and more derived camelids evolved a secondarilydigitigrade foot posture. For suiforms, unguligrade foot posture evolved ancestral to the clades studied here, and a further examination of primitively-featured suiforms might elucidate the transition to unguligrady in that group. These three transitions to unguligrade foot posture account for three instances of pollex loss, but there are two additional instances-within derived oreodonts and at the base of the protoceratid family. Neither of these groups evolved unguligrady, making the parallelism in foot morphology within artiodactyls even more striking. 'Superdigitigrady,' then, evolved at least 5 times in the group, through loss of the pollex, while three 'superdigitigrade' groups gave rise to unguligrade descendants, through further reduction of digits and modification of joint surfaces and intrinsic soft-tissues of the foot.

## CHAPTER 2: KINEMATICS OF THE FOREFOOT IN MINIPIGS (ARTIODACTYLA: SUIDAE)


#### Abstract

Unguligrade foot posture is an extremely upright configuration of foot bones maintained during the stance phase of locomotion. The joints in unguligrade feet are very ginglymal (hinge-like) and have been interpreted to restrict motion in a parasagittal plane. This study tests whether the motion in minipigs' forefoot digits is parasagittal or hinge-like and whether motion in foot bones changes between level walking and downhill steps. A novel bi-planar cinefluoroscopy data collection and analyzation procedure, called XROMM, was used to determine the 3-D positions of metacarpals, proximal phalanges, and ungual phalanges of a digit during stance in level walking, 10 cm downhill steps and 15 cm downhill steps. Analysis of motion using bone models in x - (antero-posterior), y- (medio-lateral), and z- (long-axis) axes that were fixed to bone anatomy permitted description of bone rotations. In level walking, minipigs used a small subset of possible poses at toe-on and toe-off positions and underwent large antero-posterior rotation (APR), modest long-axis rotation (LAR), and small medio-lateral rotation (MLR). Rotation between elements yielded joint motion, and the bulk of motion occurred at the interphalangeal joints rather than at the metacarpophalangeal joint. In downhill steps, toe-off poses were identical to level walking ones while toe-on positions differed. APR and MLR decreased during stance, while LAR maintained similar excursions between level walking and downhill steps. Most of the motion at joints of the digit is anatomically hinge-like, although there is a consistent MLR and LAR that makes motion of the foot non-parasagittal. Paradoxically, minipigs used straighter foot postures during downhill steps than in level walking.


## Introduction

Among even unguligrade artiodactyls, there is a range of anatomical variation in the feet. Most extant species have two central digits (III \& IV) whose metacarpals are fused into a cannon bone. Lateral digits ("side toes," II \& V) are non-functional, if present at all, and are usually only partially present (e.g., in cattle and the like, where only rudiments of distal phalangeal bones are present). The most primitive and well-studied unguligrade artiodactyls are pigs, where digits II \& V are present and potentially functional, but are too short to interact with the hard substrates during stance. Nonetheless, the lateral digits possess intrinsic adductor muscles and connections with digital flexor muscles. Central digits III and IV are unfused, and their intrinsic musculature has become entirely ligamentous. In contrast, other unguligrade groups such as camels, deer, antelopes, etc., have much more modified and derived foot morphologies. Fusion of metacarpals, loss of digits II and V, and elongated distal limb elements are all modifications of the limbs that have taken place once unguligrade stance evolved in these groups (see Ch. 1). The primitive anatomy retained by pigs makes them ideal for studying the kinematics of locomotion in an unguligrade foot. Comparing foot kinematics in pigs to those in more derived groups, like horses (Chateau et al., 2004; Clayton et al., 2007), for example, will determine whether all unguligrade taxa utilize similar mechanics or whether considerable changes in the motions of foot bones are involved in later digit loss and distal limb elongation.

Analyzing skeletal kinematics accurately is a challenge due to overlying soft-tissue structures which can mask motion. Kinematics in ungulates have traditionally been analyzed either using surface markers (Dutto et al., 2006; Lee et al., 2008), which are only estimates of skeletal motion, or using external markers fixed to skeletal elements (Chateau et al., 2004; Clayton et al., 2007), which are somewhat fragile and can only be accurate if they are
constantly visible during the motion studied. Cinefluoroscopy permits visualization of skeletal elements that otherwise would be masked by surrounding soft tissues. Moreover, biplanar cinefluoroscopy using markers implanted into bone allows unimpeded skeletal movements to be digitized and reconstructed using 3-D coordinates without wires from instrumented devices or protruding structures that may be damaged or broken.

The anatomy of the toe joints in pigs leads to some predictions about the movement at these joints during locomotion. First, the ginglymal (hinge-like) shape of these joints suggests that motion at these joints is primarily about a single axis (i.e., flexion/extension or protraction/retraction). The first hypothesis tested in this study is whether the motion of digit joints is along an anatomical flexion/extension axis. The 'anatomical' qualifier is necessary because the motion of the bones relative to each other might differ from motion of the bones in world space, if, for example, the foot is ab- or adducted or internally or externally rotated during stance. Not all of the digit joints are ginglymal with respect to either an anatomical plane or a world-space plane, such as a parasagittal plane, for example. The ginglymal curvature of the distal interphalangeal (DIP) joint is offset from that of the MCP and the proximal interphalangeal (PIP) joints. This suggests that the distal toe bones adduct during stance or as the bones extend. A 3-D analysis of the kinematics of foot bones permits measurement of motion in a flexion/extension plane in addition to ab/adduction and internal/external rotation (or long-axis rotation). Quantification of motion in multiple anatomical planes will describe the extent to which motion of the foot can be described as 'parasagittal' or 'ginglymal.'

Second, the soft-tissue structures crossing each of the three joints (MCP, PIP, DIP) differ, leading to different joint excursions that could be detected through motion of the foot bones. Muscular contraction in the deep digital flexor muscles will affect all three
joints, while the superficial flexor muscles will affect the proximal two. The additional interosseus ligaments mean that the MCP joint receives flexor moments from all three softtissue structures. Although the GRF moments should increase from distal to proximal in digital joints (due to increased moment arm from the ground reaction force, likely located under the ungual phalanx), the additive effect from tendons and ligaments should affect motion at the joints of the digits. In other words, each joint has a unique combination of soft-tissue structures and moment arm that should lead to differences in joint excursion during stance. The excursion in flexion/extension should be least in the MCP joint, due to the combined actions of the interosseus ligament and both digital flexor muscles.

The purpose of this study is to investigate the kinematics of foot bones during locomotion in an unguligrade species. Unguligrady is a derived foot posture in which the last bone of the toe supports the body during stance (or, more precisely, stance phase of locomotion), while the remaining bones of the toe and foot are elevated off the substrate. Both perissodactyls (odd-toed ungulates) and artiodactyls (even-toed ungulates) have extant species with unguligrade foot posture. In each of these groups, there is a stepwise transition to unguligrady from digitigrade ancestors (Thomason, 1986; see Ch. 1). This transition involved stabilizing the metacarpophalangeal (MCP) joint by replacing intrinsic interosseus muscles with interosseus ligaments (see Ch. 1) and making joint surfaces more ginglymal (Hildebrand \& Goslow, 2001). These anatomical changes suggest that motion at foot joints in unguligrade species became more axial and now move predominantly in flexion/extension (or protraction/retraction).

Finally, this study investigates the differences in kinematics between level walking and stepping down from two different heights. Differences in kinematics (Dutto et al., 2004; Lammers et al., 2006; Lee et al., 2008) have been described for walking on level surfaces $v$ s.
incline or decline walking in some mammals, but none have described detailed differences in the motion of foot bones. Ground reaction forces acting on a foot should increase with the height of a step descent, and the angle of approach of the body differs between level walking and stepping down. Both of these factors should alter the kinematics of the foot during stance. Descent steps should show greater extension at joints of the digit as a result of increased forces. For any gait, the ground reaction force should be directed cranial and medial to joints of these feet, creating moments which would induce joint extension. If there is a relationship between joint excursion and moment, then step-down height (and by proxy, increased force) should produce greater extension in foot joints or of the foot as a whole.

## Materials \& Methods

## Overview of XROMM

The methods in this study employ a well-tested method created by colleagues at Brown University called X-ray Reconstruction of Moving Morphology (XROMM). XROMM combines biplanar x-ray movement from two C-arm fluoroscopes, retrofitted with a high-speed motion capture system, with morphological data collected from CT-scanned specimens to produce accurate 3-D animations of skeletal movement. After implanting three radio-opaque markers in the metacarpal, proximal phalanx, and ungual phalanx, synchronized high-speed fluoroscopic videos were combined with synchronized force recordings of either unimpeded motion in a trackway or controlled motion of an isolated preparation. In the XROMM workflow, Matlab scripts were used to remove video distortion, digitize 2-D coordinates, compute 3-D coordinates by DLT (Hedrick, 2008), and calculate rigid body kinematics with the singular value decomposition (SVD) method
(Söderkvist \& Wedin, 1993). Polygonal bone models (created in Amira from CT scans of each individual) were integrated with marker movement data to yield morphologically and kinematically faithful visualizations in the animation software Maya. The XROMM analysis was applied to in vivo experiments, which had synchronized video and force data sets.

## Marker Implantation

Four juvenile Gottingen Minipigs (Marshall Bioresources, North Rose, NY) were used in this study. The size constraints of the in vivo experimental set-up required very small individuals, and this breed is the smallest available for experimental research. The minipigs used in this study were two weeks post-weaning and weighed between 5 and 6 kg during experiments. The potential drawbacks of using these pigs are that bone epiphyses and small size may alter mechanics and hamper cross-species comparisons. Visual examination did not reveal motion at bone epiphyses. For each individual, ten markers were surgically implanted into the metacarpal (4), proximal phalanx (3), and hoof (3) of the fourth digit of the right foot. During surgery, sedation was induced using IM injection of midazolam ( $0.1 \mathrm{mg} / \mathrm{kg}$ ) and buprenorphine $(0.01 \mathrm{mg} / \mathrm{kg})$. Anaesthesia was induced via facemask inhalation of $1-2 \%$ isoflurane and maintained after intubation (1-2\% isoflurane). Marker implantation in the metacarpal and proximal phalanx was carried out by making a single cutaneous incision per bone, retracting soft tissues, and making a small incision of the periosteum over the implantation site. Implantation sites were prepared using $1.0-\mathrm{mm}$ wire-pass drill bit driven by a Stryker CORE Micro Drill (Stryker Instruments, Kalamazoo, MI). Drill sites were made at least $2-\mathrm{mm}$ deep, and a single 1-mm tantalum sphere marker (Bal-Tec, Los Angeles, CA) was placed in each site. For hoof markers, implantation sites were made using the same drill and bit, but were only 1 mm deep to avoid irritation of subcuticular tissues. Hoof markers were sealed within implantation sites using Vetbond adhesive (3M, St. Paul, MN).

An effort was made to keep implantation sites consistent between individuals, but there was some variation in marker placement.

Markers were not placed in the middle phalanx due to the physical constraints of both surgery and marker implantation in such small bones. In these juvenile individuals, the middle phalanx was a little over a centimeter in total length, and the bone's epiphysis approximately bisected the bone. Marker implantation outside the epiphysis would have been extremely difficult, and the richly-innervated and vascularized growth plates would have been easily disrupted, potentially affecting normal locomotion. Additionally, the tendons of the digital extensor muscles expand mediolaterally over the middle and ungual phananges, creating the extensor hood. Marker implantation in the middle phalanx would have involved a very traumatic procedure disrupting the extensor hood and the bone's epiphysis.

## In vivo experimental set-up

A straight trackway measuring 2.4 m long X 25 cm wide was constructed for in vivo measurements (Fig. 2.1). The trackway walls were 48 cm high X 6.5 mm thick to minimize distractions for minipigs moving through the trackway. The trackway was supported at either end by sturdy tables, while the central 60 cm spanned a gap. The floor of the trackway was constructed from a single piece of 6.5 mm thick plywood. Underneath the span, a weighted ( $\sim 100 \mathrm{~kg}$ ) table supported a force platform (Kistler Type 9281B, Kistler USA, Amherst, NY). A plexiglass insert measuring 11 cm wide X 13.7 cm long X 2.2 cm thick was fixed to the surface of the force platform and raised level with the trackway surface to fit into a cutout in the trackway floor. The cutout was placed right-of-center with respect to the direction of travel for the minipigs to record from the right foot. The entire trackway surface was elevated 100 cm to accommodate a C -arm armature (described in Brainerd et al.,


Figure 2.1. Experimental set-up for in vivo steps. Top-down view (left) showing abbreviated trackway (brown) on top of forceplate (grey) with a window for the plexiglass block contacting the forceplate (aqua). Colored cones represent scope of X-ray beams to the image intensifiers. Right image shows oblique view with images from both cameras. 3-D models of metacarpal, proximal phalanx, and ungual phalanx are shown with reconstructed GRF (red) calculated from forceplate data. All objects to scale.
in reviews) with an X-ray emitter on one end and a 30 cm diameter image intensifier connected to a high-speed digital video camera on the other to collect cinefluoroscopic video. Another C-arm was placed roughly orthogonal to this, and that armature passed above the trackway. A small dog carrier was used to transport minipigs and another carrier containing a food reward was placed at the end of the trackway to encourage individuals to move through the trackway.

Two types of in vivo behaviors that resulted in single footfalls of marked feet were recorded: 1) unimpeded walking and slow trotting footfalls and 2) landing footfalls from box obstacles of either 10 cm or 15 cm height placed in the trackway. The minipigs could not be induced to produce natural fast running gaits, so to increase ground reaction forces experienced by the marked foot landing on the forceplate window within the calibrated space visible in both camera views, individuals stepped down from boxes either 10 cm or 15 cm in height. While recording single footfalls of marked feet for unimpeded walking or trotting was fairly stochastic, placing an obstacle directly immediate to the forceplate window
and calibrated camera space increased the repeatability of trials. Table 2.1 shows the sample size of individuals and steps collected in this study.

|  | level | 10 cm | 15 cm |
| ---: | :---: | :---: | :---: |
| sus03 | 4 | 4 | 3 |
| sus04 | 8 | 4 | 5 |
| sus05 | 10 | 8 | 6 |
| sus06 | 5 | 8 | 6 |
| total | 27 | 24 | 20 |

Table 2.1. Sample size for level steps, 10 cm downhill steps, and 15 cm downhill steps analyzed in this study.

Trials were recorded at $500 \mathrm{~s}^{-1}$ and 2 ms shutter using Photron high-speed digital video cameras (Photron Fastcam 1024 PCI, Photron, Inc., San Diego, CA). Stance was defined by vertical forces above 1 N . Cinefluoroscope settings for all trials were $90 \mathrm{kV} / 4.0 \mathrm{~mA}$ for camera1 and $85 \mathrm{kV} / 4.0 \mathrm{~mA}$ for camera2. Force data were recorded at 1000 $\mathrm{s}^{-1}$ using LabVIEW 8.5 (National Instruments, Austin, TX). Video and force data were synchronized using a common start trigger that initiated recording.

## Motion analysis

MATLAB scripts (available at www.xromm.org) were used to: de-distort digital videos for in vivo trials; calibrate 3-D coordinates in the space intersected by both image intensifiers; filter digitized coordinates (Butterworth 25Hz low-pass filter); calculate camera positions relative to the calibrated space; calculate 3-D positions of tantalum markers; and calculate 3-D translations and rotations for a point on each bone defined by the centroid of the markers for each bone (Hedrick, 2008; Brainerd et al., in review). This centroid was calculated through the CT models, and the models were animated according to the translations and rotations calculated from digitized coordinates.

## 3-D model generation

After in vivo data collection, experimental animals were euthanized via intravenous pentobarbital overdose per standard Brown University IACUC procedure. Marked forelimbs were then dislocated at the elbow and immediately frozen in a $0^{\circ} \mathrm{F}\left(-17.8^{\circ} \mathrm{C}\right)$ storage freezer. Once the marked forelimbs were frozen for 24 hours, they were packed in a closed Styrofoam cooler and placed in a medical CT scanner (Philips Medical System, Best, Netherlands). Scans were collected at $80 \mathrm{kVp} / 200 \mathrm{~mA}, 0.625 \mathrm{~mm}$ thickness, and 0.625 mm inter-slice interval.

