

Theropod Locomotion¹

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SYNOPSIS. Theropod (carnivorous) dinosaurs spanned a range from chicken-sized to elephant-sized animals. The primary mode of locomotion in these dinosaurs was fairly conservative: Theropods were erect, digitigrade, striding bipeds. Even so, during theropod evolution there were changes in the hip, tail, and hindlimb that undoubtedly affected the way these dinosaurs walked and ran, a trend that reached its extreme in the evolution of birds. Some derived non-avian theropods developed hindlimb proportions that suggest a greater degree of cursoriality than in more primitive groups. Despite this, fossilized trackways provide no evidence for changes in stride lengths of early as opposed to later non-avian theropods. However, these dinosaurs did take relatively longer strides—at least compared with footprint length—than bipedal ornithischian dinosaurs or ground birds. Judging from trackway evidence, non-avian theropods usually walked, and seldom used faster gaits. The largest theropods were probably not as fleet as their smaller relatives.

INTRODUCTION

Zoologists can relatively easily observe the motions of many extant animals in the field or the laboratory. For extinct species, particularly those with a body form not exactly like those of any living species, it is a different story. An extinct animal's locomotion cannot be observed directly; rather, the paleontologist must reconstruct how the creature may have moved from its morphology and other indirect sources of information.

In this paper, we summarize what has been inferred about the locomotion of carnivorous dinosaurs (*i.e.*, theropods; Fig. 1), based on the study of both body and trace fossils. Understanding how theropods moved is obviously necessary if we are to understand them as living animals. Given the likelihood that birds represent an extant subgroup of theropods, however, it is equally important that we understand how non-avian theropods walked and ran in order to

know which features of avian locomotion originated with (and within) birds, and which they inherited from their non-avian ancestors.

Our study will therefore consider theropod locomotion in a phylogenetic context. We will compare and contrast features of locomotion among different theropod groups, including ground-living birds. Although it is reasonable to suppose that theropods could have swum well enough when the situation warranted (Coombs [1980] described possible trackway evidence for this), and it is conceivable that some small-bodied theropods could have scampered about in trees—at least on occasion—without the need for obvious scansorial adaptations, we will restrict ourselves to considering what was undoubtedly the most important kind of locomotion for most non-avian theropods, namely walking and running on the ground.

THEROPOD PHYLOGENY

Modern studies of theropod phylogeny began with the question of the origin of birds, following Ostrom's observations (*e.g.*, 1975, 1976) of numerous features uniquely shared by primitive birds and

¹ From the Symposium *Evolutionary Origin of Feathers* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 6–10 January 1999, at Denver, Colorado.

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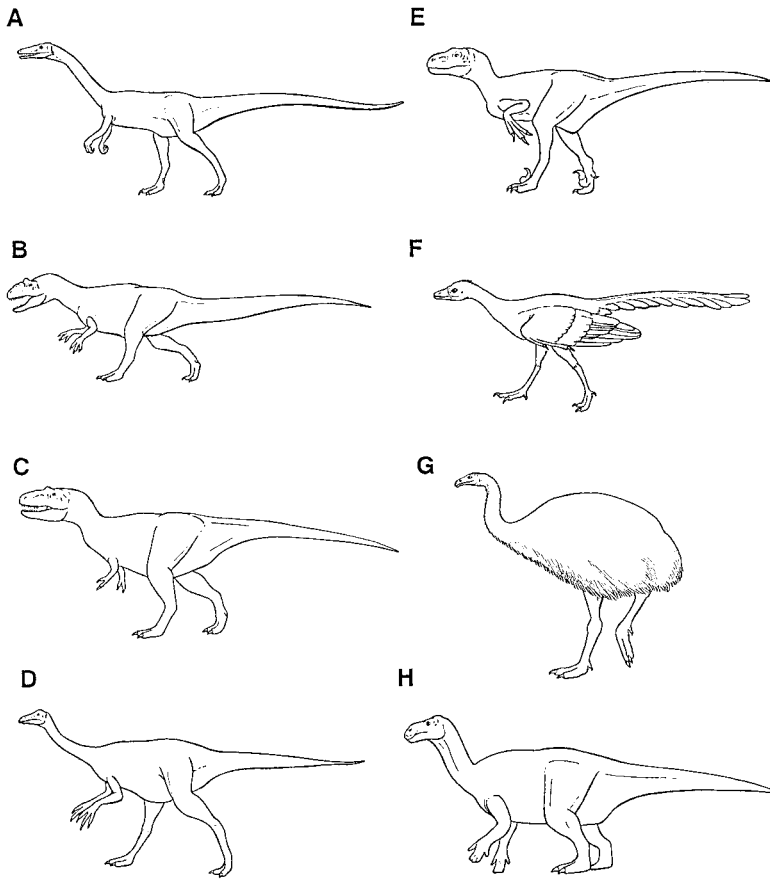


FIG. 1. Life restorations of representatives of the dinosaur groups discussed in this paper. Not to scale. A) *Coelophysis* (coelophysoid ceratosaur). Length ca. 3 m. B) *Allosaurus* (carnosaur). Length ca. 8 m. C) *Gorgosaurus* (tyrannosaurid). Length ca. 8 m. D) *Struthiomimus* (ornithomimid). Length ca. 3.5 m. E) *Deinonychus* (dromaeosaurid). Length ca. 3 m. F) *Archaeopteryx* (basal bird). Length ca. 0.5 m. G) *Dinornis* (Dinornithiformes; moa). Height ca. 2.5 m. H) *Iguanodon* (large facultatively bipedal ornithischian). Length ca. 9 m. Drawings by James Whitcraft.

various theropod dinosaurs. Most of the cladistic studies of the 1980s (Thulborn, 1984a; Paul, 1984; Gauthier, 1986) focused on the distribution of avian features among various groups of carnivorous dinosaurs. Subsequent workers conducted numerical cladistic analyses to examine the distribution of derived character states in the various subgroups of non-avian theropods (Rowe and Gauthier, 1990; Russell and Dong, 1993; Pérez-Moreno *et al.*, 1993; Holtz, 1994, 1996, 2000; Sereno *et al.*, 1994, 1996, 1998; Novas, 1996; Chargin and Milner, 1997; Sereno, 1997, 1999; Sues, 1997; Harris, 1998a; Makovicky and Sues, 1998; Padian *et al.*, 1999). Al-

though these analyses have not produced identical trees, due to differences in taxon and character choice and coding, most result in very similar patterns. The phylogenetic tree presented here (Fig. 2) represents a broad consensus of the two most comprehensive studies (Sereno, 1997; Holtz, 2000).

There is disagreement over whether *Eoraptor* and the Herrerasauridae are true theropods (Novas, 1993, 1996; Sereno and Novas, 1992, 1993; Bonaparte and Pumares, 1995; Sereno, 1997). However, all of these studies agree that *Eoraptor* and the herrerasaurids more closely resemble the ancestral dinosaurian condition, in terms of their

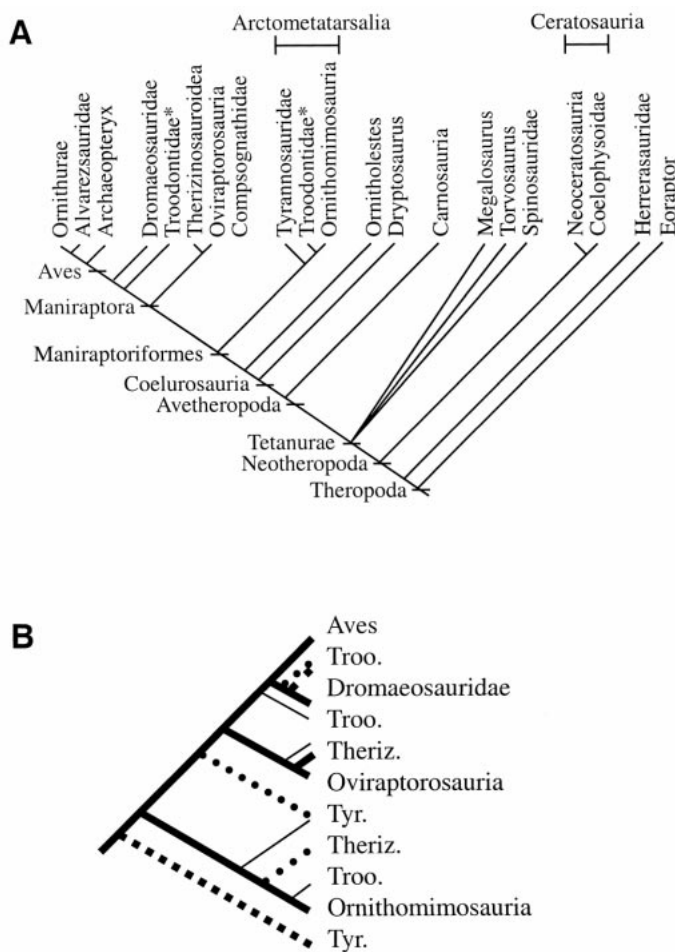


FIG. 2. A) Phylogenetic tree of Theropoda; see Holtz (2000) for details. *Asterisk indicates two equally parsimonious positions for Troodontidae. B) Conflict and congruence in current coelurosaur cladograms. Heavy solid lines represent the primary phylogenetic conclusions of Gauthier (1986), which were supported in the other studies in question. These studies differ, however, in their placement of Therizinosaurioidea (Theriz.), Troodontidae (Troo.), and Tyrannosauridae (Tyr.). The thin solid lines represent results from Holtz (1994, 2000); the dotted lines from Sereno (1997); the dashed lines from Makovicky and Sues (1998).

locomotor apparatus, than do the more advanced theropods.

Derived theropods constitute two major clades, Ceratosauria and Tetanurae (Gauthier, 1986; Sereno, 1997; Holtz, 2000). The two clades together comprise Neotheropoda.