3-D models of the marked metacarpals, marked proximal phalanges, ungual phalanges of marked digits, and the tantalum markers were made using Amira 4.1 software (Mercury Computer Systems Inc., Chelmsford, MA). Models of markers were re-registered to their corresponding bones (hoof markers were registered to the ungual phalanx).

## Anatomical axes

A set of anatomically-based axes was defined for each 3-D bone model to quantify the motion of the metacarpal, proximal phalanx, and ungual phalanx. These axes were placed on each bone and aligned according to the following procedure: a locator was created in Maya (San Rafael, California) and given x, y \& z axes. Each 3-D model (metacarpal, proximal phalanx, and ungual phalanx) was given a separate locator. The x -axis of each locator was aligned parallel to the axis of curvature of the distal articular surface for the metacarpal and proximal phalanx and the single articular surface of the ungual phalanx (Fig. 2.2). These axes did not necessarily overlap (in the case of the ungual phalanx, they never did), but they were repeatable in their position and had anatomical significance. The locators were then rotated about their x -axes until the z -axis corresponded to the long axis of the bone. The rotation order was set as $z$, then $y$, then $x$. X-axis rotations occur in an


Figure 2.2. Marker placement relative to 3-D models generated from CT data. Neutral anatomical position shown at left and representative stance pose shown at right. X-axes (red) project laterally parallel to the plane of curvature of joint surfaces. Z-axes (blue) are parallel to long axes of each bony element. Y-axes (green) are orthogonal to both of these. Rotation in the $x$-axis represents antero-posterior rotation (APR); rotation in the $y$-axis represents medio-lateral rotation (MLR); rotation in the $z$-axis represents long-axis rotation (LAR).
axis perpendicular to a plane defined by the long dimension of the trackway (i.e., direction of travel of the minipig) and the direction of gravity. That is, this is a plane in the anterioposterior direction of travel and gravity, so rotations in the axis perpendicular to this plane are termed APR (antero-posterior rotations). Y-axis rotations occur in an axis perpendicular to a plane defined by the direction of gravity and the perpendicular of the long dimension of the trackway. This dimension corresponds to a medio-lateral axis, so rotations occurring perpendicular to this second plane are termed MLR (medio-lateral rotations). Finally, z-axis rotations occur in an axis perpendicular to the floor of the trackway, roughly corresponding to long-axis rotations of the bones, so these rotations are called LAR (long-axis rotations).

## Measurement of axial rotations

The locators attached to bone models in Maya were used to measure APR, MLR, and LAR in each element. Figure 2.3 shows how these measurements were taken and how they would appear in a 'traditional' 2-D view. Panel A shows the metacarpal model in a neutral pose in both lateral and frontal views in world-space. The angular positions in the three axes of the locator (in green) are all $0^{\circ}$. The other panels show exaggerated poses that do not represent any actual poses collected in this study but are presented to show the 3-D nature of the measurements collected in this study. Panel B shows the metacarpal rotated relative to the neutral (zero) position, again in lateral (left) and frontal (right) view. The rotations in B are as follows: $45^{\circ} \mathrm{APR}, 45^{\circ} \mathrm{MLR}$, and $30^{\circ} \mathrm{LAR}$. This pose is anatomically possible; it may be attained by a pig that protracts the foot $45^{\circ}$, adducts the foot $45^{\circ}$, and internally rotates the foot (pronates) by $30^{\circ}$ from a neutral standing position.

Panel C is the result of additional $90^{\circ} \mathrm{APR}$ of the metacarpal from the pose in B. In this rotation, the same $45^{\circ}$ MLR and $30^{\circ}$ LAR are maintained. In the lateral view, $90^{\circ} \mathrm{APR}$ is apparent, and this situation could be duplicated by a living pig that retracts its foot by $90^{\circ}$ while maintaining the same adduction and internal rotation. Panel D shows the resulting pose after the same $90^{\circ}$ APR of the metacarpal in addition to $-15^{\circ}$ MLR and $-60^{\circ}$ LAR. In both lateral and frontal views, the MLR and LAR are apparent, although difficult to measure in one plane. As in C , the pose in D could be achieved by a living pig that abducted and supinated its foot during protraction.

## Data analysis

Statistical comparisons between conditions were made using 2-way ANOVAs. A pvalue of 0.05 or lower was used to indicate statistical significance. Statistical comparisons were made only within individual bones; otherwise, comparisons became meaningless (i.e.,


Figure 2.3. World-space lateral (left column) and frontal views (right column) of representative positions of metacarpal models. A) Metacarpal model shown in neutral position (i.e., $0^{\circ}$ for each axis of rotation). B) Position of metacarpal model after $+45^{\circ}$ APR, $+45^{\circ}$ MLR, and $+30^{\circ}$ LAR. C) Position of metacarpal model after further $+90^{\circ}$ APR from position in B. D) Position of metacarpal model after $+90^{\circ}$ APR, $-15^{\circ}$ MLR and $-60^{\circ}$ LAR from B. See text for details.
the statistical significance of metacarpal angles being different from proximal phalanx angles is not clear). Graphical representations of initial and final angular positions in APR, MLR, and LAR axes in a world-space coordinate system and the total angular excursion in those three axes experienced by a bone during stance were made. For the initial and final positions, angular measurements are presented at toe-on and toe-off, and an example of the axial movements is shown in Figure 2.4.


Figure 2.4. Angle distribution plots demonstrating anatomical movements. A) APR angles from lateral view with models superimposed to show representative positions. B) MLR angles from frontal view. C) LAR angles from top-down view. Positive values for each axis to the left and negative values to the right.

## Results

## Angular positions of foot bones during level walking

Figure 2.5 shows superimposed positions of foot bones in a representative level walk. Toe-on conditions during level walking steps used a narrow range of angular positions of foot bones. The metacarpal approach angle in the APR axis averaged $\sim 45^{\circ}$ (Fig. 2.6). The metacarpal begins with $\sim 6^{\circ}$ MLR and $-18^{\circ}$ LAR at toe-on. Again, the neutral position for the foot would be $0^{\circ}$ values for each axis, a position that would correspond to a foot held straight down and parasagittally. The values at toe-on represent a foot that begins protracted by $45^{\circ}$, adducted by $6^{\circ}$ and supinated (externally rotated) by $18^{\circ}$. The angular offsets between bones represent joint angles at toe on: the proximal phalanx is extended at


Figure 2.5. Superimposed poses of foot bones during stance in a representative level walk. A) Lateral view of poses every $10 \%$ of stance. B) elevated caudal view. Scaffold trackway shown for perspective. Poses at $0 \%$ and $10 \%$ of stance nearly overlap and are labeled in B to illustrate motion early in stance.


Figure 2.6. Angle distribution plots for level walking steps. A) APR (x-axis) toe-on angular positions (left) and toe-off angular positions (right). Bars represent excursion in the APR axis, with end bars representing $\pm$ s.d. B) MLR (y-axis) toe-on angular positions (circles) and toe-off angular positions (triangles). C) LAR (z-axis) toe-on angular positions (circles) and toe-off angular positions (triangles). Center point represents total mean across individuals, and outside points represent $\pm$ s.d. Top set of points are for metacarpal, middle set are for proximal phalanx, bottom set are for ungual phalanx.
the MCP joint by about $15^{\circ}$ at toe-on, while the negligible difference between the proximal and ungual phalanges indicates the digit is not flexed or extended initially. The digit undergoes MLR as a unit; the three bones maintain similar toe-on values of MLR. Also, the proximal phalanx has about $8^{\circ}$ more LAR than the metacarpal at toe-on.

At toe-off, the metacarpal has undergone $\sim 85^{\circ}$ of APR, while the proximal phalanx and ungual phalanx have undergone $\sim 80^{\circ}$ and $\sim 39^{\circ}$, respectively (Fig. 2.7). The MLR at toe-off did not differ significantly from that at toe-on for the foot (i.e., metacarpal), although


Figure 2.7. Angular excursion graphs for level walking steps. A) Angular positions in the APR axis for metacarpal (solid line), proximal phalanx (dotted line) and ungual phalanx (dashed line). B) LAR angular positions for metacarpal (solid line), proximal phalanx (dotted line) and ungual phalanx (dashed line). C) MLR axis angular positions for metacarpal. D) MLR axis angular positions for proximal phalanx. E) MLR axis angular positions for ungual phalanx. Curves represent means across individuals and grey distributions are $\pm$ s.d.
the peak values for MLR occurred during stance. That is, there was more MLR during the middle of stance than at either toe-on or toe-off. MLR of the proximal and ungual phalanges was significantly greater at toe-off from toe-on $(\mathrm{p}=0.0066 \& \mathrm{p}=0.033$, respectively), indicating that the digit underwent slight but statistically significant adduction relative to the metacarpal during stance. The MLR in the metacarpal was not different between toe-on and toe-off. The metacarpal undergoes statistically significant increases in LAR during stance $\left(\mathrm{p}=4.6 \times 10^{-19}\right)$. The peak LAR occurs near the end of stance, and approaches $18^{\circ}$. The proximal phalanx also undergoes significant LAR during stance ( $\mathrm{p}=8.9 \times 10^{-9}$ ), although it is $\sim 4^{\circ}$ less than the metacarpal. The ungual phalanx undergoes a
still smaller but significant LAR during stance $\left(\sim 10^{\circ} ; \mathrm{p}=3.7 \times 10^{-5}\right)$. The pose at toe-off corresponds to a foot that is retracted by $40^{\circ}$, adducted by $\sim 7^{\circ}$ and supinated (externally rotated) by just a couple degrees.

Significant APR between bones and LAR of all bones occurs during stance. There is an additional $5^{\circ}$ difference in APR between the metacarpal and the proximal phalanx at toeoff, indicating more extension at the MCP joint at toe-off than at toe-on. The difference in APR between the proximal phalanx and metacarpal is held fairly constant $\left(\sim 30^{\circ}-35^{\circ}\right.$ during mid-stance), indicating little extension of the MCP joint during stance. In constrast, there is $\sim 40^{\circ}$ APR between the proximal and ungual phalanges, indicating a very large extension in the proximal and distal IP joints combined during stance. There is a $4^{\circ}$ difference in MLR between the metacarpal and proximal phalanx, and a single degree difference in LAR, at toeoff $v$ s. toe-on. These motions indicate slight abduction of the proximal phalanx at the MCP joint.

The timing of motion in bones of the foot differs in all anatomical axes. In the APR axis, the metacarpal makes a nearly constant rotation until just before toe-off, when there is a faster rotation. The phalanges also show this faster rotation prior to toe-off, but they first undergo positive APR. The proximal phalanx reverses quickly, and continues negative APR slightly parallel to the metacarpal. However, the ungual phalanx maintains a slight positive rotation before a rapid negative rotation in the last portion of stance. Nearly all the APR in the ungual phalanx takes place in the last $20 \%$ of stance.

Similar differences in timing of rotations can be found in other axes. The ungual phalanx diverges strongly from the metacarpal and proximal phalanx in maintaining MLR relative to the rest of the foot during most of stance before undergoing MLR to an angle similar to its original position at toe-on. The metacarpal and proximal phalanx diverged
slightly from each other during stance in MLR, where the proximal phalanx first undergoes negative MLR then later undergoes positive MLR. In LAR, there is an inversion of the rank of rotations in late stance. Early on in stance, the ungual phalanx has the greatest LAR, followed by the proximal phalanx and the metacarpal. Later in stance, the metacarpal has the most LAR, followed by the proximal phalanx then the ungual phalanx. Both the metacarpal and the proximal phalanx show slight negative LAR at the end of stance.

## Angular positions of foot bones during downhill steps

Toe-on positions in downhill steps differed from those used in level walking. The metacarpal began with a $\sim 33^{\circ}$ position in APR for both 10 cm and 15 cm step-down trials (Fig. 2.8). This differed significantly from the position in the APR axis at toe-on for level steps ( $\mathrm{p}=3.2 \times 10^{-5}$ and $1.6 \times 10^{-6}$ for 10 cm and 15 cm , respectively). The APR angle of both the proximal phalanx and ungual phalanx differ significantly in downhill steps from level walking steps $\left(\mathrm{p}=5.7 \times 10^{-8}\right.$ for $10 \mathrm{~cm}, \mathrm{p}=1.8 \times 10^{-8}$ for 15 cm in proximal $\mathrm{phalanx} ; \mathrm{p}=0.038$ for both 10 cm and 15 cm in ungual phalanx). The positions in the APR axis do not differ significantly between 10 cm and 15 cm step-down trials. In both the MLR axis and in the long axis, there were no significant differences between walks and downhill steps. Both 10 cm steps and 15 cm steps have MLR values of $5-7^{\circ}$ for the three bones (slightly lower values for the ungual phalanx-3-5 $)$, similar to the $6^{\circ}$ in level walking. The initial LARs are also nearly identical between level walking and the downhill steps $\left(\sim-15^{\circ}\right.$ to $-17^{\circ}$ for the metacarpal, $-24^{\circ}$ for the proximal phalanx, and $16^{\circ}-18^{\circ}$ for the ungual phalanx). These positions correspond to a foot that is less protracted (in world-space) in downhill steps than in level walking, while similar amounts of adduction and long-axis rotation are maintained between level and downhill walking.


Figure 2.8. Angle distribution plots for downhill steps. A) APR (x-axis) toe-on angular positions (left) and toeoff angular positions (right) for 10 cm step. Bars represent excursion in the APR axis, with end bars representing $\pm$ s.d. B) MLR (y-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 10 cm step. Center point represents total mean across individuals, and outside points indicate $\pm$ s.d. C) LAR (z-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 10 cm step. D) APR (x-axis) toe-on angular positions (left) and toe-off angular positions (right) for 15 cm step. E) MLR ( y -axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 15 cm step. F) LAR (z-axis) toe-on angular positions (circles) and toe-off angular positions (triangles) for 15 cm step. Top set of points in each graph are for metacarpal, middle set are for proximal phalanx, bottom set are for ungual phalanx.

The APR excursions during stance were less in downhill steps than in level ones.
Metacarpal and proximal phalanx rotations in this axis averaged $\sim 74^{\circ}$ in 10 cm steps and $\sim 70^{\circ}$ in 15 cm steps (Fig. 2.9). The ungual phalanx rotated almost the same amount in 10 cm steps as in level steps $\left(40^{\circ}\right)$, while it rotated less in 15 cm steps ( $\sim 33^{\circ}$, not significant). These smaller rotations produced APR toe-off positions that were very similar between level steps,

10 cm steps, and 15 cm steps. Fifteen- cm downhill trials differed from both 10 cm downhill


Figure 2.9. Angular excursion graphs for downhill steps. A) Angular position in the APR axis in 10cm step. B) Angular position in LAR axis in 10 cm step. C) MLR axis angular positions for metacarpal in 10 cm step. D) MLR axis angular positions for proximal phalanx in 10 cm step. E) MLR axis angular positions for ungual phalanx in 10 cm step. F) Angular position in the APR axis in 15 cm step. G) Angular position in LAR axis in 15 cm step. H) MLR axis angular positions for metacarpal in 15 cm step. I) MLR axis angular positions for proximal phalanx in 15 cm step. For A, B, F, \& G, solid line is for metacarpal, dotted line for proximal phalanx, and dashed line for ungual phalanx. Curves represent means across individuals and grey distributions are $\pm$ s.d.
trials and level walks in the amount of MLR during stance. All bones in level walks and 10 cm steps slightly (but not statistically significantly) increased MLR by a few degrees during stance, while 15 cm steps showed significant negative MLR during stance for the metacarpal, proximal phalanx, and ungual phalanx $\left(\mathrm{p}=8.4 \times 10^{-4}, 4.6 \times 10^{-3}, 2.6 \times 10^{-3}\right.$, respectively for walk15 cm step comparison; $\mathrm{p}=3.9 \times 10^{-3}, 0.017,0.050$, respectively for 10 cm step -15 cm step comparison). Although the MLR difference between toe-on and toe-off was significant only for the metacarpal (and not either phalanx) for the $15-\mathrm{cm}$ step down trials, the toe-off positions of the metacarpal underwent statistically significant negative MLR for 15 cm step trials. As in the walk trials, the peak of MLR occurred during stance before decreasing to rotations close to toe-on values at toe-off.

The difference in APR positions between the metacarpal and the proximal phalanx is $\sim 16^{\circ}$ at toe-on, indicating extension of the proximal phalanx at the MCP joint, in both downhill heights, similar to the condition in level steps. Unlike the positions used in level walking, however, the ungual phalanx used lower APR at toe-on in downhill trials relative to the proximal phalanx-there is $\sim 9-10^{\circ}$ extension between the proximal and ungual phalanx at toe-on. The APR difference between the metacarpal and proximal phalanx during stance decreased with downhill step height from level walking. Extension of the proximal phalanx at the MCP joint peaked between $29^{\circ}$ and $34^{\circ}$ in 10 cm steps and between $29^{\circ}$ and $32^{\circ}$ in 15 cm steps. Similar to level steps, the angular excursions between bones in the downhill steps occurred predominantly in the APR axis, while motions in the MLR and LAR axes paralleled each other between bones.

The LAR experienced during level steps was repeated for both 10 cm and 15 cm downhill steps, although its magnitude was slightly less. Each bony element for the downhill steps averaged $\sim 8^{\circ}$ LAR between toe-on and toe-off. The ungual phalanx for 15 cm
downhill steps underwent $\sim 16^{\circ}$ LAR between toe-on and toe-off. These reductions in LAR for step-down trials were reflected in larger (but still rather significant) p -values $\left(8.0 \times 10^{-4}\right.$, $4.8 \times 10^{-4}, 0.013$ for metacarpal, proximal phalanx, and ungual phalanx, respectively, for 10 cm steps; $8.8 \times 10^{-4}, 3.3 \times 10^{-4}, 3.5 \times 10^{-5}$ for metacarpal, proximal phalanx, and ungual phalanx, respectively, for 15 cm steps). Additionally, the metacarpal for 15 cm step-down trials showed a slightly statistically significant negative LAR compared to both walks and 10 cm step-down trials ( $\mathrm{p}=0.047$ for level $/ 15 \mathrm{~cm}$ step; $\mathrm{p}=0.0054$ for 10 cm step $/ 15 \mathrm{~cm}$ step).

The timing of rotations follows similar patterns to those in walks. There is a similar initial positive APR of the proximal phalanx relative to the metacarpal at the very beginning of stance, indicating initial and brief extension of the MCP joint. Again, most of the APR of bones in the digit during stance takes place in the combined proximal and distal interphalangeal joints. The ungual phalanx maintains constant APR until the very end of stance while the metacarpal and proximal phalanx continue rotating throughout stance. For both step-down heights, the ungual phalanx experienced negative MLR relative to the proximal phalanx during stance, before returning to a more similar MLR near toe-off, similar to the condition in level walks. The metacarpal and proximal phalanx undergo MLR together slightly during stance for both step-down heights while the ungual phalanx undergoes MLR in the opposite direction. Finally, similar to the pattern in level walks, the magnitude of LAR flipped near midstance in the 10 cm step-down trials. Early in stance, the ungual phalanx experiences the greatest positive LAR (indicating pronation), while the metacarpal experiences the least. Late in stance, the metacarpal has undergone the greatest positive LAR, while the ungual phalanx has undergone the least. This pattern of long axis rotation holds for the most part in the 15 cm step-down trials until the very latest stance, when the ungual phalanx undergoes a rapid, brief positive LAR and the metacarpal
undergoes a more prolonged negative LAR. This late movement in the metacarpal likely accounts for the significant difference in long axis rotation at toe-off between the 15 cm stepdown trials and both the level walks and the 10 cm step-down trials.

## Discussion

## Parasagittal motion at digit joints

Most studies of ungulate locomotion have been carried out using a 2-D analysis and have relied on an underlying assumption that the motion in limbs is hinge-like or parasagittal (Fischer, 2001; Lee et al., 2008). There is a distinction between hinge-like motion, which occurs primarily in a single axis, and parasagittal motion, which occurs parallel to the anatomical sagittal plane. The world-space x -axis rotations (APR) in this data set are the same as 2-D rotations collected in a perfectly lateral view (Fig. 2.5A). Thus, the difference between the angular positions in the APR axis between the metacarpal and the proximal phalanx serve as a 2-D measurement of MCP joint angle. Alternatively, an anatomical reference plane was used to measure MCP joint angle (see Ch. 3). Briefly, this method utilized a measurement plane which was affixed to the abaxial surface of the metacarpal and aligned parallel to the long axis of the bone and perpendicular to the axis of curvature of the distal metacarpal condyle (the x -axis in this study). The long axes of both the metacarpal and the proximal phalanx were calculated from least moments of inertia, and the long axis of the metacarpal was aligned with this anatomical reference plane. The angular difference between these two long axes is a 3-D measurement of MCP joint angle, since it measures the long axis of the proximal phalanx relative to the long axis of the metacarpal regardless of the position in space of the two bones. Using the same data set, a lateral 2-D MCP joint angle can be compared to a 3-D angle to test the assumptions of planar data and the resulting joint
angles. Figure 2.10 shows the MCP joint angles calculated for walk trials, 10 cm step-down trials, and $15-\mathrm{cm}$ step-down trials. The 2-D joint angles are strikingly similar to (but consistently below) the calculated 3-D angles. The variation (shown as $\pm$ s.d.) of the two methods almost entirely overlap, indicating that a 2-D estimation of motion at this joint is entirely adequate, despite $10^{\circ}-20^{\circ}$ of LAR and modest MLR.


Figure 2.10. Metacarpophalangeal joint angle for global rotations (solid line) representing 2-D view and anatomically-based rotations (dashed line) representing anatomical joint angles. $\pm$ s.d. shown for anatomically-based (light gray) and world-based (dark gray) angles. A) Level steps. B) 10 cm downhill steps. C) 15 cm downhill steps.

The joints of the digit undergo different amounts of APR during stance. The metacarpal continues a consistent APR during all of stance which accelerates during the last $10 \%$ of stance, indicating protraction of the foot as the body passes over. The proximal and
ungual phalanges, however, undergo slight positive APR early in stance in all trials before reversing to follow the metacarpal in negative APR (Fig. 2.11). This brief positive motion in the APR axis for the proximal phalanx indicates the MCP joint is being extended, placing


Figure 2.11. Solid model representing toe-on positions of representative walk with shadows of foot bone positions at $5 \%, 25 \%$, and $50 \%$ of stance. Note the collapse (extension) at metacarpophalangeal joint that occurs very (at $5 \%$ ) early in stance.
strain on the soft-tissues crossing the joint such as the digital flexor muscles and interosseus ligaments. These soft-tissue structures, which are responsible for maintaining erect foot posture during stance, permit ca. $5^{\circ}$ extension at the MCP joint during the middle two-thirds of stance, after permitting an initial rapid extension. While the metacarpal and proximal phalanges continue rotating in a negative direction in the APR axis, the ungual phalanx maintains a narrow range of APR angles during most of stance. The bulk of APR in the digit occurs in the combined movements at the PIP and DIP joints, since the proximal phalanx continues to rotate around a mostly planted ungual phalanx. To use walks as an
example, at $80 \%$ stance, ca. $30^{\circ}$ of the total ca. $75^{\circ}$ of APR is taken up by the rotation at the MCP joint (i.e., between the metacarpal and proximal phalanx). The MCP joint angle is a very poor estimate of motion in the digit in these pigs or of motion between the metacarpal and the substrate. These results are consisted with measurements in horse digits by Chateau et al. (2004) and Clayton et al. (2007), and those studies show the DIP joint as the major point of compliance in the digit.

Further, with some exceptions (Chateau et al., 2004; Dutto et al., 2006; Clayton et al., 2007; Vereeke \& Aerts, 2008), the MCP (or MTP) angles reported in most papers concerning limb mechanics (e.g., McGuigan \& Wilson, 2003; Bobbert \& Santamaría, 2005; Day \& Jayne, 2007; Rubenson et al., 2007; Lee et al., 2008) are actually the angle made between the metacarpal and the ground. The foot, including the digits, is a multi-jointed structure, and the presence of multiple joints, with constellations of muscles and ligaments which cross them, permits changes in timing of muscle-tendon unit strain and production of joint moments, at least for muscles crossing multiple joints (Vereecke and Aerts, 2008). The bulk of cranio-caudal (anterior-posterior) rotations (protraction/retraction, or flexion/extension) in the pigs studied here occurred between the proximal phalanx and the ungual phalanx, rather than between the proximal phalanx and the metacarpal. Since the MCP, PIP, and DIP joints have different muscular and ligamentous structures crossing them (see Ch. 1), the implications from foot motion on muscle-tendon unit function cannot be deduced simply from MCP joint motion.

## Non-parasagittal motion at digit joints

The overwhelming majority of motion at the MCP joint is in APR, or flexion/extension of the proximal phalanx. The angular excursions in MLR and LAR are nowhere near as great as in the APR axis, but there is some motion occurring in those axes
during stance (Fig. 2.12). While the motions in MLR (in particular) are small, there does appear to be a pattern of strong MLR of the ungual phalanx during stance in all conditions.

Data in this study were collected from the $I V^{\text {th }}$ digit of the right foot, which is lateral with respect to the foot. If the two stance digits of the foot act symmetrically, then the ungual phalanges would spread apart during stance. Splayed digits may contribute to the stability of the foot in camelids (Janis et al., 2002), and they may do the same in pigs by increasing the surface area of the fibrofatty, cutaneous digital pad underlying each hoof (the 'frog' in


Figure 2.12. Caudal views of foot bone positions during stance. Toe-on and mid-stance positions shown in A and poses at each $10 \%$ of stance shown in B to illustrate extent of MLR during stance in a typical walk sequence.
horses). The metacarpal and proximal phalanx begin stance with slight positive MLR (suggesting adduction), with the metacarpal slightly more so. The proximal phalanx then undergoes more MLR during stance than does the metacarpal, which would act to bring the proximal phalanges together, assuming digit symmetry. This phenomenon was observed in walks, 10 cm step-down trials, and in 15 cm step-down trials.

The LAR observed during stance was much more consistent and was parallel in the three bony elements. At the onset of stance, both the metacarpal and the proximal phalanx maintain positive LAR angles (suggesting supination), while the ungual phalanx maintains negative LAR angles (suggesting pronation). This occurs because the anatomical axes were placed with respect to the curvature of joint surfaces. There is a medial twist in the joint surfaces between the proximal and ungual phalanges, which accounts for much of the differences in LAR between those two elements of the digit. The offset in axes of curvature of the joints in the digit also permit ungual phalanx contact in both stance digits and forward motion of the pig while the remainder of the manus is adducted and slightly offset from a purely parasagittal plane. While the hooves splay (through MLR) during stance, they rotate inward toward the digit midline (through LAR). The proximal phalanx also moves inward toward the midline through MLR (possibly related to digit extension, discussed above) while undergoing positive LAR in concert with the metacarpal. While these movements appear small, they may contribute to stability in the foot during stance.

The $10^{\circ}-20^{\circ}$ internal rotation reported here is greater than what has been reported in horse digits. Clayton et al (2007) reported a maximum $9^{\circ}$ internal (positive long-axial) rotation during stance, and Chateau et al. (2004) reported internal (positive long-axial) rotation of just over $13^{\circ}$ during stance for the whole foot, with rotations of a couple degrees at MCP, PIP \& DIP joints. Rubenson et al. (2007) reported positive LARs ca. $30^{\circ}$ for
another (primarily) monodactyl species, the ostrich, although no ab-/adduction (MLR) was reported. In both of these groups, ginglymal joints, especially in the distal elements, are a hallmark of their cursoriality (Hildebrand \& Goslow, 2001). The LAR of the whole foot during stance in the pigs studied here follow a similar pattern of internally rotating distal segments during stance, but the LAR of the ungual phalanx relative to the rest of the foot may reflect a specialization in a didactyl foot.

Foot motions in level steps versus downhill steps
The greatest differences between walks and downhill steps occurred in the APR and MLR axes. There is very little difference in the LAR between level walking and stepping down from a height. Initially, the feet approach at smaller APR angles and with a more flexed digit in the step-down trials. That is, the APR angles of the phalanges relative to those of the metacarpal are less at toe-on. At toe-off, there is no difference between the height of the step in the angles in the APR axis used by the foot as a whole or the by the digit. This translates into less flexion/extension at the MCP, PIP, and DIP joints during stance, even though the step height is higher and GRF are higher. Although there is no statistical difference between the two step heights in either initial angles at toe-on or final angles at toe-off, the peak in MCP joint angles are slightly different between the two heights. Changing the height of the step does affect the kinematics of the foot, although mostly for the initial conditions. Contrary to our initial hypothesis, however, MCP joint extension decreases with step-down height, since the feet maintain a more flexed (i.e., less extended or more erect) posture during stance for downhill steps compared to level walking steps.

The differences in the MLR axis are consistent with increased forces from increased height inducing greater adduction during stance. The only statistically-significant differences at initial or final positions between step height (except for the toe-on positions of the
metacarpal only in 15 cm steps and of the proximal and ungual phalanges in walks, curiously) were in the toe-off positions in 15 cm steps. During stance, the variation in MLR was much smaller in level steps. The more intuitive change between level walking and stepping down from a height was the greater abduction, or lateral splaying, of the ungual phalanx in downhill steps. This difference is consistent with greater magnitude GRF acting to deform the digit during stance. There is also a flip between the metacarpal and the proximal phalanx as to which has higher MLR during stance. At the beginning of stance, both bones undergo positive MLR slightly, but the metacarpal changes to negative MLR around midstance while the proximal phalanx continues its positive MLR (Fig. 2.13). These motions are consistent


Figure 2.13. MLR axis angular positions of metacarpal (solid line) and proximal phalanx (dotted line). A) Level walking steps. B) 10 cm downhill steps. C) 15 cm downhill steps. Vertical dotted lines demonstrate \%stance values where MLR axis angular position of proximal phalanx becomes greater than that for metacarpal.
with the proximal phalanx moving toward the midline of the foot relative to the metacarpal. This appears as an adduction of the proximal phalanx at the MCP joint in this digit (the $I V^{\text {th }}$, although if the opposite digit of the foot carries out a similar, but mirror-image, movement it would appear as an abduction for that digit. Again, if this motion was symmetrical within the foot, then the proximal phalanges may move toward each other, a move that may increase digit stability (discussed above). Powered flexion, involving the digit flexor muscles, which would occur after peak extension of the MCP joint, may be responsible for the difference between the metacarpal and proximal phalanx. The alternative is that this motion is directed by the joint surface itself, which is unlikely given the change in timing of the phalangeal motion. Interestingly, the flip between which bone has more positive MLR occurs earlier with increased step height. If the powered flexion of the MCP joint acts to adduct the proximal phalanx, then the increased height and increased force in higher step-down heights may be responsible.

# CHAPTER 3: MECHANICS OF THE METACARPOPHALANGEAL JOINT DURING STANCE IN LEVEL VERSUS DOWNHILL STEPS IN MINIPIGS (ARTIODACTYLA: SUIDAE) 


#### Abstract

Unguligrade stance in minipigs is facilitated not only by digital flexor muscles but also by interosseus ligaments in the foot that potentially conserve energy by providing force without expending metabolic energy. This study tests the hypotheses that the interosseus ligaments resist the majority of ground reaction force torque at the metacarpophalangeal joint and that force provided by the ligament increases in downhill steps compared to level walking. A novel bi-planar cinefluoroscopic data collection and analysis system (XROMM) was used to collect kinematic data synchronized with kinetic data collected both in vivo and ex vivo experiments. A unique data analysis configuration using 3-D bone models and an anatomically-based reference plane was used to determine joint torque. Mechanical behavior of isolated interosseus ligaments shows some spring-like properties despite large amounts of hysteresis. Individuals varied greatly in the proportion of joint torque taken up by interosseus ligaments during stance, peaking at about two-thirds of the stance phase of locomotion. Differences were primarily due to the angle of extension at the MCP joint used during the stance phase. The proportion of joint torque taken up by interosseus ligaments decreased with increasing downhill step height. The shape of torque $\nu s$. angle curves indicate a braking function of the MCP joint during stance, and when GRF increases, the braking function of the joint is increasingly taken up by digit flexor muscles rather than interosseus ligaments. The function of the ligament is primarily to support standing with an erect foot posture with little metabolic input to muscle contraction.