Ceratosauria is divided into two groups: the more gracile, long-necked coelophysoids (e.g., the Late Triassic *Coelophysis* and the Early Jurassic *Syntarsus*) and the more robust neoceratosaurs of the Late Jurassic (*Ceratosaurus*) and Cretaceous (abel-

isaurids). Although neoceratosaurs share with tetanurines some features not found in coelophysoids, the current weight of evidence supports uniting neoceratosaurs and coelophysoids in a monophyletic group (Holtz, 2000).

Most of the tetanurine groups belong to the clade Avetheropoda (or Neotetanurae; Sereno *et al.*, 1994), but several taxa possess tetanurine features yet lack the derived traits of avetheropods. Most of these are "megaloosaurs" (e.g., *Torvosaurus*, *Eus-treptospondylus*, *Piatnitzkysaurus*, and *Me-*

galosaurus) that lack any particular distribution of derived features favoring one phylogenetic arrangement over others.

Avetheropods are divided into two major groups, Carnosauria and Coelurosauria. Carnosaurs are united mainly on cranial features, and for the most part do not differ in locomotor features from the condition of more basal tetanurines; this group includes the well-known *Allosaurus* and gigantic forms like *Carcharodontosaurus* and *Giganotosaurus*.

Coelurosaurs are the most anatomically diverse group of theropods, even if birds are excluded from consideration. A basal plexus includes small and large forms like *Ornitholestes*, *Proceratosaurus*, *Dryptosaurus*, and *Deltadromeus* that lack the features of derived coelurosaurs. The latter constitute the Maniraptoriformes. Although Sereno (1997), Makovicky and Sues (1998), and Holtz (2000) disagree over particular relationships within this advanced coelurosaurian clade (Fig. 2), they agree on the composition of this taxon, which includes many of the most specialized groups of theropods: ornithomimosaurs; tyrannosaurids, troodontids, therezinosauroids, oviraptorosaurs, dromaeosaurids, and avialians (living birds and their extinct relatives).

Inclusion of birds among the coelurosaurs is a contentious matter (see, for example, Welman [1995] and Feduccia [1996] for dissenting views). Debate over this topic is as much about methodology as it is about evolutionary relationships per se. Should functional explanations be predicated on phylogenies, or should functional interpretations provide a means of evaluating phylogenetic hypotheses? Is it reasonable to let a phylogeny based on a large number of characters be “trumped” by one or a few putatively paramount characters seemingly at variance with it (see, e.g., Burke and Feduccia, 1997; Ruben *et al.*, 1997; Wagner and Gauthier, 1999; Feduccia, 1999)?

Such questions cannot be answered in a paper like this. However, the majority opinion among us is that a close phylogenetic relationship between birds and coelurosaurs (particularly dromaeosaurids) is the most robust hypothesis about avian origins presently available (Gauthier, 1986; Holtz,

1994, 2000; Chatterjee, 1997; Forster *et al.*, 1998; Sereno, 1997; Padian and Chiappe, 1998). If true, then some of the characteristic features of birds that are related to locomotion, such as striding bipedalism, digitigrady, elongated hindlimbs, consolidation and fusion of limb bones, thin-walled long bones, furculae, specialized carpal bones, a large ilium, retroverted pubis, an increased sacral vertebral count, and a reduced tail, all arose within non-avian, derived theropod dinosaurs. If this hypothesis turns out to be wrong, and birds in fact arose from very basal theropods, basal dinosaurs, or even pre-dinosaurian archosaurs, the many features that advanced coelurosaurs share with primitive birds would constitute a remarkable case of parallel or convergent evolution—perhaps surpassing even that of nimravid and neofelid sabertooths among predatory mammals (Martin, 1998).

To avoid cladistically correct but awkward, space-consuming circumlocutions such as “non-avian theropods,” in the remainder of this paper we will use the term “theropod” in quotation marks to refer to members of the Theropoda exclusive of birds. Without quotation marks the term is used in a monophyletic sense.

TRENDS AND VARIATIONS IN THE LOCOMOTORY ANATOMY OF THEROPODS

“Theropods” shared a common locomotor design. All were digitigrade bipeds with fully adducted hindlimbs and functionally tridactyl feet. This commonality can be seen in the relative lengths of the femur, tibia, and metatarsus: Despite an enormous range in body sizes, “theropods” all had very similar hind limb proportions, compared to the wide range of proportions evolved by birds (Gatesy and Middleton, 1997; Carrano and Sidor, 1999); there is no evidence among “theropods” for limbs highly specialized for diving, paddling, wading, perching, or vertical clinging. This conservatism supports the notion that “theropods” were primarily adapted for terrestrial bipedalism. Even so, there are distinctive variations on the overall “theropod” morphological theme among the various groups.

The tails of basal members of most di-

nosaur lineages, like those of other reptiles, do not show marked differentiation into sections, beyond diminution of the size of the centrum, neural spine, and chevron size posteriorly. "Theropod" caudal vertebrae, however, show a marked trend toward transformation of the tail into different functional sections. "Theropod" tails have a distinct "transition point" (Russell, 1972; Gauthier, 1986). The neural arches and transverse processes become strongly reduced tailward, and are absent in at least the distal half of the tail. In tetanurines this transition point occurs in the proximal half of the caudal column, and in avetheropods is accompanied by a dramatic change in chevron shape: Distal chevrons lose the typical gentle curve of the primitive condition to take a distinct "L"-shape. The prezygapophyses are elongated in the distal caudal vertebrae of avetheropods, increasing the interlocked nature of the posterior tail. In advanced coelurosaurs the number of caudals is reduced from the primitive count of 50 or more to 44 or fewer, the prezygapophyses extend more than half the length of the preceding vertebra, and the distalmost chevrons are even more transformed, becoming very shallow dorsoventrally but elongated anteroposteriorly. In troodontids, dromaeosaurids, and avialians the transition point migrates even further headward, becoming located somewhere in the first nine caudals. This trend was taken further still in *Confuciusornis* and ornithomimosaurs, in which the distalmost caudals are fully interlocked as a single unit, the pygostyle.

These changes result in a tail that is stouter and more mobile proximally, but thinner and stiffer distally. This segmentation presumably transformed the distal portion of the tail into a dynamic stabilizer, perhaps as an aid during turning (Gauthier, 1986), that in dromaeosaurids may also have been employed for counterbalancing the body while attacking prey (Ostrom, 1969), in a manner reminiscent of a tight-rope-walker's pole. Development of this dynamic stabilizer incorporated progressively more of the tail, from the primitive condition in ceratosaurs through basal tetanurines

and carnosaurs, to more profound transformations in coelurosaurs.

Changes in the size and shape of the tail had additional effects on locomotion. The tail's length and mass affected the way "theropods" balanced. As obligate bipeds, "theropods" had to stand with the body's center of mass over the feet in order to maintain equilibrium. A nose-down pitch caused by the body in front of the hip joint was counterbalanced, at least in part, by the nose-up rotation imparted by the tail. The tail's ability to counter the weight of the front part of the body depended on its mass, as well as on the distribution of that mass along its length. "Theropods" more closely related to birds underwent a reduction in tail size (Gatesy, 1995; Gatesy and Dial, 1996). The above-noted progressive reduction in the number of caudal vertebrae was accompanied by a reduction in tail diameter, particularly distally. These changes likely affected the location of the body's center of mass, shifting it forward relative to the hip joint and forcing the limbs to reorient in order to position the feet further forward.

In addition, changes in tail size have implications for the function of the caudofemoral musculature (Gatesy, 1990). The caudofemoralis longus is a muscle running from the tail to the femur in living saurians (i.e., lizards, *Sphenodon*, crocodilians, and birds). Because of its large size and attachments, this muscle plays an important role during locomotion in both lizards (Reilly, 1995, 1998) and crocodilians (Gatesy, 1990). Osteological evidence of both origin and insertion indicates that a substantial caudofemoralis longus was the ancestral condition for "theropods."

"Theropods" more closely related to birds (e.g., ornithomimosaurs, dromaeosaurids, troodontids) show features indicative of a reduction in caudofemoral musculature. The smaller number of caudal vertebrae, reduced transverse processes, and distal specialization of the tail restricted the origin of the caudofemoralis longus to a smaller area of the tail base. Similarly, reduction or loss of the caudofemoral insertion scar, the fourth trochanter of the femur, indicates a reduction in muscle size. This pattern of change suggests that the caudo-

femoral retraction system was primitively important in “theropods,” but became less so in forms closely related to birds. Birds continued this trend by reducing the tail still further, and losing the caudofemoralis longus entirely in some species.

Theropod hips and hindlimbs show marked morphological changes (Fig. 3) that are consilient with functional changes during their evolution: (1) The antitrochanter repositioned from its primitive archosaurian location on the ischium, facing craniodorsally, to a more craniolateral orientation on the ischium and ilium in dinosaurs and their closest relatives. The antitrochanter then enlarged and re-oriented to face cranioventrally in birds. (2) The femoral head shifted from a craniomedial orientation in basal theropods to a more offset medial orientation in avetheropods, especially birds. (3) The ectocondylar tuber of the distal femur enlarged in “theropods” and moved distally from the proximal popliteal region onto the distal lateral condyle in birds. (4) The main weight-bearing axis of the crus shifted medially in theropods onto the tibia as the fibula and calcaneum were reduced, and elements of the knee and ankle joint became more rigidly appressed. (5) The fibular tubercle, the insertion of the knee flexor *M. ilio-fibularis* (Müller and Streicher, 1989), moved from a plesiomorphic craniolateral position on the proximal fibula in “theropods” to a caudolateral position in birds, consistent with a change in the action of this muscle related to increased knee flexion.

Unlike human beings, which have a distinctive walk/run transition, a shift between gaits is less clear in many ground dwelling birds (Gatesy and Biewener, 1991). Although the presence of an aerial phase is traditionally used to define running, birds are able to move very quickly without an aerial phase. Guineafowl, for example, do not employ an aerial phase below speeds of 2 m/sec (Gatesy, 1999). It appears that birds, particularly small forms, are able to maintain contact with the ground even at high speeds because of their highly compliant limbs. Such a “soft” limb spring allows birds to use a running mechanism (defined by the energy fluctuations of the cen-

ter of mass), while maintaining a double support phase. Such a running style has been called “Groucho running” (McMahon *et al.*, 1987) after the famous Marx brother’s bent-legged locomotor style. A question that remains unanswered is when this compliant form of avian locomotion evolved. Did all theropods have it, or is it unique to birds? An increase in limb compliance may have accompanied the reorientation of the femur into a more horizontal position, but this hypothesis awaits testing.