## Introduction

Unguligrade foot posture is a key anatomical innovation in ungulate mammals. Unguligrade foot posture is one where the distal, or ungual, hoofed phalanx is the only bony element lying along the ground during stance. All unguligrade feet lack a pollex, and most living species, such as ruminants and horses, are characterized by additional digit loss and considerable fusion of remaining elements (Hildebrand \& Goslow, 2001). Even-toed unguligrade groups (artiodactyls) stand on digits III and IV, while digits II and V (the "side toes") are reduced to various degrees.

Unguligrade feet possess a set of ligaments often called "spring ligaments" in veterinary literature. These ligaments develop from intrinsic interosseus muscles of the feet and are more properly called interosseus ligaments (see Ch.1). The anatomy of the interosseus ligaments suggests that these ligaments resist extension at the metacarpophalangeal (MCP) joint and likely have spring-like properties. The interosseus ligament originates proximally on the proximo-volar surface of the metacarpals and extends distally to a dual insertion site. The bulk of the ligament attaches to the proximo-volar surface of the proximal phalanges, just distal to the metacarpophalangeal (MCP) joint and resists extension of the MCP joint. A much smaller attachment for the interosseus ligament is on a laterally widened portion of the tendons of the digit extensors on the dorsal aspect of the proximal phalanges called the extensor hood (a mediolateral expansion of the extensor tendons) and might facilitate extension at the interphalangeal joints when strained by placing tension on the widened extensor tendons.

The MCP joints in unguligrade animals have often been modeled as a spring, especially in horses (McGuigan \& Wilson, 2003). More recent studies (e.g., Dutto et al., 2006; Lee et al., 2008) have modeled spring-like, damping, and force-generating behavior at
the MCP joint. During the stance phase of locomotion, the MCP joint extends and strains the structures along the volar side of the joint, such as interosseus ligaments and digit flexor muscles. The interosseus ligament is the only element crossing the volar surface of the MCP joint that cannot generate force and maintains consistent material properties, unlike digital flexor muscles which can modulate their stiffness and spring properties based on fiber activation (Roberts et al., 1997). That said, McGuigan \& Wilson (2003) showed that distal limb stiffness is not affected by digital flexor muscle activation in horses. If their results are the case for all ungulates, then passive ligamentous structures such as the interosseus ligament are the key structures maintaining an erect, unguligrade foot posture during stance.

Pigs (Sus scrofa, Suidae), while being unguligrade, represent an intermediate morphology between digitigrade groups, such as dogs, and derived unguligrade groups, such as ruminants. Pigs lose digit I (pollex) and develop interosseus ligaments, but they retain digits II-V that are reduced to a non-functional role in locomotion. More derived artiodactyls have extremely reduced (mostly absent) $\mathrm{II}^{\mathrm{nd}}$ and $\mathrm{V}^{\mathrm{th}}$ digits, fuse the metapodials of digits III and IV into a single bony element (the cannon bone), and elongate the metapodials and accompanying interosseus ligaments. These changes evolved in groups that already evolved unguligrade foot posture, and they likely affect the mechanics of the MCP joint and of the soft-tissues crossing the joint (see Ch. 1). Because pigs do not have such a derived foot, they are ideal for studying the functional contribution of the interosseus ligament to maintaining unguligrade stance without other specializations such as fusion and extreme elongation.

This study examines the mechanical significance of the interosseus ligament of forefeet in artiodactyl locomotion. I hypothesize that the interosseus ligament provides a significant amount of torque during stance at the MCP joint. There are three sets of soft-
tissue structures that cross the MCP joint and are capable of producing torque at the MCP joint: the 1) superficial and 2) deep digital flexor muscles and the 3 ) interosseus ligaments. The digital flexor muscles need to be active during stance in order to prevent hyperextension at the proximal (PIP) and distal interphalangeal (DIP) joints, making it impossible for the interosseus ligaments to provide all the torque during stance. However, any torque provided by the interosseus ligament does not require metabolic energy in the form of muscle contraction and would represent an energy savings over a condition in which all the joint torque came from muscle activity. If the interosseus ligaments provide a significant amount of torque at the MCP joint, then that performance advantage could explain the evolution of such a derived foot posture in artiodactyls.

This study combines in vivo and ex vivo data to determine the contribution of passive ligamentous structures to total joint force during stance. Measurements of in vivo MCP joint flexion/extension and the GRF moments resisted by soft-tissue structures crossing the joint in minipigs during unimpeded locomotion in a trackway are compared to the moments acting to resist extension at the MCP joint against interosseus ligaments in an ex vivo reduced preparation. These two data sets are compared to determine the contribution of interosseus ligaments to total joint force.

## Materials \& Methods

This study used the same minipigs and XROMM system described in the previous chapter. The kinematics of level and downhill steps collected from the trackway data and analyzed in MATLAB and Maya were imported into this study and combined with a kinetic analysis from the under-trackway forceplate.

## Kinetic analysis

Force data were recorded at $1000 \mathrm{~s}^{-1}$ using LabVIEW 8.5 (National Instruments, Austin, TX). Voltage measurements from the force platform were calibrated manually, Butterworth filtered in MATLAB (50Hz low-pass), and converted into a resultant vector (i.e., GRF) with center-of-pressure coordinates relative to the surface of the force plate window. Video and force data were synchronized using a common start trigger that initiated recording. The table-top forceplate configuration was stabilized in the direction of travel (parallel to the trackway) using wall-mounted box beams clamped to the table. Vertical stability was provided by affixing the forceplate to the weighted table using Bondo fiberglass resin (3M, Atlanta, GA). However, due to the space constraints of the fluoroscopic C-arms, no additional lateral (with respect to direction of travel) stability could be added to the forceplate. As a result, transverse oscillations were present in the force recordings. Horizontal force component calculations had a variable-frequency oscillation that could not be filtered out and increased the error in lateral (with respect to direction of travel) force measurements and in center-of-pressure coordinates. This variability made the kinetic data unreliable for a complete 3-D analysis to accompany the 3-D kinematics of foot bones, but the in-travel and vertical force components were adequate for the planar analysis carried out here (see below). Further, the motion of the MCP joint is primarily flexion/extension (see previous chapter), and the interosseus ligament resists this motion. The horizontal oscillations would not affect the force resisted by the interosseus ligaments, since they occurred transversely with respect to the orientation of the foot in space.

## Ex vivo experimental setup

After in vivo data were collected, experimental animals were euthanized by IV administration of pentobarbital according to Brown University ACF protocol. Marked
forelimbs of each individual were harvested and stored in a $0^{\circ} \mathrm{F}\left(-17.8^{\circ} \mathrm{C}\right)$ freezer. After thawing, marked feet were skinned and dissected. Phalanges were disarticulated at the proximal interphalangeal joint, and the manus was disarticulated at the radiocarpal joint. These isolated preparations were prepared such that the only remaining intact major structure crossing the metacarpophalangeal joint was the interosseus ligament. The preparations were not dissected further, in order to prevent accidental damage to the interosseus ligament. The proximal region of metacarpals III and IV of the isolated preparations were fixed to 6.033 cm diameter PVC pipe (ASTM D1785 Schedule 40, North American Pipe Corporation, Elkhart, IN ) using 25 g surgical steel suture (Ethicon, Somerville, NJ ). Distal regions of the metacarpals were stabilized using 10 cm plastic cable ties. The other end of the PVC pipe was clamped to a rig made from 80/20 (80/20 Inc., Columbia City, IN ) which was then clamped to a lab table. A 1 mm drillbit was passed through the distal articular condyles of the proximal phalanges, and a non-compliant string was tied to the drillbit between the two phalanges. This string was passed through an angled guide of 80/20 attached to the rig, passed over a plastic pulley, and tied to a single-element force transducer (Kistler Type 9203, Kistler USA, Amherst, NY). The force transducer was attached to a custom-made aluminum rod that permitted manual tension to be applied through the force transducer and inelastic string to the interosseus ligament. The image intensifiers of the C-arms used in in vivo trials were arranged roughly dorsoventrally and mediolaterally with respect to the isolated foot preparation. Ex vivo trials consisted of manually pulling on the aluminum rod and inducing extension at the MCP joint. Cinefluoroscopic digital video and force recordings through the single-element transducer of ex vivo trials were collected at $500 \mathrm{~s}^{-1}$.

## 3-D analysis in Maya

The trackway floor, the force platform, the force platform window, and virtual cameras were constructed in a virtual scene according to their relative global positions and real-world dimensions in the software package Maya (Maya 8.5, Autodesk, San Rafael, CA). Views of the force platform window and force platform edges from the two digital videos were hand-aligned to the force platform and window models in the virtual scene. The translations and rotations necessary to convert the calibrated "C-arm" space to "force platform" space were recorded and entered into a transformation matrix that was applied to all digitized in vivo data. The resultant GRF and center-of-pressure positions which were calculated in force-platform-space were then properly aligned to the motion of the 3-D models of the metacarpal, proximal phalanx, and ungual phalanx animated in in vivo sequences.

For ex vivo sequences, undistorted views of individual trials were used to hand-align a point of application of force between the two proximal phalanges on the drillbit. No other elements of the ex vivo apparatus were constructed in a virtual scene. The vector of the applied force was hand-aligned to follow the orientation of the inelastic string connecting the drillbit and the single-element force transducer. These two elements are analogous to the center-of-pressure and GRF magnitudes calculated through the force platform measurements.

## Anatomical reference plane

A set of inertial axes was created for each metacarpal model and each proximal phalanx model. These sets of axes indicated the axis of greatest inertia (an x -axis), the axis of least inertia (a z -axis), and an axis orthogonal to the first two (a y -axis). The axis of least inertia represented a repeatable measure of the long axis of a bone, while the other two axes
varied somewhat between individuals. The inertial axes on the metacarpal models were rotated about the axis of least inertia (i.e., the long axis of the bone) until the axis of greatest inertia was aligned to a position parallel to the axis-of-curvature of the distal metacarpal articular surface. That is, the x -axis of the bone was adjusted until it was parallel to the curved plane defined by the MCP joint surface. The axes were translated along this axis until the axis of least inertia was adjacent to the adaxial surface of the metacarpal. That is, the $z$ axis was slid along the x -axis until it lied on the adaxial metacarpal surface. This realignment of the inertial axes created a set of anatomical axes that corresponded to 1 ) the long axis (the axis of least inertia, or z -axis) 2) the adaxial/abaxial axis (parallel to the center of curvature for the MCP joint, or x -axis) and 3 ) the dorsal/volar axis (orthogonal to the first two, or $y$-axis) of the metacarpal. A plane was then constructed using the long axis (zaxis) and the dorsal/volar axis ( y -axis) of the metacarpal. Motion along this plane represents pure flexion/extension of the MCP joint, which involves the digital flexors and the interosseus ligament, since those structures limit extension during stance. For in vivo sequences, the GRF vector was projected into this plane, and a moment arm from the MCP joint center-of-rotation (on the adaxial/abaxial axis) was calculated to yield a total joint torque in the anatomic reference plane. For ex vivo sequences, the hand-aligned applied force was projected in the anatomic reference plane with a moment arm from the MCP joint center-of-rotation to yield a torque resisted by the interosseus ligament alone. For both in vivo and ex vivo scenarios, MCP joint angle was calculated as the angle between the two long axes of the metacarpal and proximal phalanx $\left(0^{\circ}\right.$ was defined as the two axes in perfect alignment in the anatomic reference plane). For each digitized frame, a MCP joint angle and a torque was calculated. In the in vivo sequences, this torque represented a total joint torque,
and the ex vivo torque calculations represented a proportion of total joint torque applied by the interosseus ligament alone.

## Torque/angle curves

Data generated in this study are analyzed in graphs demonstrating the torque $\nu$ s. angle relationship. These curves resemble work loops like those used to analyze muscle function (Josephson, 1985). The angle values on the abscissa are proxies for a strain measurement of the soft tissues resisting extension of the MCP joint. The torque values on the ordinate represent the rotational force resisted by the joint, either in the isolated preparation or in the intact limb. These torques are opposite and equal to either manuallyapplied forces (in ex vivo sequences) or ground reaction forces (in in vivo sequences). Clockwise loops indicate work absorbed by a system, which are expected for both isolated ligaments (Nordin et al., 2001) and forefeet during locomotion (Dutto et al., 2006).

The data flow for in vivo and ex vivo trials are shown in Figure 3.1. Section A shows 3-D models of a metacarpal, proximal phalanx and ungual phalanx at $25 \%, 50 \%$ and $75 \%$ of stance. The magnitude and orientation of the GRF is shown in red, and the surface of the forceplate window is shown in aqua. Section B shows the 3-D models and GRF in position at $25 \%, 50 \%$ and $75 \%$ stance in the anatomic reference plane. In the anatomic reference plane view, all motions take place relative to the stationary metacarpal. In the left panel of B ( $25 \%$ stance), the moment arm measured from the joint center of rotation to the GRF is labeled ' $a$ ' and the magnitude of the GRF projected into the anatomic reference plane is labeled 'b.' At each time-step, the planar GRF (b) and the normal from the GRF to the center-of-rotation (i.e., the moment arm, a) is calculated in Maya. Also, the angle between the long axes (calculated as moments of least inertia) of the metacarpal (shown in green in

middle panel of B) and the proximal phalanx (shown in blue) is calculated in Maya at each time-step. Panel C shows the outputs of these calculations: force in Newtons in the anatomic reference plane (left panel, red trace), moment arm in millimeters (left panel, green trace), joint moment in Newton*meters (the product of moment arm, a, and planar force, b , from B; middle panel), and joint angle in degrees as a function of stance time. Finally, for each time-step, the joint moment and joint angle are plotted against each other, shown in Section D. Arrows indicate the direction of data points during stance. For in vivo sequences, both the angle of MCP extension when maximum torque was reached and the torque at
which maximum angle was reached (indicated by orange lines in D ) were determined for each sequence. These values were averaged by individual.

Sections E, F, and G of Figure 5 show identical calculations for a representative ex vivo trial. Identical planar force, moment arm, and joint angle measurements are made, even though the 'simulated GRF' is applied at the end of the proximal phalanx rather than at the ungual phalanx. Section E shows the relative positions of the metacarpal, proximal phalanx, and applied force in the anatomic reference plane at $25 \%, 50 \%$, and $75 \%$ of stance. Section F shows the planar force and moment arm (left), joint moment (middle), and joint angle (right) calculated at each time-step during a trial. The resulting curve in $G$ shows joint moment as a function of joint angle, and a power-fit curve derived from that trial is shown in a dotted line. For each ex vivo trial, an exponential curve was fit to the entire sequence. New curves were generated using the intercept ( $\mathrm{y}_{0}$ ), constant (a), and exponent (pow) calculated from curve fitting for the range $0^{\circ}-40^{\circ}$ extension. The values generated from these curves were averaged at every $0.1^{\circ}$ across and between individuals. Thus, average curves from ex vivo data are not generated directly from equation variables but are averaged from the values generated by those variables in each curve.

## Results

## Ex vivo preparations

For individual trials, the difference between loading and unloading curves stayed around 0.1 Nm for the middle regions of the curves. This difference represented a significant reduction in force in unloading the ligament-around $25 \%$ of the force produced by the ligament during loading was lost when unloading the ligament. The difference between the loading an unloading portions of curves peaked around $0.12-0.15 \mathrm{Nm}$, although
this difference was obviously less at peak torques. The variability in curve-fit constants is given in Table 3.1.

| sequence | $\mathrm{y} 0 \pm$ | a $\pm$ | pow $\pm$ |
| :---: | :---: | :---: | :---: |
| 0304a | $0.051607 \pm 1.68$ | $3.4901 \mathrm{e}-007 \pm 1.22 \mathrm{e}+6$ | $4.5471 \pm 1.29$ |
| 0304b | $-0.11172 \pm 2.7$ | $4.4224 \mathrm{e}-005 \pm 7 \mathrm{e}+4$ | $3.3179 \pm 9.79$ |
| 0304c | $-0.026886 \pm 1.9$ | $1.5102 \mathrm{e}-007 \pm 1.19 \mathrm{e}+7$ | $5.1068 \pm 5.61$ |
| 0305a | $-11.215 \pm 55.3$ | $9.3362 \pm 54.3$ | $0.078955 \pm 0.379$ |
| 0305b | $-0.10754 \pm 2.46$ | $6.0874 \mathrm{e}-005 \pm 4.38 \mathrm{e}+4$ | $3.2505 \pm 8.26$ |
| 0307a | $0.17221 \pm 3.66$ | $1.0911 \mathrm{e}-008 \pm 3.58 \mathrm{e}+8$ | $5.7279 \pm 12.8$ |
| 0307b | $0.04749 \pm 0.0613$ | $7.7443 \mathrm{e}-008 \pm 7.79 \mathrm{e}-8$ | $5.2098 \pm 0.296$ |
| 0307c | $-0.32709 \pm 0.0819$ | $0.00016331 \pm 6.18 \mathrm{e}-5$ | $2.9859 \pm 0.105$ |
| 0401b | $-0.86332 \pm 5.21$ | $0.01986 \pm 509$ | $1.4489 \pm 33.1$ |
| 0401c | $-1.0387 \pm 7.05$ | $0.004549 \pm 5.17 \mathrm{e}+3$ | $1.9593 \pm 81.2$ |
| 0404a | $-0.43558 \pm 3.79$ | $0.0010638 \pm 5.65 \mathrm{e}+3$ | $2.2734 \pm 19.8$ |
| 0404b | $-0.85446 \pm 5.77$ | $0.0021968 \pm 7.53 \mathrm{e}+3$ | $2.0868 \pm 58$ |
| 0404c | $-0.66155 \pm 6.97$ | $0.00012577 \pm 2.37 \mathrm{e}+5$ | $2.8847 \pm 110$ |
| 0406a | $-0.11556 \pm 4.5$ | $1.8164 \mathrm{e}-006 \pm 4.54 \mathrm{e}+6$ | $4.0866 \pm 28.4$ |
| 0406b | $-1.0044 \pm 5.6$ | $0.0037144 \pm 4.48 \mathrm{e}+3$ | $1.9616 \pm 58.1$ |
| 0406c | $-0.10105 \pm 4.99$ | $1.883 \mathrm{e}-006 \pm 8.58 \mathrm{e}+6$ | $4.064 \pm 58.1$ |
| 0502a | $-0.18902 \pm 2.06$ | $5.1699 \mathrm{e}-005 \pm 3.86 \mathrm{e}+4$ | $3.0908 \pm 6.58$ |
| 0503a | $-0.57649 \pm 4.18$ | $0.00064501 \pm 1.24 \mathrm{e}+4$ | $2.4429 \pm 27.4$ |
| 0503b | $-0.04551 \pm 0.0374$ | $1.1444 \mathrm{e}-007 \pm 6.78 \mathrm{e}-8$ | $4.8365 \pm 0.164$ |
| 0503c | $-0.044708 \pm 0.0411$ | $1.5582 \mathrm{e}-007 \pm 7.13 \mathrm{e}-8$ | $4.7208 \pm 0.124$ |
| 0504a | $-0.13746 \pm 1.26$ | $1.6011 \mathrm{e}-005 \pm 5.14 \mathrm{e}+4$ | $3.4397 \pm 2.63$ |
| 0504b | $-0.50136 \pm 3.5$ | $0.00024025 \pm 3.44 \mathrm{e}+4$ | $2.7146 \pm 28.6$ |
| 0504c | $-2.363 \pm 9.31$ | $0.038651 \pm 1.52 \mathrm{e}+3$ | $1.4243 \pm 214$ |
| 0507c | $-0.99487 \pm 7.46$ | $0.0014873 \pm 4.12 \mathrm{e}+4$ | $2.3178 \pm 230$ |
| 0601b | $-0.048617 \pm 1.19$ | $7.2261 \mathrm{e}-005 \pm 1.32 \mathrm{e}+4$ | $3.1666 \pm 2.96$ |
| 0601c | $-2.8906 \pm 4.46$ | $2.1157 \pm 7.32$ | $0.19942 \pm 41.4$ |
| 0602b | $-0.23909 \pm 0.0558$ | $0.00012135 \pm 3.14 \mathrm{e}-5$ | $2.9842 \pm 0.0692$ |
| 0601b | $-0.20703 \pm 0.0486$ | $0.00018839 \pm 3.47 \mathrm{e}-5$ | $2.834 \pm 0.048$ |
| 0603b | $-1.3133 \pm 2.65$ | $0.96677 \pm 4.64$ | $0.23305 \pm 11.8$ |
| 0604b | $-0.38812 \pm 4.86$ | $0.00073356 \pm 2.77 \mathrm{e}+4$ | $2.4721 \pm 73.5$ |

Table 3.1. Curve-fit constants for ex vivo sequences. Data were fit to the equation $x=y_{o}+a^{\text {pow }}$.

Torque resisted by the interosseus ligament increased curvilinearly with angle (Fig.
3.2A). Below $15^{\circ}$ extension at the MCP joint, torque resisted by the interosseus ligament is
negligible. At $40^{\circ}$ extension, the average torque resisted by the interosseus ligament was 0.63 Nm . The variability in trials increased steadily with angle and was quite high at the


Figure 3.2. Ex vivo curve fits from experimental data. Grand average of all ex vivo trials (A) and individual averages (B). Colors correspond to individuals (green - sus03; blue - sus04; red - sus05; orange - sus06), and upper and lower thin curves indicate $\pm$ s.d.
highest angles analyzed (ca. 0.1 Nm ). Fit curves calculated from ex vivo data are conservative estimates of the torque generated by the interosseus ligament because the hysteresis experienced by the ligament is taken into account when generating fit curves. Peak torque was reached very quickly (within 100 ms ) for ex vivo trials, while relaxation of the ligament to zero force was considerably longer, further biasing the fit curves to lower estimates of force. A conservative estimate of ligament torque is useful, since stance in in vivo trials lasts longer than the time to peak force production from ligamentous structures. These estimates are likely more realistic.

Because negative values could be calculated from the fitted power curves but were not observed from actual force recordings (this would mean the ligament or string was "pushing" on the force transducer), negative values from power curves were discarded and registered as zero values. This makes estimates below $15^{\circ}$ extension unreliable, although the real values are likely zero. Thus, the optimum range for estimating interosseus ligament mechanics for the MCP joint is $15^{\circ}-35^{\circ}$ extension.

## In vivo trials

The MCP joint increased total joint torque as joint angle increased (Fig. 3.3). Every trial employed a clockwise torque $v$ s. angle loop, indicating that the joint absorbed work or acted as a brake during stance. Individuals used a range of speeds in walks, using an average speed of $0.71 \mathrm{~m} / \mathrm{s}$ and a range from $0.34 \mathrm{~m} / \mathrm{s}$ to $1.40 \mathrm{~m} / \mathrm{s}$. Overall, peak joint torque generally increased with increased speed, although not in every case. Maximum torque also increased in step-down trials from $0.68 \pm 0.27 \mathrm{Nm}$ in walks, $0.75 \pm 0.20 \mathrm{Nm}$ in 10 cm steps, and $0.84 \pm 0.26 \mathrm{Nm}$ in 15 cm steps (Fig. 3.4). However, the joint torque at maximum joint extension remained similar between walks $(0.618 \pm 0.166 \mathrm{Nm})$ and 10 cm steps ( $0.616 \pm 0.170 \mathrm{Nm}$ ) while increasing in 15 cm steps $(0.684 \pm 0.274 \mathrm{Nm})$.


Figure 3.3. Individual torque $v s$. angle curves. Each graph represents all experimental trials from each individual. Colors are as follows: black - ex vivo curve for each individual $\pm$ s.d.; red - level steps; blue 10 cm steps; green -15 cm steps. sus03 in $A$, sus04 in $B$, sus 05 in $C$, sus06 in D.

MCP joint extension showed an inconsistent relationship with speed across all individuals. The average peak angle was $30.8 \pm 4.8^{\circ}$ extension, and the average angle at peak
torque was $29.9 \pm 4.9^{\circ}$ extension for walking trials. Both maximum angle and peak angle at maximum torque decreased with step height to $28.5 \pm 6.3^{\circ}$ and $26.5 \pm 7.3^{\circ}$, respectively, for 10 cm steps and $27.2 \pm 4.5^{\circ}$ and $25.0 \pm 5.3^{\circ}$, respectively, for 15 cm height (Table 3.2).

Individuals used straighter leg postures (i.e., less extended MCP joint angles) and experienced higher total joint torque as step height increased.




Figure 3.4. Total MCP joint torque showin in dark gray, +s.d. in light gray. Proportion of total MCP joint torque taken up by interosseus ligament (red) +s.d. (orange) overlain. Values for level steps (A), 10 cm step (B), and 15 cm step (C) at point where maximum torque was reached. Values for level steps (D), 10 cm step $(E)$, and 15 cm step $(F)$ at point where maximum angle is reached.

Across all walk sequences, the interosseus ligament provided approximately a third of total MCP joint torque during stance ( $44.6 \pm 23.9 \%$ at peak angle, $35.7 \pm 19.7 \%$ at peak torque, Table 3.3), although results compared across individuals were highly variable. The combination of reduced joint extension and higher joint torques decreased the proportion of torque provided by the interosseus ligament during step-down sequences. For 10 cm steps, the proportion of joint torque provided by the interosseus ligament was $35.6 \pm 23.3 \%$ at peak angle and $25.7 \pm 20.8 \%$ at peak torque. For 15 cm steps, the proportion provided by the

| angle © max torque | grand ave | sus03 ave | snus04 ave | sns05 ave | sus06 ave |
| :---: | :--- | :--- | :--- | :--- | :--- |
| walks | $29.9 \pm 4.9$ | $34.0 \pm 2.8$ | $24.4 \pm 1.5$ | $34.3 \pm 1.3$ | $26.7 \pm 2.4$ |
| 10 cm | $26.5 \pm 7.3$ | $29.8 \pm 1.9$ | $25.9 \pm 2.5$ | $33.9 \pm 3.3$ | $17.9 \pm 21$ |
| 15 cm | $25.0 \pm 5.3$ | $29.4 \pm 1.6$ | $25.3 \pm 2.5$ | $29.0 \pm 2.2$ | $18.4 \pm 3.4$ |
| angle © max angle |  |  |  |  |  |
| walks | $30.8 \pm 4.8$ | $34.5 \pm 2.3$ | $25.2 \pm 1.3$ | $35.2 \pm 1.4$ | $27.9 \pm 1.5$ |
| 10 cm | $28.5 \pm 6.3$ | $30.8 \pm 1.1$ | $28.8 \pm 1.1$ | $34.9 \pm 2.1$ | $20.7 \pm 1.7$ |
| 15 cm | $27.2 \pm 4.5$ | $30.5 \pm 1.6$ | $26.8 \pm 2.4$ | $31.5 \pm 1.4$ | $21.7 \pm 2.2$ |

Table 3.2. Measurements of MCP joint angle when maximum torque is reached and when maximum angle is reached. Grand average is taken across all individuals, and values are given in degrees $\pm$ s.d.

| \%@ max tonque | grand ave | 03 ave | 04 ave | 05 ave | 06 ave |
| :---: | :---: | :---: | :---: | :---: | :---: |
| walks | $35.7 \pm 19.7$ | $38.1 \pm 17.9$ | $14.2 \pm 2.9$ | $54.7 \pm 10.5$ | $30.3 \pm 12.5$ |
| 10 cm | $25.7 \pm 20.8$ | $19.4 \pm 6.1$ | $13.4 \pm 4.4$ | $52.3 \pm 11.7$ | $8.5 \pm 2.7$ |
| 15 cm | $16.1 \pm 9.1$ | $14.2 \pm 7.3$ | $13.5 \pm 2.9$ | $26.3 \pm 8.2$ | $9.2 \pm 5.2$ |
| \%@ max angle |  |  |  |  |  |
| walks | $44.6 \pm 23.9$ | $43.7 \pm 19.5$ | $18.3 \pm 3.5$ | $68.4 \pm 12.4$ | $40.1 \pm 15.7$ |
| 10 cm | $35.6 \pm 23.3$ | $24.7 \pm 5.2$ | $25.8 \pm 4.2$ | $64.9 \pm 15.6$ | $16.8 \pm 2.8$ |
| 15 cm | $25.3 \pm 10.8$ | $18.1 \pm 8.5$ | $20.8 \pm 3.1$ | $37.6 \pm 10.7$ | $20.5 \pm 5.6$ |

Table 3.3. Measurements of MCP joint torque when maximum torque is reached and when maximum angle is reached. Grand average is taken across all individuals, and values are given in percentages $\pm$ s.d.
ligament was $25.3 \pm 10.8 \%$ at peak angle and $16.1 \pm 9.1 \%$ at peak torque. The values between peak joint angle and peak joint torque differ significantly due to the open-ness of the torque $v$ s. angle curves. Peak total joint torque was most often reached at a lower angle than peak angle, leading to a smaller proportion of the total joint torque being provided by the ligament.

The results of the in vivo experiments varied greatly both by individual and by behavior. Each of the four individuals used a different set of torque and angle values during walks and step-downs. Moreover, each pig showed a different response to increased speed during level steps. The results given below are described per individual, with all measurements comparing ligament mechanics to whole-joint mechanics taken from the same individual.

The first individual (sus03, Fig. 3.3A) utilizes in vivo torque/angle loops for steps that are fairly close in the loading and unloading portions. The walking sequences for this pig show very tight curves, and the angle at peak torque is fairly close to the peak extension angle of the MCP joint. Three of the four curves use similar torque/angle excursions which use about a third of the joint torque from the interosseus ligament ( $29.5 \%$ at peak torques, $34.0 \%$ at peak angles). The outlying walk sequence uses a much higher proportion of planar joint torque from the ligament ( $63.9 \%$ and $72.8 \%$ ). The step-down sequences used more open curves that reach higher torques at shallower (more flexed) MCP joint angles. The range of extension angles at peak angles and torques decreased from $30^{\circ}-37^{\circ}$ in walk trials to $27^{\circ}-32^{\circ}$ in step-down trials. Concomitantly, peak torques increased from $0.8 \mathrm{Nm}-1.1 \mathrm{Nm}$ in walks to $0.8-1.3 \mathrm{Nm}$ in step-downs. Because higher torques are reached at lower angles, stepdowns in this individual used much smaller proportions of planar MCP joint torque from the interosseus ligament. The lowest percent of joint torque coming from the ligament in walk sequences was close to the peak ligament proportion for the step-down sequences, and the proportion of torque produced by the interosseus ligament at peak angles and torques was as low as $10 \%$ in step-downs.

One other individual (sus05, Fig. 3.3C) utilized a broadly similar pattern of torque/angle relationships. For this individual, curves from walking trials generally paralleled the ex vivo curve. The peak angles and torques used in walking trials generally increased with increased speed. This individual relied much more on the interosseus ligament to provide torque for the MCP joint in level steps than any other individual. The proportion of force provided by the interosseus ligament averaged $54.7 \%$ at peak torque for a sequence and $68.4 \%$ at peak angle. This proportion is higher on average than any other individual. These walking trials used relatively low peak torques ( $\sim 0.4-0.6 \mathrm{Nm}$ ) and relatively
high angles ( $\sim 32^{\circ}-37^{\circ}$ extension) compared to other individuals. Additionally, this individual chose the slowest walking speeds and employed the most extended MCP joint.