Holtz (1995) showed that arctometatarsalians (tyrannosaurids, ornithomimosaurs, and possibly certain other derived coelurosaurs) markedly increased the length of distal hindlimb elements relative to the femur length (Fig. 4A), as compared with other “theropods.” In addition, these derived “theropods” also developed a tightly interlocked proximal metatarsus that more effectively transmitted locomotory forces from the foot to the lower leg than did the ancestral theropod metatarsus. Holtz concluded that arctometatarsalians were probably capable of a greater degree of cursoriality than were other “theropods.”

Cursoriality is like pornography, however: We’re not sure what it is, yet we think we know it when we see it in animal morphology. How do “cursorial” adaptations actually relate to locomotor performance? Would more cursorial animals be expected to have a longer stride, and a faster top speed and/or walking speed, than less cursorial animals of the same body size? Is cursoriality related mainly to maximal sprint speed, or stamina, or the cost of transport (Garland and Janis, 1993; Janis and Wilhelm, 1993; Steudel and Beattie, 1995; Carrano, 1999)? The answers to these questions are not clear, and this makes interpretation of the locomotor performance of extinct animals like “theropods” especially difficult.

FOOTPRINTS, TRACKWAYS, LIMB CARRIAGE, AND GAITS

Much can be learned about “theropod” locomotion from anatomical studies of skeletons, but such inferences are necessarily indirect. Fossilized footprints and trackways directly record the movements of the

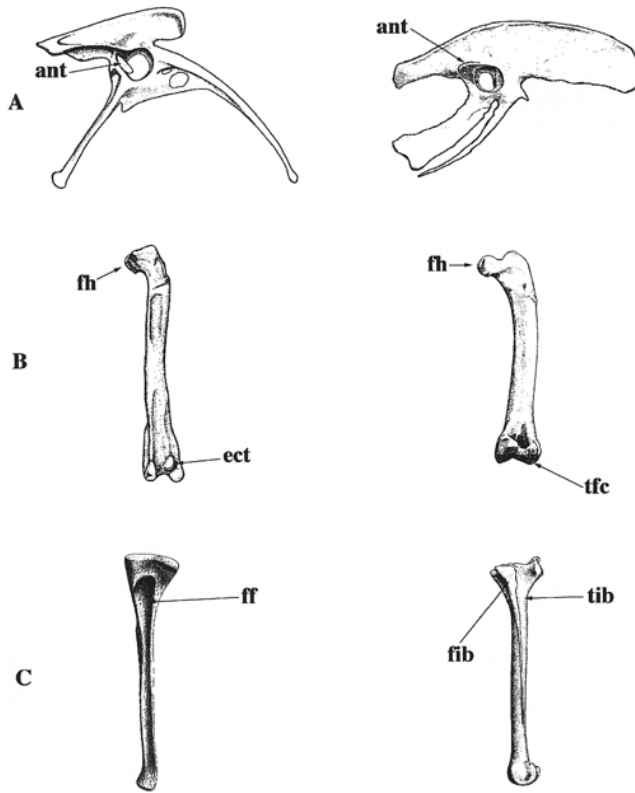


FIG. 3. "Theropod" (left) and bird (right; kiwi [*Apteryx*]; after McGowan, 1979) hindlimb elements, all from the right side. A) Pelves in lateral view: *Coelophysis* (after Rowe and Gauthier, 1990) and kiwi; arrow roughly indicates the orientation of the antitrochanter. B) Femora in caudal view; *Syntarsus* (after Rowe and Gauthier, 1990) and kiwi; arrow roughly indicates the orientation of the femoral head. C) *Allosaurus* (after Madsen 1993) fibula in medial view (left) and kiwi tibiotarsus in lateral view. Abbreviations: ant = antitrochanter, ect = ectococondylar tuber, ff = fibular fossa, fh = femoral head, fib = fibula, tfc = tibiofibular crest (homolog of ectococondylar tuber; Chiappe 1996), tib = tibia.

animals that made them, thus complementing the skeletal record.

Footprint shape and hindlimb carriage

Although trackways of small quadrupeds have been attributed to juvenile "theropods" (Wright, 1996), quadrupedal locomotion was probably rare at best in carnivorous dinosaurs. More common, but still infrequent, are trackways attributed to "theropods" that were walking flat-footed, with the entire metatarsus touching the ground (Thulborn and Wade, 1984; Kuban, 1989; Pérez-Lorente, 1993). Most "theropod" footprints confirm the conclusion that would be drawn from pedal osteology, that these dinosaurs usually walked in a digitigrade fashion.

Despite the greater number of phalanges (five) in the outer digit IV than in the inner digit II (three phalanges) of the main toes in both "theropods" and most large ground birds, the aggregate lengths of these toes are much the same. The ostrich, which has lost digit II, is a dramatic exception. However, this symmetry is not seen in most well-preserved footprints attributed to "theropods." The impression made by digit II is commonly much shorter than that of digit IV, resulting in a conspicuous notch along the medial edge of the print (Fig. 5A, B). The posterior margin of the "theropod" footprint seems to have been made by a pad beneath the metatarsophalangeal joint of digit IV (Baird, 1957; Thulborn, 1990). The most proximal digital pad of both digits II

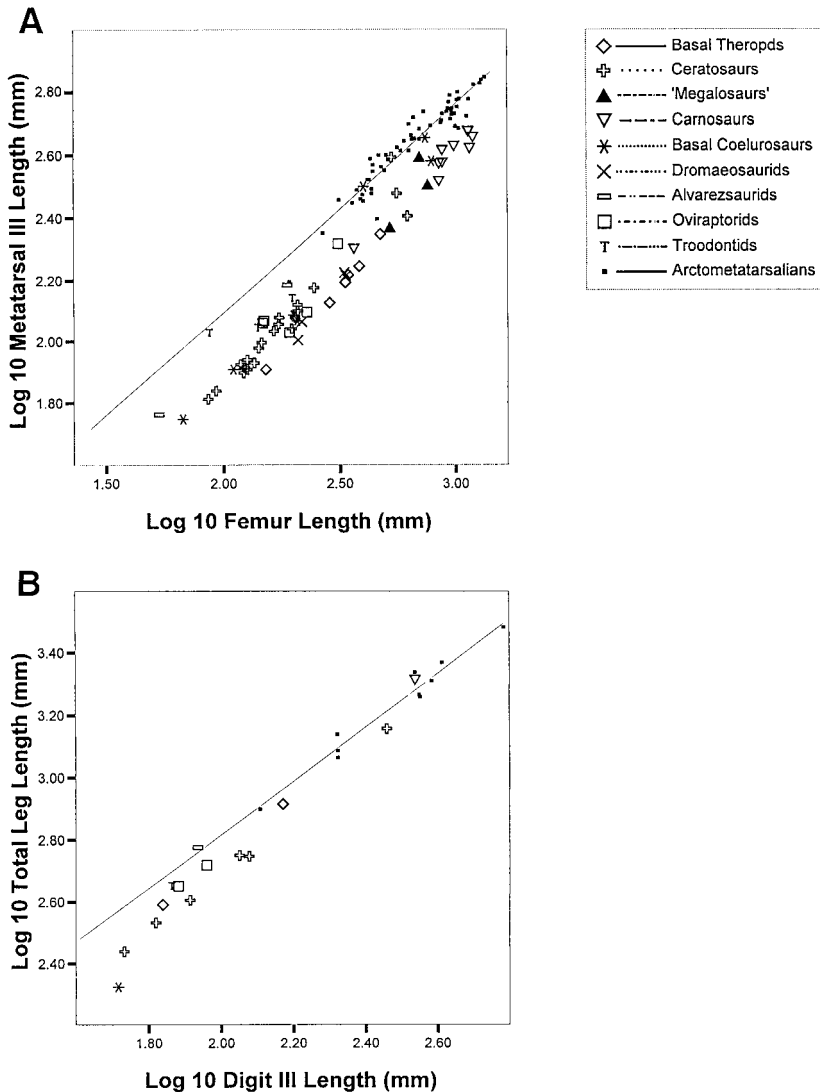


FIG. 4. Limb proportions in "theropods." A) Plot of the length of metatarsal III against femur length. Note the tendency for arctometatarsalian coelurosaurs (tyrannosaurids and ornithomimosaurs, and possibly troodontids), as compared with other groups, to lengthen the metatarsus relative to the femur. Modified from Holtz (1995). The regression line is for arctometatarsalians: \log_{10} metatarsal III length = $0.664 \log_{10}$ femur length + 0.765 ; $r^2 = 0.91$. However, this and other regression equations reported in this paper should be taken with caution; data cases are individual specimens, and particular species are represented by different sample sizes. For a list of the genera that represent the various groups in this and other graphs, see Appendix 1. B) Total leg length (femur + tibia + metatarsal III) as a function of the aggregate length of the phalanges of digit III. In contrast to the comparison of proximal and distal limb segment lengths, the present relationship shows no marked difference between arctometatarsalians and other "theropods." Regression line for arctometatarsalians: \log_{10} total leg length = $0.864 \log_{10}$ digit III length + 1.088 ; $r^2 = 0.966$.

and III that is commonly recorded in footprints was situated beneath the joint between the first and second phalanges of the digit.