Step-down sequences for this individual showed a pattern of increased joint torque yet more flexed MCP joint angles. Step-downs from the smaller ( 10 cm ) height used similar torque/angle relationships to walk sequences, except the curves are more open (i.e., the loading and unloading regions of the curve are farther apart). The proportion of planar joint torque taken up by the ligament in the smaller step-down sequences approached that for walking sequences ( $52.3 \%$ at peak torque, $64.9 \%$ at peak angle). However, the higher ( 15 cm ) step-down produced curves that were much more open and used more flexed angles. Because shallower angles were used for these sequences, the proportion of joint torque taken up by the ligament decreased to $26.3 \%$ at peak torque and $37.6 \%$ at peak angle.

Another pattern of torque/angle relationships in walks is in a third individual (sus06, Fig. 3.3D). At the slowest speed, this individual used a similar proportion of joint force from interosseus ligaments at peak planar joint torque and peak angle as the two previously described individuals ( $46.7 \%$ and $62.5 \%$, respectively, at $0.7 \mathrm{~m} / \mathrm{s}$ ). As this individual used faster walking speeds, planar joint torque generally increased, and the torque/angle curves became more open. Moreover, as this individual increased speed, it did not increase the MCP joint angles used during walking steps, unlike the previous two described individuals. Peak angles generally decreased with increasing speed, especially at peak torque. This individual never used angles of MCP extension greater than $30^{\circ}$, and the highest angles used by this individual were in walking steps. The proportion of planar joint torque taken up by the interosseus ligament was around $1 / 3$ ( $30.3 \%$ at peak torque, $40.1 \%$ at peak angle).

There was little difference between step-down trials by height in this individual, although step-down trials in toto differed from walk trials in using more flexed MCP joint
angles. The range of joint torques used in step-down trials was within the range for walking trials, except for two sequences. Thus, the reduction in the proportion of planar joint torque taken up by the interosseus ligament overall in step-down trials ( $8.8 \%$ at peak torque, $18.6 \%$ at peak angle) is a result of the decrease in angles used.

Finally, a fourth individual used a different set of torque/angle relationships (sus04, Fig. 3.3B). The walk steps for this individual were similar to step-down sequences in most other individuals. The curves for walking trials were the most open of any individual, and the peak MCP joint angles were the most flexed while the speeds this individual used were slower than average. Faster speed did not affect either peak torque or peak angle. The proportion of planar joint torque taken up by the ligament was lowest in walking trials in this individual ( $14.2 \%$ at peak torque, $18.3 \%$ at peak angle).

Torque/angle graphs from step-down sequences maintained similar overall shapes to the walking sequences, although higher peak angles and torques were reached. The proportions of planar MCP joint torque provided by the interosseus ligament for step-down sequences in this individual were similar to the average for step-down trials in all individuals. At peak torque, step-down sequences for this individual averaged similar proportions of planar joint torque from the interosseus ligament as in walk sequences $(13.4 \%$ for $10-\mathrm{cm}$, $14.1 \%$ for 15 cm ). The ligament proportion of planar joint torque increased slightly at peak angle for step-down sequences ( $25.8 \%$ and $20.3 \%$ ), largely as a result of a few sequences undergoing the highest MCP joint extension.

## Discussion

## Braking function of MCP joint

A spring model of leg function (Farley et al., 1993) during locomotion predicts that greater joint torques produce greater leg compression, expressed here as MCP joint extension. The individuals studied here showed an opposite pattern: the peak joint angles decreased overall during high-force activities, either through faster steps or through higher step-down trials. Also, the interosseus ligament was significantly engaged in producing joint torque resisting the GRF at slow speeds for some individuals and at high angles of extension for all individuals. The increased open-ness of torque-angle curves at higher planar joint torques suggests a stiffer yet less spring-like MCP joint than at lower torques. An increasingly greater proportion of planar joint torque is taken up by active contractile elements (such as the superficial and deep digital flexors) rather than passive elements, such as the interosseus ligament, and the joint takes on a greater role as an actuator.

The proportion of total joint force provided by the interosseus ligaments combined with the clockwise direction of the torque/angle graphs indicates that the MCP joint does not act as an effective spring in these minipigs. The proportion of joint torque not provided by the interosseus ligaments must be provided by the muscle-tendon units of the digital flexors, which would require at least some metabolic energy to provide these forces. The implication for the evolution of this derived foot posture and the modification of interosseus muscles is that the morphological changes in the feet of unguligrade animals, at least at first, may not have been to create effective springs. Pigs represent the most primitively-featured extant unguligrade animals, since they possess the bare minimum of unguligrade foot posture but retain unfused digits II-V and intrinsic adductors of reduced digits II and V. The braking function of unguligrade limbs is emphasized in this morphology, as indicated by
very open torque/angle curves that show very different amounts of torque when the joint is being loaded (absorbing forward kinetic energy at the beginning of stance) compared to when the joint is being unloaded (producing force for forward motion at the end of stance).

Other workers have shown that in other and more derived unguligrade species, such as horses, the compliance of the MCP joint is fixed, regardless of contraction of digital flexors (McGuigan \& Wilson, 2003). If this were the case in the minipigs studied here, then torque-angle curves would maintain similar shapes between trials and would take a similar parallel trajectory toward peak angles and peak torques at increased speed and/or force. A similar scenario to this was the case for two individuals during level steps (sus03, Fig. 3.3A; sus05, Fig. 3.3C), where loading and unloading portions of the torque/angle curves were somewhat close to each other. Also, the interosseus ligaments help simply to maintain an elevated MCP joint, while (especially) the proximal and distal interphalangeal joints are also elevated above the walking surface through the action of digital flexor muscles. If digital flexors were not active during stance, then (at least) the proximal IP joint would collapse, or hyperextend. In horses, the interosseus (i.e., "suspensory") ligaments cross both the MCP and proximal IP joints, permitting a spring-like system capable of maintaining fixed compliance without muscular digital flexor activity. However, in artiodactyls, the interosseus ligaments cross only the MCP joint and cannot resist extension in proximal or distal IP joints, which are flexed only by digit flexor muscles. The actions of these muscles in the minipigs studied here and in the goats of Lee et al. (2008) change the function of the MCP joint from primarily a spring (at level walking at slow speeds) to primarily an actuator (at high speeds or step-down trials with high planar joint torques), rather than entirely a spring as in horses.

In quadrupedal locomotion forelimb landing takes place cranial to the center of mass and thus has a net braking effect on forward motion (Biewener, 2003, and references therein). Forelimbs in ungulates experience higher GRFs than hindlimbs do (Gustas, et al., 2004), produce a net braking force (Dutto, et al., 2004), and absorb work during stance (Dutto, et al., 2006). This braking effect manifests itself in torque-angle curves whose loops are more open. The torque-angle curves analyzed in this study that were more open, were, for the most part, also at lower MCP joint angles and engaged less of the interosseus ligament than were the curves that were less open or more spring-like. These open curves are evidence of negative work being done on the forelimb, and larger loops indicate a larger amount of work absorbed by the joint during stance than less open curves. That the shape of ex vivo curves differs so greatly from the very open or 'loss-y' curves during low-angle behaviors further indicates little reliance upon the interosseus ligaments during the stance phase of locomotion in those trials.

Engaging the interosseus ligament would provide passive torque and could serve as a potential energy saving mechanism. Although the ligament does not display ideal spring behavior, the properties of the ligament are fixed (at least during a stride), and relying upon digital flexors for torque production at the MCP joint permits greater plasticity during stance. Spring-like behavior of the foot would probably engage a large proportion of the interosseus ligament, creating a pogo-stick-like limb that has been modeled in many running vertebrates (Alexander, 1988). The observation that the individuals studied here "choose" to use straighter (more erect) foot posture and more actuator-like behavior of the MCP joint suggests that there are benefits to relying more on muscular action of the digit flexors at high joint torques, such as absorbing force in muscles during decline (Gabaldón, et al., 2004) which would avoid an inappropriately 'over-springy' foot.

Reduced proportional interosseus ligament contribution to increased forces at the MCP joint may also be an artifact of a necessary increase in force produced by digit flexor muscles to maintain an erect PIP joint. Since there is no passive structure akin to an interosseus ligament at the PIP joint, the only way to increase flexing moments resisting GRF is to increase forces produced by either the superficial digit flexor muscle (which attaches to the middle phalanx after crossing the MCP joint and the PIP joint) or a combination of both the superficial and deep digital flexors (the deep flexor additionally crosses the DIP). From kinematic data presented in Chapter 2, the angular positions and excursions experienced by the proximal phalanx do not suggest that the PIP joint collapses in situations when GRF is increased. Rather, the bone maintains similar positions in higher force conditions as it does in lower force ones. In order to maintain similar digit posture in the face of a higher moment induced by the GRF, then digit flexors would necessarily have to produce more force. So, the apparent observed increase in stiffness of the MCP joint and decreased proportion of force provided by interosseus ligaments in high-force conditions may simply be the upstream result of an increased force applied by the digit flexor muscles to maintain erect posture at the IP joints.

## Power curve estimation of ligament torque

The power-fit curves generated from ex vivo preparations are likely conservative estimates of torque produced by the interosseus ligament alone. The power fit was taken for the entire loading-unloading cycle. The majority of data points are concentrated in the unloading portion of the curve, and this would weight the fit toward the lower of two possible values during an ex vivo cycle (either of the loading or unloading). While an effort was made to keep ex vivo cycles roughly the same duration as in vivo ones, the distribution of data points between these two differed substantially. The ligament isolated preparations
unloaded very slowly and experienced significant hysteresis. The "unloading" of in vivo sequences was often very rapid and frequently overlapped with hindfoot landing on the forceplate, making torque measurements for the MCP joint inaccurate. This makes estimations from ex vivo data more conservative.

One explanation for why the interosseus ligaments are less stiff and show so much hysteresis and such slow unloading compared to isolated tendon and ligament preparations described elsewhere might be that they are derived from muscular precursors. Veterinary anatomists have long documented the development of interosseus ("suspensory") ligaments from interosseus muscles (Cunningham, 1885), and the pigs used in this study were rather young. The development of interosseus ligaments has been studied extensively in veterinary literature (see Nickel et al., 1986), and, even when the ligament is fully developed and has lost all of its muscle tissue, the remnants of muscle tissue exist as vacuoles or multi-nucleate cellular spaces with no tensile resistance (Callegari, 1968). These factors combine to produce interosseus ligaments used in this study that could not be expected to be as stiff as pure ligaments or interosseus structures in adult or mature specimens. Aging also has a clear stiffening effect even on pure ligaments and tendons (Kannus, et al., 2000) to which these ligaments would never have undergone. Again, these particular specimens studied may serve as the most conservative estimate of torque production at the MCP joint since there is a developmental progression making the interosseus ligaments stiffer and these ligaments are expected to be the least-stiff possible for a locomoting ungulate.

## Individual variation in in vivo trials

Individual variation in the in vivo trials was higher than expected. Each individual used a separate pattern of both planar MCP joint torque and proportion of planar joint torque taken up by the interosseus ligament. All individuals increased planar joint torque
with increased speed and increased step-down height, but the MCP joint angles used showed some variation in response to increased torque.

First, for level steps, there are two qualitatively different torque-angle scenarios and three qualitatively different responses to increased speed (or, as a rough proxy, increased planar joint torque during walk sequences). Individuals employ either relatively closed loops that have up to twice the torque of the ligament, or they use more open loops that are further away from the ex vivo curve. In vivo torque-angle loops that were more open also had lower peak angles than loops that had loading and unloading sections closer together. When faster speed and/or higher planar joint torque was achieved, torque-angle curves either followed a similar trajectory within an individual to their slower curves while maintaining a similar degree of 'open-ness,' or they became more open. Two individuals (sus03, Fig. 3.3A; sus05, Fig. 3.3C) maintained torque-angle relationships that followed a similar trajectory along a consistent torque-angle path when planar joint torque increased. Due to the curvilinear nature of the ex vivo curve, a higher proportion of the planar joint torque can be taken up by the interosseus ligament at higher speeds and/or higher planar joint torques when high extension angles at the MCP joint are used. This situation creates the possibility that the interosseus ligament serves as an energy saving mechanism during fast locomotion in these individuals, in that a passive ligament takes up a majority of the stance-phase torque of the MCP joint rather than metabolically-active muscles such as the digital flexors.

Cursorial adaptations improving locomotor performance at high speed have been a descriptive hallmark of ungulates for decades (Gregory, 1912; Hildebrand \& Goslow, 2001), and reliance upon the interosseus ligaments to produced force at the MCP joint during high speed or high force activities would be one line of evidence for cursorial adaptation.

However, the other two individuals (sus04, Fig. 3.3B; sus06, Fig. 3.3D) demonstrate an
opposite pattern to the two previously discussed. One of the two (sus06, Fig. 3.3D) increases planar joint torque without appreciably increasing MCP joint angle, while the other (sus04, Fig. 3.3B) increases both torque and angle but always uses very low MCP joint angles that engage very little interosseus ligament strain. Both of these individuals support more recent research (Janis \& Wilhelm, 1993; Reilly et al., 2007) that suggest the morphological features of ungulate limbs have evolved for efficient locomotion at slower speeds. All individuals in the present study show the highest proportion of planar MCP joint torque being provided by the interosseus ligament at the slowest level steps and at the lowest peak planar joint torques.

Next, step-down sequences showed a much simpler pattern. Every individual demonstrated more open torque-angle curves for step-downs compared to walks. Again, there was a varied response to increased torque, or increased height, of the step down. All individuals used higher torques for a given angle during a step compared to walks (comparing within an individual). The peak angles used in step-downs were generally lower than for walks. One individual (sus05, Fig. 3.3C) had a similar (but slightly lower) range of peak angles at downhill steps compared to level walks, and another individual (sus04, Fig. 3.3B) used both higher peak torques and peak angles during step-down sequences than level steps, producing curves much more open than those used in walks. This individual also had the lowest peak angles during walks of all individuals studied. Overall, individuals mostly used more flexed (less extended) angles during step-down sequences, resulting in a foot that was more upright than during walks. These individuals used straighter leg postures and greater ground reaction forces (and greater planar joint torques). This pattern differs slightly from similar measurements in other artiodactyls (goats), where downhill walking produced larger joint excursions at lower forces (Lee et al., 2008). Also, that study showed torque-
angle curves that were significantly more open at deviations from level walking, yet peak torque and peak angles shifted in opposite directions in the goats studied in Lee et al. (2008) from the minipigs studied here.

## CHAPTER 4: STUDIES IN THE EVOLUTION AND MECHANICS OF UNGULIGRADY IN ARTIODACTYLS


#### Abstract

Traditional analyses of the derived limbs in ungulates have postulated that elongated distal segments and hinge-like joints evolved for faster locomotion. This morphology may instead reflect passive maintenance of stance rather than stance maintained through forces generated by metabolically-active muscle. Faster locomotion through these limbs is more costly for these mammals, when compared to mammals using digitigrade or plantigrade foot postures during locomotion, even though many extant ungulates are indeed fast runners. The combination of 1) mechanical specialization for inexpensive standing, such as development of interosseus ligaments, and 2) sequential developmental releases during digit loss permitting distal limb elongation indicate that exaptation played a large role in the evolution of the derived limbs of most extant artiodactyls, if their current morphology is interpreted as an adaptation for fast locomotion. The key mechanical change in unguligrade foot posture involves moving points of compliance in the limb from the wrist to the metacarpophalangeal (MCP) joint. When the MCP joint is elevated during stance, the compliant wrist is stiffened, further making a functionally longer distal limb. The key developmental change initiating the evolution of unguligrady is loss of the pollex. The ecological drivers of distal limb elongation likely involved, or coincided with, the evolution of the large fermenting gut. Data from organismal energetics indicates that mammals maintain a mass-specific cost of locomotion, and the derived limbs of modern ungulates may be the result of increasing the mass of the gut (and its contents) at the expense of the locomotor system.


## Fast running hypotheses of unguligrady

Unguligrady is the most specialized foot posture found in mammals. The mechanical demands of maintaining a fully erect foot with only distal (ungual) phalangeal segments in contact with the ground have resulted in specialized anatomical changes. Some of these changes may be associated with cursoriality (a high degree of mobility), or for fast and efficient locomotion, while others might not be. High-speed running locomotion has traditionally involved a suite of morphological or morphometrical changes in limbs (Steudel \& Beattie, 1993; Carrano, 1999). Of course, high-speed locomotion is a comparative characteristic (i.e., the fastest lion needs only to outrun the slowest antelope, \&c.), and teasing apart the specific morphological features (not to mention physiological ones) that facilitate fast running is complicated when comparing animals across a broad range of morphologies and performances. For example, digitigrade mammals, such as extant canids and felids are almost always considered specialized runners (whether or not speed is actually measured) due to long limbs and distal limb muscles with relatively short muscle fibers and relatively long tendons-features that may or may not necessarily correlate with limb posture, or how the limb is held during stance.

Biomechanical texts contain an old refrain: upright limbs that have long distal limb segments, hinge-like joints, and long distal limb muscle tendons have evolved for fast running. Hinge-like joints supposedly permit fast limb recycling during swing phases of locomotion (Howell, 1944), and upright posture moves muscle moment arms closer to joint centers-of rotation so that a given muscle shortening results in faster motion at the joints (Maynard-Smith \& Savage, 1956). The long tendons belonging to the distal limb muscles in these limbs further facilitate efficient locomotion by storing elastic energy at the beginning of stance to help power toe-off (Alexander et al., 1982). The mechanical experiments carried
out in previous chapters have sought to describe the mechanical behavior of the structures immediately responsible for maintaining unguligrade stance in the foot, namely the motion at purportedly hinge-like joints and potential elastic energy storage at the MCP joint by interosseus ligaments.

The fact that all living unguligrade species incorporate a suite of morphological changes compared to their digitigrade ancestors makes it difficult to tease apart the specific structures that give specific performance advantages. Features specific to unguligrady are hinge-like digit joints combined with a ligamentous interosseus system. Other changes, such as hooves; elongated zeugopodia (radii+ulnae/tibiae+fibulae), and autopodia (esp. metacarpals) (Howell, 1944); reduction of proximal muscle fiber length and increase in tendon length (Alexander et al., 1982); and highly erect leg posture which reduces muscle moment arms and maximizes speed (Maynard-Smith \& Savage, 1955) occur in both digitigrade and unguligrade mammals. As has been shown in Chapter 1, the derived unguligrade limbs of extant artiodactyls have evolved from ancestral limbs that are already fairly specialized in terms of long distal limb segments and hooves, and at least a modicum of fast running locomotion has been inferred in some of these basal groups based on this morphology (Gregory, 1912; Rose, 1982). Tylopods (camels and the like), basal ruminants, and ancestors of modern horses (hyracotheres) had already evolved hooves, relatively elongated distal limb segments, and supposed fast running posture-erect, straight-legged, and upright (at least digitigrade).

Extant species of pigs (suids) and peccaries (tayassuids) are not generally regarded as fast runners, yet their foot posture is, in fundamental ways, as derived and specialized as in more fleet-footed groups, such as antelopes and deer. Suoids (pigs and peccaries) have evolved an unguligrade foot posture accompanying a moderate amount of distal limb
lengthening. The fundamental morphological indicators of unguligrade foot posture are present in pigs, yet they retain fully-developed (although reduced) $\mathrm{I}^{\text {nd }}$ and $\mathrm{V}^{\text {th }}$ digits. Many wild pig species, such as warthogs, are fast-running only for short periods of time (Schaller, 1972) and do not have the large home ranges requiring constant movement that other more derived artiodactyls have (Cumming, 1975). So, compared to antelopes or deer, for example, pigs do not have the same reputation as fast runners. Again, because fast locomotion is a relative measure, suoids are fleet of foot if they are compared to, for example, giant anteaters, but they are not very fast if they are compared to, for example, pronghorns. This makes suoids an ideal group for studying the performance differences between digitigrady and unguligrady, since the unguligrade foot posture in suoids appears to be uncoupled from specializations for fast running. Pigs have the anatomical changes necessary to maintain an unguligrade foot posture without the extremely elongated distal segments found in nearly every other living unguligrade mammal.

In the experiments carried out in this project, it appears that unguligrade feet take advantage of passive force mechanisms in the foot during slow locomotion or standing (Fig. 4.1). These data do not describe a system involving more efficient or spring-like locomotion at high speed and high force conditions. When speeds or forces applied to the feet are increased, the increased ground reaction force experienced by the joint is countered by force from muscles, rather than by the passive interosseus ligament system. Similarly, during the two recorded trials of stationary standing (Fig. 4.1, green traces), the proportion of MCP joint torque taken up by the interosseus ligament is similar to that in the slowest walks. These ligaments do not appear to be used primarily as sources of elastic energy storage, since the shape of the torque $v$ s. angle loops are fairly open (indicating energy loss). Rather, the joint appears to become stiffer at higher speeds based on these data. MCP joint angles
decrease or remain the same when speed and/or force increase, while the proportion of joint torque provided by the interosseus ligaments decreases, significantly in some cases.


Figure 4.1. Torque vs. angle graphs for four individuals. Each graph shows the torque vs. angle loops used in the fastest (blue) and slowest (red) level walking trials. Graph labels indicate the speed which produced that loop and the \%torque provided by the interosseus ligament (upper range taken at peak angle, lower range taken at peak torque). Ex vivo fit curves (see Ch. 3) for each individual shown in black. A - sus03; B - sus04; C - sus05; D - sus06.

The studies carried out here suggest that unguligrady (in pigs) is not ideal for efficient locomotion at high speeds since there is a reduction in the reliance upon cheap and springy elements, such as ligaments, in the foot at high speeds and forces. The smaller joint extension angles seen at higher speeds and forces cannot be carried out by passive ligaments (which cannot actively contract) and must be carried out by digit flexor muscles. These muscles preferentially take up the braking role of the foot while the ligament is best-
employed to provide force in low-force stance situations. Unguligrade foot posture involving forefoot ligaments has evolved in a (generally) low-performance group of animals similar in anatomy to the earliest unguligrade artiodactyls (see Ch. 1), so the mechanics of the metacarpophalangeal joint (see Chs. $2 \& 3$ ) at least suggest that the initial benefit of unguligrade foot posture is inexpensive standing and stance at slow speeds.

Other workers have suggested the same phenomenon: unguligrady may not be an adaptation for fast running and is more (or at least equally) energetically advantageous at slower speeds. Garland \& Janis (1993) demonstrated that elongated distal segments did not correlate with faster running speed among cursorial carnivorans and ungulates, especially since ungulates had extremely high ratios of distal limb segments to proximal limb segments but were not the fastest species. Janis and Wilhelm (1993) showed that relatively long distal segments in hindlimbs correlated with large home-range size, indicating, or at least suggesting, a reliance on consistent but slow locomotion rather than sprint speed.

One of the most conspicuous results of unguligrade foot posture is a longer step length, both because distal elements such as metapodials and phalanges are elongated, relative to digitigrade groups, and because erect digit posture (as opposed to limb posture) facilitates longer steps. Heglund \& Taylor (1988) found that stride frequency is inversely proportional to body mass and that each stride incurred similar mass-specific metabolic costs. That is, larger animals take fewer steps that are each equally-relatively costly than the more frequent steps of smaller animals. Indeed, unguligrade foot posture may be a mechanism to increase step length over digitigrade foot posture and reduce stride frequency in ungulates in order to minimize locomotor costs over a series of steps. That said, increasing step length would increase speed if stride frequency is kept constant, and longer step lengths are found in both slow and fast gaits in unguligrade groups (Steudel \& Beattie,
1993). In two otherwise identical animals, one digitigrade and one unguligrade, the unguligrade one would have an energetic advantage over the digitigrade one simply because longer steps reduce the per-distance cost of locomotion (that is, unless it is more costly to maintain unguligrade stance over digitigrade stance). So, even if we disregard the potential impact(s) on overall locomotor energetics, the increased step length in unguligrade limbs appears to be the strongest evidence that unguligrady has evolved for faster locomotion, even if that argument is not particularly compelling.

More recently, Reilly et al. (2007) determined that the erect limb (and foot) posture in horses incurs higher relative metabolic costs at high speeds than in other mammals. They found that horses (the only unguligrade species in their sample) were the only animals for which running gaits were not more economical than walking gaits (Fig 4.2). The shift from


Figure 4.2. Cost of walking gaits (W), trotting gaits (T), and gallops (G) (black bars, left axis) showing increased relative cost of running gaits in horses. Top bars \& right axis shows increased use of pendular mechanics in horses. Taken from Reilly et al. (2007).
pendular mechanics to spring-like mechanics occurs in the walk-to-trot transition, and the data in Reilly et al. (2007) suggest horses maintain a metabolic advantage over other mammals when using relatively stiff-legged pendular mechanics at slow gaits but suffer metabolic disadvantages compared to other mammals when using spring-like mechanics at fast gaits. They also found that horses do not decrease metabolic costs of locomotion with increasing body size, counter to the trend for mammals in general, using data from Griffin et
al. (2004) and Minetti et al. (1999). This comparison is skewed, since Reilly et al. (2007) make a comparison between horses of different body sizes with mammals of different body sizes, but there may be a general trend from the comparison. First, Biewener (1989) detailed how mammals of increasing body size use increasingly more upright or erect limb posture to maintaining tolerable metabolic costs of locomotion. Next, the mass-specific force muscles produce scales negatively with body size, if muscle architecture is kept constant (force correlates with cross-sectional area, which increases with the square of increased linear dimension, whereas mass increases with the cube of linear dimension). Finally, erect posture compensates for muscles that produce relatively smaller forces at larger body sizes by moving muscle moment arms closer to joints, increasing the effective mechanical advantage of muscles (an effect purportedly for increasing limb speed in Maynard-Smith \& Savage, 1956). However, if a limb is already erect and foot posture is unguligrade, then there is no more erect or straight-legged posture to adopt to increase the effective mechanical advantage of muscles in the foot. Reilly et al. (2007) argue that since the cost of fast locomotion (as trotting gaits and galloping gaits) increases as body size increases in horses while the opposite is true for walking gaits, the energetic benefits of unguligrade posture are realized only at slow speeds. The energy savings that unguligrady provides during standing and walking appear to be countered by an increase in the costs associated with fast locomotiona notion certainly counter to earlier ideas focused on unguligrady as a facilitator of fast locomotion.

## Didactyl cetartiodactyl taxa and the role of exaptation

Terrestrial artiodactyls with a didactyl manus are all derived from tetradactyl taxa which, in turn, are derived from pentadactyl taxa. The key osteological changes in didactyl
feet of derived artiodactyls are the loss of digits II and V and the reduction of the basal volar process of the metacarpal. This process serves as the proximal attachment site of the interosseus muscles/ligaments and lies on the proximal-most region of the metacarpals immediately distal to the carpometacarpal articulation. The anatomy of extant derived artiodactyls is well-understood: veterinary literature adequately describes manus anatomy for bovids (and by inference, all pecorans), and Lesbre (1903) describes the manus anatomy in camels, a member of the other didactyl clade of extant artiodactyls. Extant camelids have their own unique specializations of the manus, namely their secondarily digitigrade stance and splayed $\mathrm{III}^{\text {rd }}$ and $\mathrm{IV}^{\mathrm{th}}$ digits (Webb, 1972). That said, there are extinct camelids with manus anatomy almost identical to extant pecorans (except for the complete distal metapodial keel), such as Poëbrotherium ${ }^{\dagger}$ and possibly Stenomylus ${ }^{\dagger}$. Later camelids, including all extant taxa, have very characteristic features of the digits and metapodials that indicate secondary digitigrady (Janis, et al., 2002). Since lateral digits are so reduced in camelids and in pecorans, the accompanying interosseus ligaments and adductor muscles that attached to them have been lost. This likely accounts for the reduction in the size of the metacarpal volar process.

Although some didactyl artiodactyls, such as medium-sized antelopes, deer, and pronghorn, are generally considered more fleet of foot than almost any other terrestrial mammals, the key features presumed to contribute to their fast locomotion first appear in other taxa that are either slower, have unknown locomotor performance, or are not considered fast at all. Loss of the pollex, distal limb element elongation, and specialization of musculotendinous structures available for elastic energy storage all appear first in tetradactyl taxa, even in those that are digitigrade. Digitigrade ('subunguligrade') taxa among those, such as derived oreodonts and all protoceratids, are not reconstructed as particularly
fast (although protoceratids sometimes are, largely because they are reconstructed incorrectly). Even unguligrade tetradactyl taxa, such as extant pigs, peccaries, and tragulids, are commonly left out of discussions of fast-running mammals, despite their obvious limb specializations. As discussed above, it may be the case that tetradactyl taxa represent a significant improvement in running performance from their pentadactyl ancestors; certainly similar changes have taken place in extant canids, where perhaps the fastest and widestranging species, the hunting $\operatorname{dog}$ (Lycaon), also is tetradactyl, while other canids retain a reduced pollux or 'dew claw' (Kingdon, 1977). There appears to have been an underlying assumption in older explanations of the evolution of highly derived, didactyl limbs that any improvement gained by tetradactyl taxa was taken to an extreme by the didactyl taxa (see Gregory, 1912; Howell, 1944). The argument goes: if the evolution of digit loss, hinge-like joints and elongated distal limb elements first evolve in fast running artiodactyls and are kept in the very fast running extant ones, then they must initially be adapted for fast and/or efficient locomotion (i.e., "cursoriality"). However, the most important features, from a functional standpoint, that take place in the manus first appear in taxa that are not very cursorial and are taken to an extreme in taxa that are. So the initial adaptive function of digit loss and elongation and hinge-like joints may not have been locomotor speed. The exaptation of these anatomical changes is the central feature of the evolution of limbs in a highly derived group of artiodactyls.

Exaptation likely played an important role in the morphology of unguligrade limbs. Because unguligrade limbs are so uniquely modified for locomotion, the performance advantages of specific morphological changes can likely be determined. Any confounding effects from limbs that perform many functions, such as grasping, climbing, \&c., are at least reduced in ungulates, since ungulates in general do not carry out those accessory limb
functions. If ungulate limbs are adapted for fast running, or if the morphology of unguligrady in all taxa facilitates an improvement in running performance and energetics, then we could predict that force production at the metacarpophalangeal joint is predominantly produced by interosseus ligaments and that these ligaments provide increasing amounts of force as speed increases. If interosseus ligaments produce most of the force at the metacarpophalangeal joint during stance, then there is an energetic benefit of unguligrady since metabolically-active muscle is not needed to maintain stance. This energetic benefit is carried over at faster speed if the interosseus ligament produces most of the force at the metacarpophalangeal joint even at higher speed. The growing evidence that unguligrade foot posture may be a response to selective pressures favoring energetically cheap stance and slow locomotion (Janis \& Wilhelm, 1993; Reilly et al., 2007; see Chs. 1 \& 3) suggests that morphological features associated with fast locomotion in unguligrade species may be exaptive. The morphological changes necessary to maintain unguligrade foot posture first appear in taxa with foot morphologies similar to pigs (i.e., with relatively short legs), suggesting that unguligrady is adaptive for efficient locomotion at slow speeds, since this may be the case in pigs. Structures like interosseus ligaments likely evolved for (i.e., are adapted for) efficient slow locomotion and stance requiring little muscular input. Features, such as hinge-like joints and long distal limb segments, that have been presumed to facilitate fast running are instead exapted for fast running after evolving first for inexpensive slow locomotion. The fact that hinge-like joints permit fast, uniaxial motion of the limb itself in fast-running mammals indicates only their current use and appeals to our own sense of engineering and design rather than their evolutionary significance. Hinge-like joints also likely reduce the muscle input required for lateral stability of joints, and they may not be
related to running speed at all, since they are found in cursorial and non-cursorial ungulates alike.