In order to make prints of this shape, the metatarsophalangeal joints of digits II and III had to have been held clear of the ground, while digit IV was impressed over

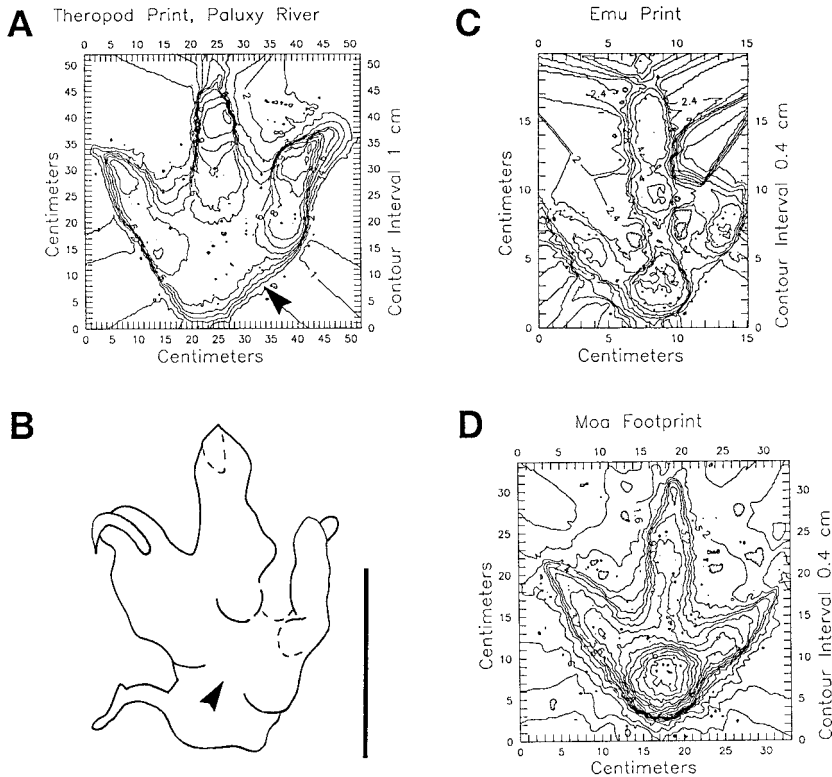


FIG. 5. Footprints of "theropods" and large ground birds. A) Topographic map of a large Early Cretaceous "theropod" footprint from the Paluxy River of Texas. Arrow points to the notch along the inner rear margin of the digit II impression created by failure of the proximal end of phalanx 1 of digit II to impress. B) *Tyrannosaurus* (by convention, names assigned to footprints refer to the prints themselves, and not to the creatures that made them), a very large Late Cretaceous footprint from New Mexico. Due to the great depth of the track, there is a clear (and unusual) impression of digit I (left of the arrow). Arrow points to the medial embayment along the inner rear margin of the print. Scale bar = 50 cm. Redrawn from Lockley and Hunt (1994). C) Footprint of an emu (*Dromaius novaehollandiae*). Note the well-developed, symmetrically positioned metatarsal pad impression in this and the next footprint. D) Moa footprint from the Pleistocene of New Zealand.

its entire length. This resulted in an asymmetry of the proximal (posterior) portion of the footprint that can be seen in "theropod" prints small and large. (We will designate the proximal end of "theropod" and bird footprints as the "heel" for descriptive purposes, but it should be kept in mind that this region of the print was not made by the anatomical heel, which would usually have been held clear of the ground in these digitigrade animals.) The same asymmetry can be seen in footprints (e.g., *Anomoepus*) attributed to primitive ornithischians (Lull, 1953; Thulborn, 1990, 1994; Olsen, 1995), and so this may be a primitive feature for dinosaurs generally.

In contrast, the proximal end of Cenozoic

ground bird footprints is much more symmetrical (Fig. 5C, D). The "heel" is formed by a thick metatarsal pad located beneath the distal end of the digit III trochlea of the tarsometatarsus (Lucas and Stettenheim [1972]; Cannon [1996]; in ostriches, however, this pad commonly does not touch the ground). The metatarsophalangeal joints of digits II and IV are elevated off the ground.

Padian and Olsen (1989) observed that the proximal ends of the digits do not register in footprints of rheas and other ratites. They noted the relatively longer metatarsus of birds than of "theropods," and suggested that a longer metatarsus would have to be more vertically oriented than in typical "theropods" to keep the animal's center of

mass positioned above the feet. Padian and Olsen (1989) further speculated that the avian metatarsus might have elongated "to move the center of support farther forward to compensate for (1) the increased pectoral muscle mass of birds . . . and (2) the loss of the long, fleshy tail of their dinosaurian ancestors" (Padian and Olsen, 1989, p. 234).

However, the situation is probably more complicated than that. Lengthening the metatarsus with no other changes in limb segment lengths or inter-segmental angles would indeed shift the animal's mass backwards, causing the animal to tend to fall backward with respect to the point where its foot touched the ground. Shortening the tail with no other changes, in contrast, would cause the animal to fall forward. Having both changes occur simultaneously might cancel out their effects, obviating the need for a more vertical metatarsus.

Another complicating factor, though, is the size and orientation of the femur. Padian and Olsen (1989) argued that "theropods," like birds, held the femur in a nearly horizontal fashion. In contrast, Gatesy (1991) noted the relatively elongate, slender shape of the femora in "theropods" as compared with avian femora, and argued that the thigh in "theropods" was not stoutly enough constructed to withstand the stresses to which it would have been subjected had it been held horizontally. Carrano (1998) extended this argument by demonstrating that a horizontal femur experiences considerably greater torsional strains than a vertical femur. In birds, this results in a very short, stout femur that is very unlike the relatively slender femur of non-avian theropods (Gatesy, 1991; Carrano, 1998).

In birds, most of the motion of the leg during protraction–retraction at slow speeds occurs at the knee, rather than the hip (Tarsitano, 1983; Gatesy, 1990; Carrano, 1998). The considerable shortening of the tail in birds forces the center of mass forward, and a walking bird balances its weight over the knee, and not the hip. Perhaps this has contributed to the more vertical orientation of the metatarsus in birds than in "theropods," but how the more horizontal femur would interact with tail shortening and metatarsal

lengthening to elevate the latter bone is unclear.

Yet another change during theropod/bird evolution was the above-mentioned reduction of the fibula and the increased importance of the tibia in weight-bearing. Early archosaurs had rather large fibulae, and stood/moved with digit I and V touching the ground (Serenio, 1991). Theropods changed this by (1) claspings the fibula to the tibia with a big crest, ligaments, and a proximally shifted interosseus muscle, (2) lifting digits I and V off the ground, and (3) linking the tibia and the astragalus via the ascending process of the latter bone, while reducing the fibula and calcaneum. More derived birds than *Archaeopteryx* eventually reduced the fibula still further, and fusion of the metatarsals into a single tarsometatarsus may have occurred in association with a more evenly distributed carriage of body weight across the proximal end of the foot as the metatarsus became elevated.

In any case, a more vertical orientation of the metatarsus is very likely the reason for the more symmetrical shape of the "heel" in footprints of birds as opposed to most "theropods"; a more vertical carriage of the metatarsus would presumably lift the metatarsophalangeal joint of digit IV off the ground. Further evidence for differences in metatarsal carriage comes from differences in shape between footprints made by "theropods" and birds walking on very soft substrates (Gatesy *et al.*, 1999). It would be interesting to know when in the course of theropod evolution this elevation of the metatarsus happened. Would footprints of the first birds have looked like those of most small "theropods," with an asymmetrical "heel"? Did the evolution of a pronounced metatarsal pad at the rear edge of the print occur after birds emerged as a distinct clade? Or would such features have been seen in prints made by "theropods" close to birds?

"Theropod" and Cenozoic ground bird footprints commonly differ in the angle formed by the impressions of digits II and IV (Table 1). "Theropod" prints tend to have low values of this interdigital angle, while prints of birds often have higher val-

TABLE 1. Values of interdigital angle II–IV (measured as best-fit lines through digit impressions in photographs or on tracings drawn from footprint casts on plastic sheets; numbers in degrees) in footprints of selected large birds and dinosaurs. Data from the senior author's unpublished observations. Moa footprints are from the Pleistocene of New Zealand, and dromornithid prints from the mid-Tertiary of Tasmania. Dinosaur footprints from the Amherst College Collection and Dinosaur State Park are Early Jurassic, and dinosaur tracks from the F⁶ Ranch and Glen Rose Limestone sites are of Early Cretaceous age.

Trackmaker(s)	Minimum	Maximum	Mean	Number of footprints
Female greater rhea (<i>Rhea americana</i>)	42	77	57.0	7
Male lesser rhea (<i>Rhea pennata</i>)	38	49	44.0	3
Juvenile emus (<i>Dromaius novaehollandiae</i>) ^a	57	111	85.1	41
Adult emus ^b	55	119	80.8	53
Cassowaries (<i>Casuarius casuarius</i>) ^c	36	51	46.5	6
Kiwis (<i>Apteryx australis</i>) ^d	104	119	111.3	4
Unidentified moa	64	109	89.9	10
Unidentified dromornithids	78	125	101.4	5
Phasianids ^e	57	144	110.8	56
Male kori bustard (<i>Ardeotis kori</i>)	61	82	73.7	3
Amherst College 9/14 <i>Anchisauripus</i>	21	48	29.2	38
Dinosaur State Park (Rocky Hill, CT) "theropods"	31	87	54.3	113
F ⁶ Ranch site (Fort Terrett Formation, Kimble County, Texas) "theropods"	17	53	32.1	25
Glen Rose Limestone (various localities, central Texas) "theropods"	29	54	40.1	28

^a Data for 21 captive individuals.

^b Data for at least 16 captive or free-living individuals.

^c Data for two captive individuals.

^d Data for two captive individuals.

^e Data for at least 26 captive individuals of 19 species.

ues. However, there is overlap between the two groups; rheas and cassowaries have low interdigital angles for birds, and some prints attributed to "theropods" have interdigital angles as large as those of any bird (Harris, 1998b).

Several types of small Mesozoic footprints have been attributed to birds (Lockley *et al.*, 1992), and some of these show features like those of Cenozoic bird prints. Interdigital angle II–IV is usually rather large in footprints attributed to Mesozoic birds, and digits II and IV extend outward from a symmetrical "heel." In addition, there is often a clear impression of the hallux, with a large angle formed between this impression and that of digit II. Most Mesozoic bird prints were made by waterbirds, and as in many modern waders the toe-marks are very slender.