## Unguligrady and points of compliance in the foot

One of the central biomechanical features of limbs during stance is the compression of limbs induced by ground reaction force moments (Geyer et al., 2006). This compression, acting across compliant joints, can be stored as elastic strain energy in muscles, tendons, and (perhaps) in ligaments to be recovered during toe-off (Farley et al., 1993). Different foot postures (by definition) maintain different erect foot segments during stance, changing the potential number of points of compliance in the limb. Rotation in multiple compliant joints during stance results in limb compression. Plantigrade species, like gibbons for example, can utilize a foot with multiple compliant joints to decouple strain in ankle flexor muscles from strain in digital flexor muscles, two multi-jointed muscle groups that both have effects in the foot (Vereecke \& Aerts, 2008). Digitigrade species, such as dogs, plant the metacarpophalangeal joint along the ground, rotating the limb over that joint during stance. Immediately proximal to the planted metacarpophalangeal joint, dogs maintain a compliant wrist (carpus) that extends during stance (inferred from photos in Muybridge, 1957; Fig. 4.3) in response to the ground reaction force moment. In unguligrade species, the wrist is stabilized against extension through extensive ligaments on the volar carpal surfaces such that motions at the joint are minimized during stance (inferred from Muybridge, 1957; Lee et al., 2008) while still accommodating flexion during swing. The wrist is effectively noncompliant during stance. The distal interphalangeal joint becomes the planted joint over which a limb rotates in unguligrade posture, while the metacarpophalangeal joint is held off the ground during stance. Rather than rotating the body over a planted


Figure 4.3. Mid-stance poses of digitigrade and unguligrade mammals. Digitigrade mammals in top row, from left to right: dog, dog, lion. Unguligrade artiodactyls in bottom row, from left to right: eland, goat, guanaco, pig. Red arrows indicate position of the wrist. Note how the wrist is extended past vertical in digitigrade mammals while it is held straight in unguligrade mammals. From Muybridge (1957).
metacarpophalangeal joint the way digitigrade mammals do, unguligrade mammals rely on an elevated metacarpophalangeal joint whose flexion/extension during stance (compliance) contributes to limb compression. This change in the points of limb rotation and compliance has potentially important consequences for the energetics and mechanics of locomotion.

The strain transferred to the digital flexor muscles and interosseus ligaments in unguligrade species derives solely from digit extension at the metacarpophalangeal and interphalangeal joints during stance now that the wrist is locked. In digitigrade limbs during stance, the muscle-tendon units of the digital flexors strain both when the limb rotates over a planted metacarpophalangeal joint and when the compliant wrist extends. This contrasts with the straight-wrist posture in unguligrade limbs. The tightly interlocking connections of carpal bones and the extremely dense transverse carpal ligaments in unguligrade limbs make the metacarpal segment of the manus act like a functional elongation of the forearm, making the metacarpophalangeal joint the next point of limb compliance distal to the elbow and analogous in locomotor function to the wrist in digitigrade species. The observed increased stiffness of distal leg segments of unguligrade mammals, such as in horses (McGuigan \&

Wilson, 2003), may be simply a result of restricting points of compliance distal to the elbow to the unguligrade digit.

A close examination of the foot posture of digitigrade animals (as shown photographically in Muybridge, 1957), demonstrates that even digitigrade mammals are unguligrade for at least the very end of stance prior to toe-off. Although foot posture categories are defined by static posture, there are points in a stride when statically-plantigrade and -digitigrade animals are unguligrade at instants in locomotion. A more dynamic definition of foot posture would imply that unguligrady shifts the foot posture seen at the end of stance in digitigrade forms, where stance is maintained on the most distal toe elements, to a position earlier in stance to take advantage of mechanical benefits of an erect limb, such as reduced moment arms. A more erect limb has smaller muscle moment arms and is cheaper to maintain in stance in terms of required muscle mass (Biewener, 1989). Reduction of muscle fibers combined with elongation of the attached tendons makes digital flexor muscles stiffer and less energetically costly (Alexander, et al., 1982; McGuigan \& Wilson, 2003), and interosseus ligaments further reduce costs of stance by providing force from non-metabolic sources. Thus, the anatomical changes necessary to maintain erect limb and foot posture might involve reducing costs of stance by decreasing total limb compliance by reducing joint degrees of freedom during stance.

The kinematic analysis in Chapter 2 describes hinge-like motion at joints of the digit, although those hinge-like motions are not exactly parasagittal. As stated earlier, one of the morphological indicators of unguligrade foot posture is hinge-like joints in the digit. Another is reduction of intrinsic muscles of the foot. The ginglymal joints in unguligrade feet may reduce compliance of joints through passive mechanisms by restricting motion to a single axis. Even though the bones of the foot do not move in a parasagittal plane, the
motions at the metacarpophalangeal joint and the combined interphalangeal joints move about a single axis, even if that axis itself moves during stance. Rather than stiffening joints in the direction of travel, such as occurs in the unguligrade wrist, stiffening joints against multiple axes of rotation (i.e., reducing degrees of freedom) reduces total joint compliance. Almost any joint could potentially show hinge-like motion at a joint (i.e., rotation about a single axis), but unless there is some bony or ligamentous mechanism preventing other rotations, then the stabilization at the joint is provided by muscles and incurs a metabolic cost. The evolution of joints that move passively predominantly in flexion/extension might reduce costs of stance by reducing stabilizing forces provided by muscles. This is accomplished in unguligrade taxa both by changes in bony morphology of the joint surface and in the transformation of the interosseus muscles into stiffened ligaments.

## Future studies of the evolution of unguligrady

## Loss of the pollex

In pentadactyl artiodactyls, the pollex is always reduced. Even in the most primitive artiodactyls, the pollex is reduced to a digit that is clearly taken out of a locomotor role in the manus (as in canids). In extant canids, the reduced pollex or "dew claw" has a full suite of intrinsic muscles (mm. abductor pollicis brevis, flexor pollicis brevis, and adductor pollicis) (Evans, 1993), even though these muscles do not perform any straightforward function in a digit so small and seemingly functionless. Of course, even though the pollex is reduced, the remaining intrinsic musculature of the manus (i.e., mm . abductor digiti quinti, flexor digiti quinti brevis, adductor digiti quinti, interossei) suggests that there are other functions that the foot may carry out other than locomotion (grasping, digging, etc.). The intrinsic musculature of the manus is symmetrical with the presence of a pollex, in that both digits I
and V possess the same suite of intrinsic muscles while the remaining digits retain interosseus muscles. There may be developmental constraints that maintain a pollex, even in a reduced state and regardless of the functions that intrinsic muscles of the foot carry out. That is, maintenance of the pollex may necessarily mean that all the intrinsic muscles of the foot develop, and loss of the pollex may necessarily mean that other intrinsic muscles of the foot are lost. Further, the pollex may have to be lost before interosseus muscles can be stiffened into ligaments.

All unguligrade mammals are derived from ancestors that lose the pollex, and the pollex is always the first digit lost when toe reduction happens. The loss of the pollex may represent a developmental release upon constructional constraints that affect digit number and intrinsic soft-tissues of the manus. All amniotes are constrained to develop five digits, and taxa with fewer than five digits undergo additional regressive development in the manus once the anlage of all five digits have undergone considerable development (Galis, et al., 2001). This regression also may be true for intrinsic musculature of the manus; the musculature that accompanies each digit may be constrained to undergo a proscribed development that may be modified only after a certain point. Also, there may be developmental mechanisms that ensure specific intrinsic musculature accompanies specific digits, i.e. the formation of a pollex is necessarily accompanied by the development of its intrinsic musculature. It may be developmentally impossible to separate the development of the skeleton of the pollex from the musculature accompanying it. Testing whether the retention of a pollex mandates the presence of a full suite of intrinsic musculature of the manus which cannot be modified into ligaments would determine the significance of a pollex, even in a reduced state.

Unguligrade artiodactyls have lost most of the non-locomotor functions of the feet, since there is little or no intrinsic musculature to carry out fine motor activities. The evolution of hooves may have facilitated this loss-of-function in the manus and pes of nonunguligrade artiodactyls. Extant non-unguligrade ungulates, such as tapirs and rhinos, certainly do not have multifunctional use of either the manus or pes, but their large body sizes confounds a useful comparison with the kinds of comparable taxa in artiodactyls, such as derived oreodonts and protoceratids. The only non-unguligrade extant artiodactyls, the hippos, maintain interosseus muscles (Fisher et al., 2007), despite having graviportal limbs that carry out few, if any, non-locomotor functions. Loss of the pollex may occur simultaneously with loss of non-locomotor functions, such as grasping and climbing. The loss of the pollex may also indicate a developmental release on constraints that dictate digit number and intrinsic muscle rearrangement and/or loss-loss of other digits in the foot may be impossible without loss of the pollex.

There is considerable development involved in making interosseus ligaments from interosseus muscles, which continues ex utero (Callegari, 1968; Nickel et al., 1986). The loss of the pollex may be a pre-requisite for the 'involution' (Callegari, 1968) of the interosseus tissues of the foot; the presence of the pollex may create such a multi-jointed and mobile structure that ligamentous replacement of muscular tissue becomes untenable. Once the capacity to developmentally eliminate the pollex evolved, that same developmental machinery may have released constraints placed on other digits of the manus and their associated soft-tissue structures, leading eventually to an elongated, nonmuscular, didactyl manus. These hypotheses could be tested either by monitoring foot development in a growth series or by experimental modification of developing digits to understand the effect of pollex loss on ultimate foot morphology.

The evolutionary sequence that led to the derived limbs in artiodactyls began with the loss of the pollex and increasingly straight limbs possessing joints that are more ginglymal (hinge-like) in parasagittal motion. There are developmental scenarios (see above) that might suggest that the loss of the pollex is a lynchpin for later developmental changes in the musculoskeletal makeup of the manus. Further evidence for the importance of pollex loss can be found in other mammalian ungulates that have undergone a convergent reduction of digits accompanying the evolution of unguligrade foot posture. In perhaps the most famous and best-studied example, modern monodactyl horses are the descendants of an evolutionary chain of events roughly similar to the ones in their even-toed cousins: pentadactyl 'condylarths' gave rise to tetradactyl hyracotheriine equids, which gave rise to tridactyl anchitheriine equids, which gave rise to the anatomically modern monodactyl, unguligrade equine equids (MacFadden, 1992). Interestingly, artiodactyls first evolved unguligrade foot posture within tetradactyl groups that later gave rise to extremely derived didactyl groups (see Ch. 1); unguligrady evolved within tridactyl equids that eventually gave rise to extremely derived descendants (Thomason, 1986). The reduction in the number of digits in equids also accompanied relatively longer foot elements in taxa with fewer digits. Finally, the derived monodactyl feet of extant horses possess an ligamentous configuration derived from interosseus muscles that is analogous to the system in artiodactyls (Camp \& Smith, 1942), suggesting further the developmental and evolutionary importance of pollex loss in the evolution of unguligrade foot posture. Additionally, determining the extent of developmental convergence between unguligrade artiodactyls and perissodactyls might underscore the interplay between digit loss and unguligrady.

## Proportional body mass in cursorial herbivores

The mass-specific cost of transport decreases logarithmically with body size in mammals (Taylor et al., 1982, Fig. 4.4). Included in their analysis are carnivorans and artiodactyls of similar body sizes. These two orders of mammals are expected to differ


Figure 4.4. Mass-specific metabolic cost of locomotion in similarly-sized carnivorans and artiodactyls. Taken from Taylor et al. (1982). Values in parentheses are normalized for speed and size ( $\mathrm{mL} \mathrm{O}_{2}$ per meter per kilogram).
substantially in the proportion of body mass dedicated to different organ systems (e.g., digestive and locomotor), yet they follow a broadly similar pattern with respect to locomotor costs at a given body size. Herbivorous mammals, especially ruminants, have a much more specialized and enlarged digestive tract compared to the relatively simple tract of carnivorous mammals. The body mass devoted to gut mass (and gut contents) should be much higher in herbivores than in carnivores, due to the enlargement of the organs themselves, the greater
volume of food consumed, and the longer gut transit times that herbivores have. An increase in the proportion of body mass devoted to the gut translates into a decrease in the proportion of other organ systems, if body size is kept constant. That is, a 40 kg antelope has relatively more gut than a 40 kg dog, while they both have similar mass-specific locomotor costs, according to the dataset of Taylor et al. (1982), an idea first proposed by C. Janis (pers. comm.). Conversely, the 40 kg antelope has a smaller mass devoted to the locomotor system (presumably in the form of reduced muscle mass) than the 40 kg dog.

The ruminant digestive system seen in extant artiodactyls most likely first evolved as a response to the increased seasonality of the late-middle Eocene, when a foraging strategy of selecting more sparse deciduous vegetation of higher quality was more suited to the foregut fermentation of artiodactyls than to the hindgut fermentation of perissodactyls (Janis, 2007). Selenodont dentition (indicating a strictly herbivorous diet) and, interestingly, more derived foot morphologies (e.g., digitigrade feet lacking a pollex and later groups clearly having unguligrade foot posture), appeared during this same period in both tylopods (Honey et al., 1998) and in ruminants (Métais \& Vislobokova, 2007). Suoids, meanwhile, maintained bunodont dentitions, and likely omnivorous diets (Harris \& Liu, 2007), and do not have the immense fermentation chambers of ruminants despite foot specializations resulting in unguligrady. For herbivorous artiodactyls, the later part of the Eocene heralded the appearance of a new morphotype of artiodactyl (from brachydont and pentadactyl groups such as anthracotheres and primitive oreodonts to more derived descendants that lose the pollex) and in the composition of large terrestrial herbivore communities (from predominantly perissodactyls to predominantly artiodactyls) (Janis, 2007). That pigs lie in between these two conditions makes them ideal for studying the performance advantages of unguligrady alone, as detailed in previous sections and Chapters.

The rise of selenodont artiodactyls may have also signaled the onset of selective pressures favoring foot posture that was cheaper to maintain during stance and slow locomotion-the upright foot posture in unguligrady. Again, these same changes were paralleled in the evolution of modern horses-specialized teeth for folivory and tridactyl feet appeared concomitantly in the earliest anchitheriines, such as Mesohippus. Testing whether large guts, unguligrade feet, folivorous diets, and large home ranges co-incide in independent lineages of artiodactyls, perissodactyls, and notoungulates (extinct South American ungulates) would suggest there may be integrated, organismal selection requiring unguligrady with the ecology of ungulates, represented today by modern ruminants, camels, and horses.

As ruminants increase in size, there is a slight positive allometric increase in gut size (Clauss et al., 2007), suggesting that larger ruminants would have proportionally less body mass devoted to the locomotor apparatus. The reduction in muscle mass in distal leg segments devoted to locomotion in ungulates (Alexander et al., 1982) might be a two-fold response to: 1) having proportionally less to work with, since increasingly large amounts of body mass are being devoted to the gut and 2) making a more efficient standing leg used to move slowly during foraging. Although the selective pressures leading to unguligrady and the performance measures improved by it remain enigmatic, there are clearly suites of ecomorphological traits accompanying unguligrady. The coincident appearance of wide-ranging folivores and unguligrade taxa in different artiodactyl lineages (in addition to at least one perissodactyl lineage and perhaps at least one notoungulate lineage) suggests that a folivorous and slow-moving ecology may be involved in the adoption of erect foot posture. The "large-gutted," folivorous, wide-ranging herbivores first appearing in the late-middle Eocene may have found themselves in a situation like the Red Queen: they had to evolve more and more derived limb morphologies simply to stay in the same place, energetically-
speaking (on the mass-specific cost of locomotion curve, Fig. 4.4). Limbs adapted for standing for long periods of time with little muscle input could not lose the ability to run fast, but their locomotor system had to become more and more specialized to accommodate an increasingly large fermentation system.

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