However, some Mesozoic footprints, both large and small, are harder to categorize as having been made by "theropods" or birds (Fig. 6). The Late Cretaceous ichnotaxon (footprint taxon) *Saurexallopus* (Harris *et al.*, 1996; Harris, 1997) has a fair-

ly deep "heel" mark that is similar to the metatarsal pad of bird prints; the ichnotaxon is also characterized by the distinct impression of a long (albeit unreversed) hallux, large interdigital angles, and possibly interdigital webbing—yet more birdlike features. If the *Saurexallopus*-maker was a bird, it would have been comparable to large ratites in size. Harris *et al.* (1996) rejected the hypothesis that the trackmaker was a bird in part on the basis of the size of the prints, citing the absence of big birds from the osteological record of the Late Cretaceous, but the recent discovery of an ostrich-sized bird from the Late Cretaceous of Europe (Buffetaut and Le Loeuff, 1998) weakens this objection. If, however, the *Saurexallopus*-maker was in fact a "theropod", it was a form whose feet were unusually birdlike.

Magnoavipes from the Lower Cretaceous of Texas (Lee, 1997) is even more birdlike than *Saurexallopus*, and like the latter was made by an animal comparable in size to a large ratite. There seems to be a metatarsal impression about which digits II and IV are

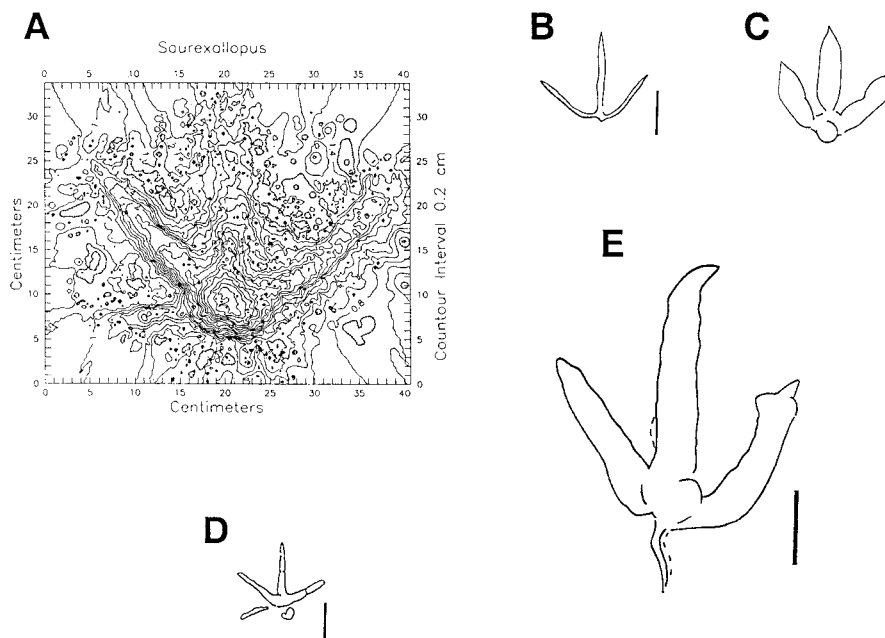


FIG. 6. Mesozoic tridactyl footprints of uncertain affinities. A) Topographic map of *Saurexallopus*, a large “theropod” or bird print from the Late Cretaceous of Wyoming (Harris *et al.* 1996). The footprint is deepest in the “heel” region, with a symmetrical metatarsal pad impression and a large digit I impression (extending to the left in this view); print depth diminishes distally along the toemarks. B) *Magnoavipes*, a large bird (?) footprint from the Early Cretaceous of Texas; scale bar = 10 cm. Redrawn from Lee (1997). C) *Fuscinapedis*, a large “theropod” (?) footprint from the Early Cretaceous of Texas; note the apparently well developed metatarsal pad impression. Scale bar = 10 cm. Redrawn from Lee (1997). D) *Trisauiropodiscus*, a bird or birdlike “theropod” footprint from the Early Jurassic of Africa. Scale bar = 10 cm. Redrawn from Lockley *et al.* (1992). E) *Plesiornis*, a bird or birdlike “theropod” footprint from the Early Jurassic of Poland. Scale bar = 1 cm. Redrawn from Gierlinski (1996).

symmetrically arranged, interdigital angle II–IV is rather large, and the toemarks are slender. *Fuscinapedis* from the same fauna is even bigger, with footprints some 38 cm long—comparable in size to large moa footprints. Lee (1997) attributed *Fuscinapedis* to a “theropod,” but it has a marked metatarsal impression.

Even more perplexing are the ichnogenera *Trisauiropodiscus* and *Plesiornis*, very birdlike footprints from the early Mesozoic (Lockley *et al.*, 1992; Weems and Kimmel, 1993; Gierlinski, 1996). Such prints show the same features used to assign later Mesozoic prints to avian trackmakers. Most of these tracks are only a few centimeters long, but some are comparable in size to heron footprints. Intriguingly, these tracks are older than *Archaeopteryx*. Interpreting them as having been made by birds would imply a rather earlier origin of birds than

conventionally accepted (Padian and Chiappe, 1998), but would be compatible with more heterodox notions of when the first birds evolved (Chatterjee, 1991, 1997).

However, it is difficult to integrate information from footprints like *Saurexallopus*, *Magnoavipes*, and *Trisauiropodiscus* into discussions of “theropod” and avian locomotion, simply because we cannot be certain of the affinities of their makers. Were these creatures in fact birds, or rather theropods that had independently evolved a very birdlike pedal configuration? Such questions illustrate the weakness that accompanies the strength that footprints bring to interpreting dinosaur locomotion: What one gains in the ability to “observe” the stance and motions of a trackmaker, one loses in taxonomic resolution about who that trackmaker was.

Trackway patterns and limb proportions

Trackways show that “theropods” were striders rather than hoppers (Thulborn, 1990). “Theropod” trackways are usually (but not always; Lockley *et al.*, 1996) very narrow, indicating that their makers generally walked with the feet placed close to the body midline. Footprints often angle slightly inward with respect to the trackmaker’s direction of travel, but can also point straight ahead, or angle slightly outward (Farlow, 1987; Farlow and Galton, 2000). Tail marks are only rarely seen.

Trackway data suggest conservatism in some aspects of locomotor activity during “theropod” evolution. Figure 7A examines stride length as a function of footprint length in trackways attributed to “theropods.” Unsurprisingly, bigger animals (with footprint length as a proxy for overall size) tend to take longer strides than do smaller animals (Thulborn, 1990; Pérez-Lorente, 1996). The data plot in a broad band. Nearly all of the small later Mesozoic “theropod” points at the upper edge of the band come from a single locality, the Lark Quarry site in Queensland, where a host of small dinosaurs is thought to have been panicked by the approach of a large carnivorous dinosaur (Thulborn and Wade, 1984). Other dinosaur points along the upper margin of the band likewise show unusually long strides for a given footprint length. Unless one wishes to postulate the existence of “theropods” with much longer legs than any known from skeletal evidence, points along the top edge of the band probably represent trackways made by running animals, and those along the lower edge of the band presumably correspond to trails of animals walking in a more leisurely fashion.

The trackway data provide no evidence for changes in stride lengths (at least as compared with footprint length) during walking or running in comparisons of early as opposed to later Mesozoic “theropods.” One might have expected progressively more cursorial groups (Holtz, 1995) of “theropods” to have longer limbs for a given foot length; progressively more cursorial animals might reduce the amount of the

foot contacting the ground by increasing the degree of digitigrady (*cf.* Coombs, 1978). This would then translate into longer stride lengths for a given footprint length.

The presently available trackway data provide no evidence for this. However, most of the later Mesozoic trackways are of Early Cretaceous age; there are few available trail measurements from times and places when arctometatarsalians (predominantly known from the Late Cretaceous of Asia and western North America) would constitute the likely trackmakers. If such data did exist, they might indicate relatively longer strides during walking and running than in the data examined here.

On the other hand, although the data are scant, conservatism also seems to characterize the relationship between total leg length and a very rough proxy for footprint length, the aggregate length of the phalanges of digit III. Ceratosaurs have a relatively short leg length for a given digit III length, but there is otherwise no obvious phylogenetic pattern in this relationship (Fig. 4B). Derived groups seem not to have relatively longer legs than more primitive groups. This suggests the possibility that relative stride lengths did not lengthen appreciably—at least for walking animals—during the course of “theropod” evolution. A relatively longer stride may have been used only during flat-out running (although the trackway data provide no evidence for this).

“Theropods” may not differ much among themselves in the relationship between stride and footprint length, but they do differ from other kinds of bipedal archosaurs. Figure 7B summarizes data for “theropods,” extant and extinct ground birds, and bipedal ornithischians. The many points for small ornithischians with long strides are from the Lark Quarry site. Although large ornithischian (probably mainly ornithomimid) points show considerable overlap with those of “theropods,” there is a clear tendency for large ornithomimids to take shorter strides for a given footprint length. Bird points likewise show much overlap with “theropods.” However, many of the avian trackmakers were zoo captives that seemed agitated about being driven across

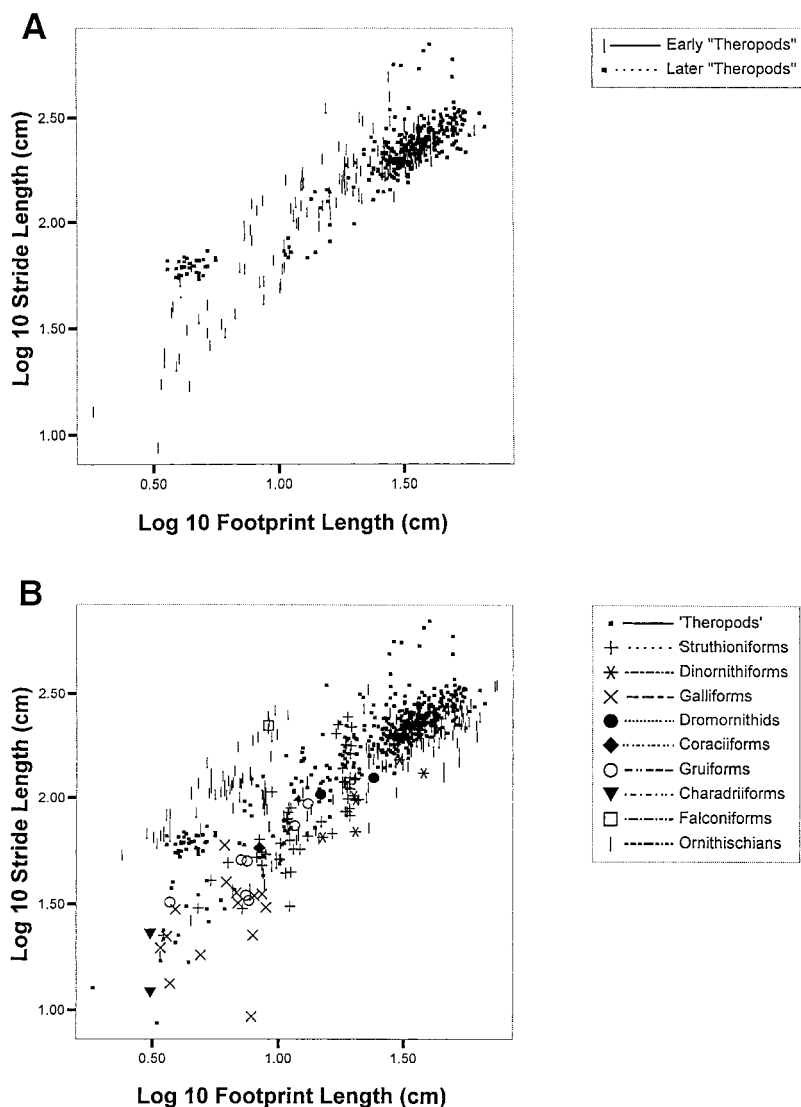


FIG. 7. Stride length (distance from one footprint to the next footprint made by the same foot) as a function of footprint length. A) Early (Late Triassic-Early Jurassic) and later (Late Jurassic-Cretaceous) Mesozoic trackways attributed to "theropods." Data compiled from numerous published sources and the senior author's unpublished observations. B) Stride length as a function of footprint length in "theropods," birds, and bipedal ornithischians. Bird trackway data mainly from the senior author's work on zoo and free-living animals, but also from the literature. Although it is unlikely that any individual non-avian dinosaur is represented by more than one point in the graph, many of the struthioniform points represent repeated trackmaking episodes by a small number of individual emus.

substrates prepared for recording footprints; these birds were moving at faster than their normal walking speeds. Among these discontented birds were emus (*Dromaius novaehollandiae*) responsible for the longer struthioniform strides; the same individual emus are also represented by lower-plotting

stride lengths in the graph. Note, too, that the dinornithiform trackways—which were unquestionably made without human interference—plot toward the bottom of the cloud of points associated with walking "theropods." It seems, then, that ground birds, when moving without harassment,

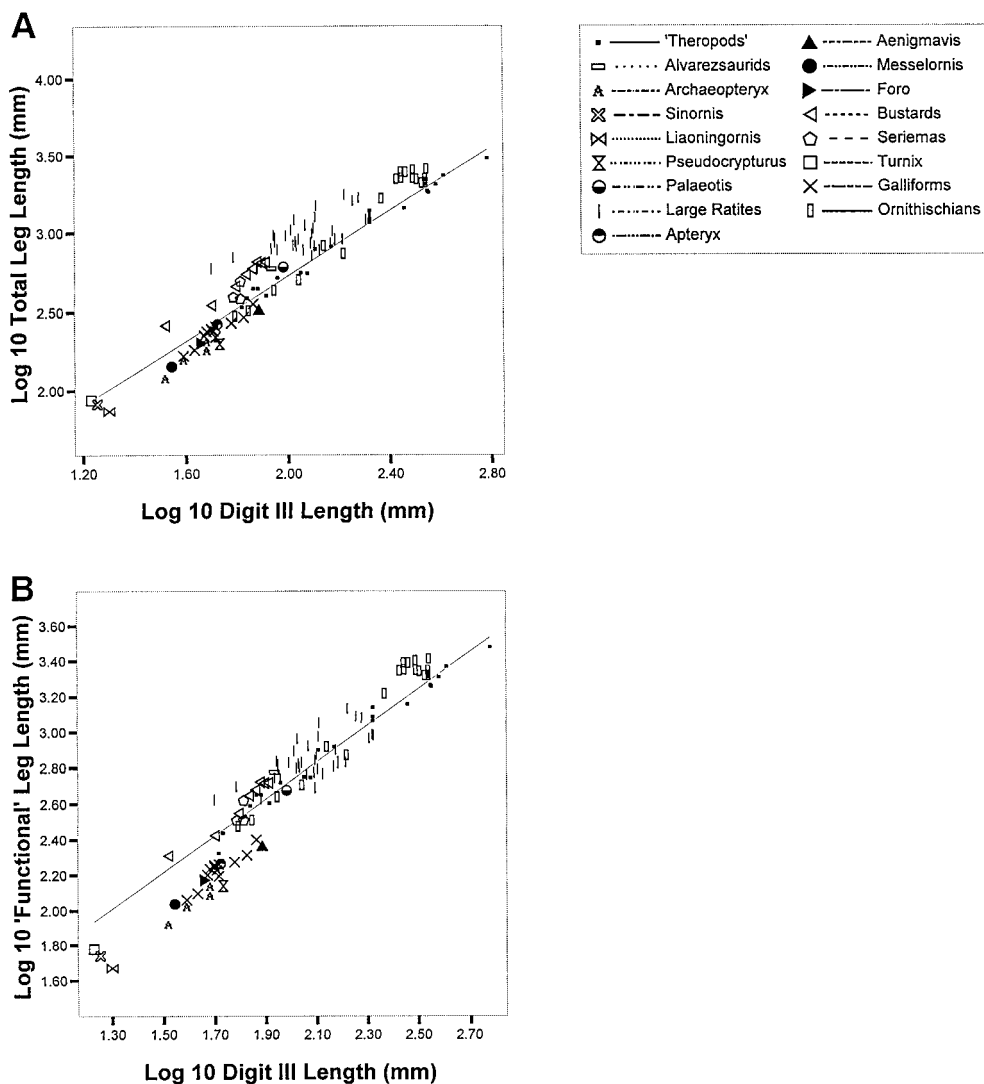


FIG. 8. Leg length as a function of digit III length (a proxy for the portion of the foot likely to touch the ground) in “dinosaurs” and birds. A) Total leg length (femur + tibia [or tibiotarsus] + metatarsal III [or tarsometatarsus]) vs. digit III length. B) “Functional” leg length vs. digit III length in “dinosaurs” and birds. In “dinosaurs” “functional” leg length is the same as total leg length, while in birds this parameter excludes the length of the femur. Regression line for “theropods” in both graphs: $\log_{10} \text{ leg length} = 1.029 \log_{10} \text{ digit III length} + 0.670$; $r^2 = 0.981$. Some of the dinornithiform (moa) points represent composites of two individual birds of comparable tarsometatarsus length.

often take relatively shorter steps for a given footprint length than did non-avian theropods.

Conceivably this might be related to the different hindlimb carriage of “theropods” than birds, with the more vertical and relatively longer femur of the former resulting in a longer relative leg length. This hypoth-

esis can be tested by comparing the length of digit III against the combined lengths of the femur, tibia (or tibiotarsus), and metatarsus (or tarsometatarsus) in the two groups (Fig. 8A). Contrary to the hypothesis, large ground birds (most living ratites, moa, elephantbirds, bustards, seriomas) tend to have a longer leg, relative to digit

III length, than do “theropods.” However, Mesozoic and some Cenozoic birds (button-quail, kiwi, a lithornithid, *Aenigmavis*, *Messelornis*, *Foro*, galliforms) do plot among points for “theropods.” Large ornithopods, like big birds, have long legs relative to the length of digit III.

If we now consider that most of the leg action in walking birds occurs at the knee rather than the hip (Gatesy, 1990, 1991; Gatesy and Biewener, 1991), we can compare a “functional” leg length against digit III length in “dinosaurs” and birds (Fig. 8B), with “functional” leg length being equal to total leg length in “dinosaurs,” but equivalent to the combined length of the tibiotarsus and tarsometatarsus in birds. Birds that plotted among “theropod” points in the graph of total leg length against digit III length now plot below them, but the long-legged ground birds now show considerable overlap with “theropods.”

Neither total leg length nor “functional” leg length as presented here is completely realistic; we have not considered angles between limb segments or the actual motions made by the limbs during locomotion. Nonetheless the comparisons are probably realistic enough to have intriguing implications for “dinosaurian” and avian locomotion. First, “theropods” do not have relatively longer legs (relative to digit III and footprint length) than birds. If we could add the likely lengths of “theropod” tarsal elements in leg lengths, “functional” limb lengths of “theropods” would likely show even more overlap with birds in the relationship depicted in Figure 8. This means that “theropods” and ground birds may have roughly the same functional leg length for the amount of foot that touches the ground.

Second, this similarity in function, if such it is, is not something that was conserved during changes in limb carriage in the evolution of birds from “theropods.” Mesozoic and some Cenozoic birds have relatively shorter “functional” limb lengths than “theropods” (Fig. 8B). Consequently any similarity in “functional” leg length relative to digit III length between large ground birds and “theropods” reflects convergence rather than conservatism.

Large ornithopods have relatively longer legs for a given digit III length than do large theropods (Fig. 8). This may highlight a weakness in using digit III length or footprint length as a proxy for overall animal body size. If we compare digit III and leg lengths with overall body shape in large “theropods” and big ornithopods, it is clear that the latter do not have long legs so much as extremely short toes. A better comparison of leg lengths among “theropods,” birds, and ornithischians might use the total length of the dorsal vertebral series as the proxy for body size.

If birds and “theropods” of a given body size generally walk(ed) at the same speed, possibly birds have a higher stride frequency than “theropods” did. Alternatively, if the longer step lengths of “theropods” than birds do in fact translate into faster speeds, perhaps this difference in locomotion between “theropods” and ground birds has a behavioral rather than a structural explanation. Most Cenozoic ground birds have been herbivores or omnivores rather than carnivores, while most “theropods” were manifestly predators. Conceivably trackways of “theropods” were generally made during foraging bouts, when the trackmakers were actively searching for prey. In contrast, many trackways made by ground birds may record less purposeful motion. The more abundant, better dispersed nature of foodstuffs available to non-predatory animals may permit short, unhurried steps during many foraging bouts. This idea is, however, merely speculation.

“Theropod” trackways and running

In a study based on 267 trackways of bipedal dinosaurs, Thulborn (1984b) examined the frequency distribution of the ratio of stride length to estimated hip height. Unsurprisingly, he found that dinosaur trackways usually had a low stride/hip height ratio, indicating that walking predominated over faster styles of locomotion. More interestingly, Thulborn’s data suggested that the distribution of stride/hip height ratio was bimodal. He speculated that what he called a “trot” (which he defined as slow running in which the ratio of stride length to estimated hip height ranged from 2.0 to

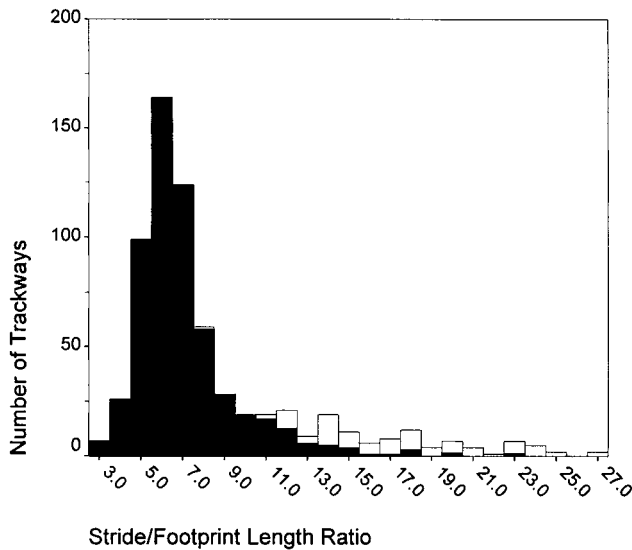


FIG. 9. Relative stride length (stride/footprint length) in trackways of bipedal dinosaurs. Unshaded histogram is for all trackways ($N = 664$), including many from the Lark Quarry site, where a large number of small dinosaurs apparently were frightened into mass flight by the approach of a large “theropod.” Shaded histogram ($N = 577$) excludes trackways from the Lark Quarry site.

2.9) was a transitional gait of high energetic cost that bipedal dinosaurs generally avoided using.

However, 92 of Thulborn’s dinosaur trackways came from his Lark Quarry site, which—as already has been noted—represent an unusual circumstance, where a large group of small dinosaurs was stampeded by the approach of a large carnivore (Thulborn and Wade, 1984). Figure 9 plots the stride/footprint length ratio for 664 bipedal dinosaurs, more than twice Thulborn’s (1984*b*) sample size. There is no indication of bimodality in this larger data set. This conclusion is even stronger if data for the Lark Quarry site are excluded; if bipedal dinosaurs really had avoided a “trot,” this should be apparent in trackway data generally. The bimodality in Thulborn’s data was an artifact of the large number of trackways from a single, unusual site (a possibility that Thulborn conceded). Bipedal dinosaurs usually walked, and used increasingly faster gaits decreasingly often.

The occurrence of “Groucho” running in birds raises other questions about the gaits used by non-avian theropods. If this style of compliant locomotion actually evolved in pre-avian theropods, then some “thero-

pod” trackways with relatively long strides may not record true running. However, because some of the characteristic features associated with avian bipedalism (knee-based kinematics, horizontal femur, presence of a pygostyle) may not have been present in basal birds (Gatesy, 1990, 1991; Carrano, 1998), then—if “Groucho” running is intimately tied to a horizontal femoral orientation—it is likely that most “theropods” did not employ this style of fast locomotion. If any “theropods” were “Grouchos,” we suspect that they were small forms very closely related to birds.

Alexander (1976) published an equation that related an animal’s speed to its hip height and stride length. Because the latter two parameters can be either measured or estimated from trackways, Alexander’s equation became the basis for estimating the speeds of dinosaurs. Most such estimates for bipedal dinosaurs are 10 km/hr or less (Thulborn, 1990; Pérez-Lorente, 1996), but estimated speeds of as much as 40 km/hr have been reported (Farlow, 1981; Viera and Torres, 1995; Irby, 1996). Although these estimates seem reasonable, there is no way of testing their accuracy.

Stance, Running, and Gigantism in "Theropods"

Gigantism was a recurring theme in dinosaurian evolution (Farlow *et al.*, 1995; Sereno, 1997). The earliest theropods were small to medium-sized (1–3 m body length) animals, but tetanurines soon evolved very large forms.

Biomechanical, scaling, and kinematic studies of living tetrapods suggest that terrestrial vertebrates adopt more extended hindlimb posture at larger body sizes as compared with smaller tetrapods (Biewener, 1989; Bertram and Biewener, 1990; Gatesy and Biewener, 1991). If the pattern exhibited by mammals and birds has general application, then larger theropods should have more straightened hindlimbs than their smaller relatives.

In contrast, Paul (1988) contended that a "crouched" hindlimb stance was retained even in enormous "theropods" like *Tyrannosaurus*, basing his argument on the configuration of the hip, knee, and ankle joints. From this he concluded that *Tyrannosaurus* retained the same capacity for rapid locomotion seen in smaller, related forms like ornithomimosaur.

However, a 3D computer analysis using digitized elements of the hindlimb of *Tyrannosaurus* (J. R. Hutchinson, unpublished observations) reveals more joint mobility at the knee and hip than is evident from 2D drawings of the kind made by Paul. The hip and knee joints can be positioned in a variety of intuitively pleasing positions (Fig. 10) that span the entire "crouched vs. columnar" dichotomy without disarticulating these joints.

Christiansen (1999) estimated limb angulations of "theropods" of various sizes by measuring the angle between the femoral distal epiphysis and the long axis of the bone. In contrast to Paul (1988), his data suggested that large "theropods" did indeed have less flexed limbs than their smaller relatives, but nonetheless had less columnar limbs than elephants, suggesting somewhat greater potential for fast locomotion than in the latter.

Alexander (1985) defined an index of the bending strength of limb bones that consid-

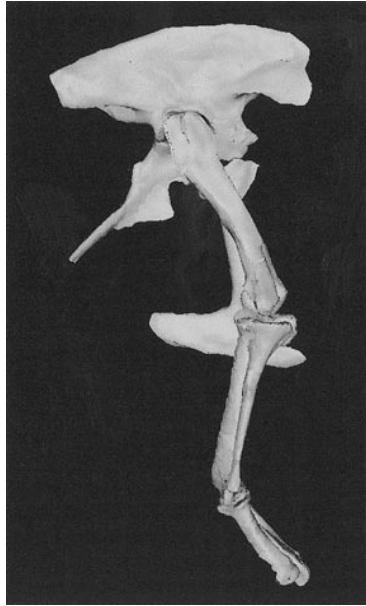


FIG. 10. One of many possible interpretations of hindlimb joint angulation in *Tyrannosaurus* that are consistent with a three-dimensional analysis of joint configurations.

ered animal mass, bone length, and the section modulus of the shaft of the bone. Modern large animals capable of rapid locomotion have high values of this "strength indicator," while slowly moving forms have low values. Applied to dinosaurs, Alexander's approach indicated that the femur of *Tyrannosaurus* was comparable in bending strength to that of an elephant, suggesting that the huge theropod was little better than an elephant at moving quickly. Farlow *et al.* (1995) recalculated Alexander's strength indicator for *Tyrannosaurus*, using better data than were available to Alexander, but nonetheless found values of the strength indicator comparable to those obtained by Alexander. Christiansen (1999) noted that a component of the strength indicator that lessens its value, limb bone length, is disproportionately longer in large "theropods" than in large mammals capable of rapid locomotion. He concluded that the limbs of enormous "theropods" were only marginally stronger than those of elephants and hippos.

Farlow *et al.* (1995) considered another issue that could have affected the locomotor

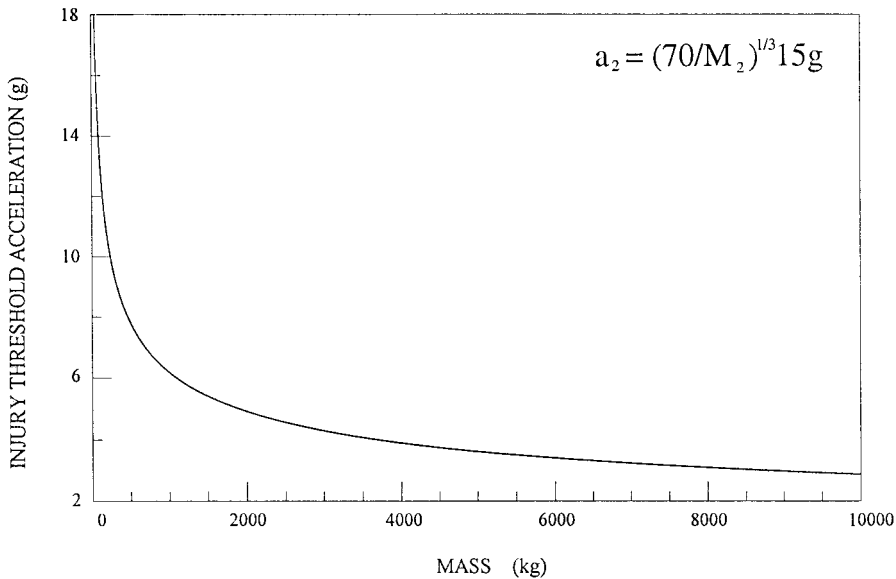


FIG. 11. Injury threshold impact acceleration a_2 as a function of animal body mass M_2 .

performance of very large “theropods”: the likelihood of injury in the event of a fall while running. Simple mathematical models based on animal mass, the height of the dinosaur’s head and torso above the ground, the depth of the hole gouged in the ground by the animal’s fall, and the animal’s ground speed suggested that the risk of serious injury or even death would have been significant had a *Tyrannosaurus*-sized “theropod” stumbled while moving at speed. Farlow *et al.* (1995) concluded that this was an additional reason for thinking that very large “theropods” did not run at sprint speeds comparable to those of smaller “theropods.”

Alexander (1996) evaluated this argument using a novel source of data: injuries sustained by humans in car crashes. From scaling arguments he calculated that, if a 70-kg human can survive an impact deceleration of 15g, a 6000-kg tyrannosaur should be able to withstand a deceleration of 3.4g. More than that and the animal would likely be seriously injured. The models presented by Farlow *et al.* (1995) estimated impact decelerations considerably greater than 3.4g, and Alexander (1996) concluded that a falling *Tyrannosaurus*

would indeed very likely risk damage to itself.

We have extended Alexander’s (1996) argument (appendix 2) to generalize the relationship between injury threshold acceleration and body mass (Fig. 11). The maximum tolerable impact deceleration a_2 decreases drastically for animals with body mass greater than 70 kg (the mass of an average-sized human being). This also means, though, that “theropods” smaller than *Tyrannosaurus* would have risked less injury in the event of a fall: a_2 for a 2000-kg animal is 4.9g; for a 1500-kg animal 5.4g; for a 500-kg animal 7.8g; for a 200-kg animal 10.6g. To the extent that injury risk was a factor in limiting locomotor performance, theropods like *Gorgosaurus* could be expected to have been somewhat more likely than *Tyrannosaurus* to engage in “Jurassic Park”-style performances, while ornithomimosaurs could safely have run at the higher speeds that their morphology suggests (Russell, 1972). Furthermore, juveniles of very large-bodied theropods could more safely have been rapid runners than their elders were.

However, Alexander (1996, p. 121) questioned “whether animals can be expected to

be cautious, or to live dangerously.” He cited the galloping of giraffes, the sprinting of ostriches, and the treetop maneuvers of gibbons as activities in which a fall might be expected to result in injury. Whether and how natural selection factors such risks before rolling the locomotory dice is a question we cannot answer. However, it does seem likely that smaller animals like gibbons and ostriches would be better able to make sudden, quick corrections of motion to correct for a potential mishap than could an elephant-sized animal moving at a rapid speed. Furthermore, Farlow *et al.* (1996) argued that a huge biped might find it harder to compensate for a misstep than could a large quadruped like a giraffe.

The trackway of a *Tyrannosaurus*-sized theropod with an enormous stride would decisively show that such animals were indeed capable of rapid sprinting. Thus far, however, the only known “theropod” trackways that suggest flat-out running were made by small to medium-sized forms (Thulborn, 1990; Irby, 1996). As noted by Paul (1988), this is merely negative evidence. However, as fossilized trails of large theropods continue to be discovered, if none of them suggests rapid locomotion, this negative evidence will become increasingly hard to ignore.

CONCLUDING REMARKS

Birds may be theropods, but “theropods” were not birds, and “the evolution of theropods was more than a ‘bird factory’” (Holtz, 1998, p. 1276). For more than 150 million years a diversity of large and small “theropods” constituted the dominant large-vertebrate predators of continental biotas. Throughout that time they showed considerable variability in adaptations for procuring and processing animal prey, with remarkable specializations of the jaws and hands. At the same time, however, their hindlimb features remained fairly conservative. Early in their history, theropods hit upon a successful style of striding, digitigrade bipedalism that they employed for the remainder of their successful reign.

Whether and how the origin of feathers relates to theropod locomotion depends on when in avian evolution these peculiar

structures first appeared, a matter that remains contentious (Chen *et al.*, 1998; Ji *et al.*, 1998; Unwin, 1998; Ruben and Jones, 2000; L. Witmer, personal communication). If feathers or “protofeathers” arose in non-volant, non-avian theropods, their initial function could not have been related to flight (Padian, 1998), and neither would there be any direct connection between feather origins and the typical striding bipedalism of “theropods.” On the other hand, bipedal locomotion freed theropod forelimbs from an obligatory connection with ground locomotion (Gatesy and Dial, 1996). The forelimb was therefore available to be pressed into service for an entirely new style of locomotion, whenever it was that feathers appeared or were elaborated in a fashion that made flight possible.

Thus one lineage of extremely specialized theropods, although they retained many of the features of theropod bipedal locomotion, nevertheless considerably modified the forelimb for flight. For these theropods, which survived whatever it was that eliminated their more conservative, ground-dwelling kin, the sky was literally the limit of their evolutionary potential.

ACKNOWLEDGMENTS

We thank Paul Maderson and Dominique Homberger for inviting us to participate in this symposium, and the National Science Foundation for travel grants to bring participants to the meeting. Matt Carrano, Kevin Middleton and two anonymous reviewers made helpful comments on the manuscript. Peggy Maceo, Kirk Johnson, Kieran Shepherd, Tony Fiorillo, and Raymond Coory provided us with useful footprint casts; Jana McClain and personnel of the Fort Wayne and other zoos helped in collecting prints of modern birds. Jim Hopson shared measurements of bird hindlimbs, and Jim Whitcraft produced some of our artwork. This research was supported by grants from the Dinosaur Society and the National Science Foundation to Farlow. This is University of California Museum of Paleontology contribution number 1723.

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APPENDIX 1

A list of the genera that represent clades and informal groups in Figures 4, 7, and 8 of this study. A given clade or informal group is not necessarily represented by the same genera in all graphs.

Basal theropods = *Eoraptor* and *Herrerasaurus*.
 Ceratosaurs = *Segisaurus*, *Procompsognathus*, *Dilophosaurus*, *Coelophysis*, *Syntarsus*, *Elaphrosaurus*, *Podokesaurus*, and *Ceratosaurus*.
 'Megalosaurs' = *Afrovenator* and *Eustreptospondylus*.
 Carnosaurs = *Sinraptor*, *Acrocanthosaurus*, *Allosau-*

rus, *Chilantaisaurus*, *Saurophaganx*, and *Szechuanosaurus*.

Basal coelurosaurids = *Compsognathus*, *Chuandongocoelurus*, *Deltadromeus*, *Dryptosaurus*, *Kiajiangosaurus*, *Ornitholestes*, and *Tugulusaurus*.

Dromaeosaurids = *Deinonychus* and *Sauornitholestes*.

Tyrannosaurids = *Maleevosaurus*, *Aublysodon*, *Gorgosaurus*, *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus*.

Ornithomimosaurids = *Ornithomimus*, *Struthiomimus*, *Dromiceiomimus*, *Gallimimus*, *Garudimimus*, and *Archaeornithomimus*.

Alvarezsaurids = *Avimimus* (questionably) and *Parvicursor*.

Oviraptorids = *Chirostenotes*, *Caudipteryx*, and *Ingania*.

Troodontids = *Sinornithoides*.

Struthioniformes = *Dromaius* and *Rhea*.

Large ratites = *Struthio*, *Rhea*, *Casuarus*, *Dromaius*, *Dinornis*, *Emeus*, *Euryapteryx*, *Megalapteryx*, *Anomalopteryx*, *Pachyornis*, and *Aepyornis*.

Galliformes (Fig. 7) = *Ammoperdix*, *Alectoris*, *Rollulus*, *Lophophorus*, *Gallus*, *Lophura*, *Phasianus*, *Chrysolophus*, *Afropavo*, *Pavo*, *Meleagris*, and *Callipepla*.

Coraciiformes = *Bucorvus*.

Gruiformes = Bustards: *Ardeotis*, *Otis*, *Eupodotis*; Seriemas: *Cariama* and *Chunga*; other gruiforms = *Grus*, *Gallirallus*, and *Psophia*.

Charadriiformes = *Charadrius*.

Falconiformes = *Sagittarius*.

Galliformes (Fig. 8) = *Phasidus*, *Numida*, *Guttera*, *Chrysolophus*, *Crossoptilon*, *Syrnaticus*, *Tragopan*, *Alectoris*, and *Francolinus*.

Ornithischians = *Lesothosaurus*, *Heterodontosaurus*, *Agilisaurus*, *Yandusaurus*, *Parksosaurus*, *Tenontosaurus*, *Iguanodon*, *Prosaurolophus*, *Saurolophus*, *Edmontosaurus*, *Anatotitan*, and *Corythosaurus*.

APPENDIX 2

Derivation of an equation relating injury threshold acceleration to body mass.

Alexander (1996) used animal mass and scaling theory to estimate how injury threshold forces depend on the mass of an animal. We expand upon this approach, which assumes that the critical factor in determining injury is the ratio of the impact force F to surface area A of the animal. This ratio is assumed to be equal at injury threshold for all animals. Thus:

$$F_2/A_2 = F_1/A_1,$$

where the subscripts 1 and 2 label two different animals. Because mass is proportional to the cube, and area to the square of the linear dimension,

$$M \propto A * L,$$

where A is area and L is the length of the animal. Therefore

$$A \propto M/L \propto M^{3/3}/M^{1/3} \propto M^{2/3}$$

Thus

$$F_2 = (A_2/A_1)F_1 = (M_2/M_1)^{2/3} F_1$$

Dividing both sides of the last equation by M_2 in order to obtain the injury threshold acceleration a_2 , we find

$$\begin{aligned} F_2/M_2 = a_2 &= (M_2^{2/3})(F_1)/(M_1^{2/3})(M_2^{3/3}) \\ &= (M_2^{-1/3})(F_1)(M_1^{1/3})/M_1^{3/3} \\ &= (M_1^{1/3})(F_1)/(M_2^{1/3})(M_1) \\ &= (M_1/M_2)^{1/3}(F_1/M_1) \end{aligned}$$

From accident data, Alexander (1996) estimated that the injury threshold acceleration F_1/M_1 for a 70-kg human is about 15g, where g is the acceleration of gravity, 9.8 m/sec². Substituting these numbers into the final expression above, we obtain the result

$$a_2 = (70/M_2)^{1/3}15g.$$