

Dinosaur Locomotion

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Many lines of evidence must be used to understand dinosaur locomotion: how extinct dinosaurs moved.

Introduction: What Evidence and Methods are Useful for Studying Dinosaur Locomotion?

Several lines of inquiry offer clues about how extinct dinosaurs moved. First, dinosaur body fossils reveal dinosaur ‘anatomy’, particularly limb bone and joint structure. In some rare cases, even soft tissues such as muscle fibres or claw sheaths are preserved. Second, fossilized footprints (called ‘trackways’) are distinctly identifiable for certain kinds of dinosaurs (**Figure 1**), offering direct evidence of locomotor behaviour in extinct dinosaurs.

The anatomy of dinosaurs reveals how the limb joints could (or could not) have moved. Muscle, tendon, and ligament attachment sites can often be located on bones and identified by comparison with living animals. A caveat with anatomical analyses is that the extent or size of many such soft tissue structures are unknown and must be estimated within reasonable bounds. Likewise, dinosaur tracks show how the feet were placed on the substrate relative to one another, what the shape of the feet (with bones and soft tissues) was like, and how much distance a dinosaur foot covered with each step. A caveat with footprint analyses is that although the footsteps are clearly preserved, motions of more proximal joints (e.g. the hip) are harder to infer.

When combined, data from dinosaur anatomy and trackways are much more informative than either is alone. From the form of the footprints and an understanding of

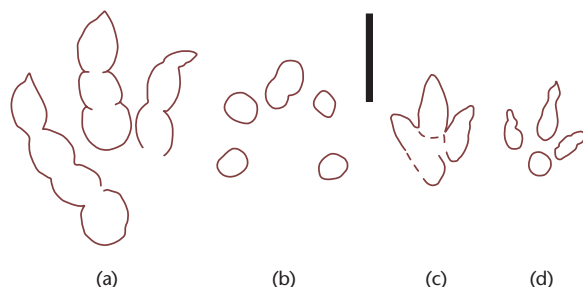


Figure 1 Fossil footprints from different Jurassic dinosaurs. Track names and possible dinosaur trackmakers: (a) *Megalosauripus* (large theropod), (b) *Ravatichnus* (sauropodomorph?), (c) *Therangospodus* (wide-toed theropod), and (d) *Dinehichnus* (ornithischian). Scale bar is 20 cm. From Lockley MG (1998) *The vertebrate track record*. *Nature* **396**: 429–432.

Introductory article

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dinosaur anatomy, it is possible to infer what kind of dinosaur made a given track. Other anatomical information can be added, such as how the limb joints could have allowed that kind of dinosaur to make those footprints – in other words, what sort of posture or limb orientation that dinosaur might have been using when it made those tracks. Methods such as biomechanical computer models, animation, comparisons with living animals, and statistical analyses of body and track dimensions can be integrated to obtain a richer picture. Together, these data are most interesting and meaningful when integrated in a ‘phylogenetic’ (evolutionary or historical) perspective (**Figure 2**), reconstructing how dinosaur locomotion evolved. This kind of multidisciplinary approach tells us a lot about how Mesozoic dinosaurs moved.

Historical Perspective

When Richard Owen coined the term ‘dinosaur’ in 1841, he envisaged this new group of reptiles as standing and moving more like mammals and birds than like ‘typical’ sprawling reptiles. He came to this conclusion by studying the limb anatomy of dinosaurs: the joints seemed to keep the feet close to the midline of the body (erect posture) and restricted most limb movements to a plane parallel to the body (parasagittal gait). For example, the head of the femur (thigh bone) sticks straight into the hip socket at a right angle to the shaft, requiring the thigh to be held close to the body. This conclusion was upheld by later discoveries of more dinosaur fossils, and by the recognition of dinosaur trackways (**Figure 3**).

None the less, our scientific view of dinosaur locomotion has changed significantly since the 1800s. Some early depictions of dinosaurs reverted to a more ‘sluggish reptile’ paradigm for reconstructing stance and gait, despite the contrary evidence, and this perspective eventually became entrenched in the scientific and public mind for many decades. Dinosaurs were frequently depicted dragging their tails and moving with a more sprawling posture, even though fossil tracks and anatomy showed that dinosaurs did not typically do this. With exceptions, this view held from the late 1800s to the later 1900s.

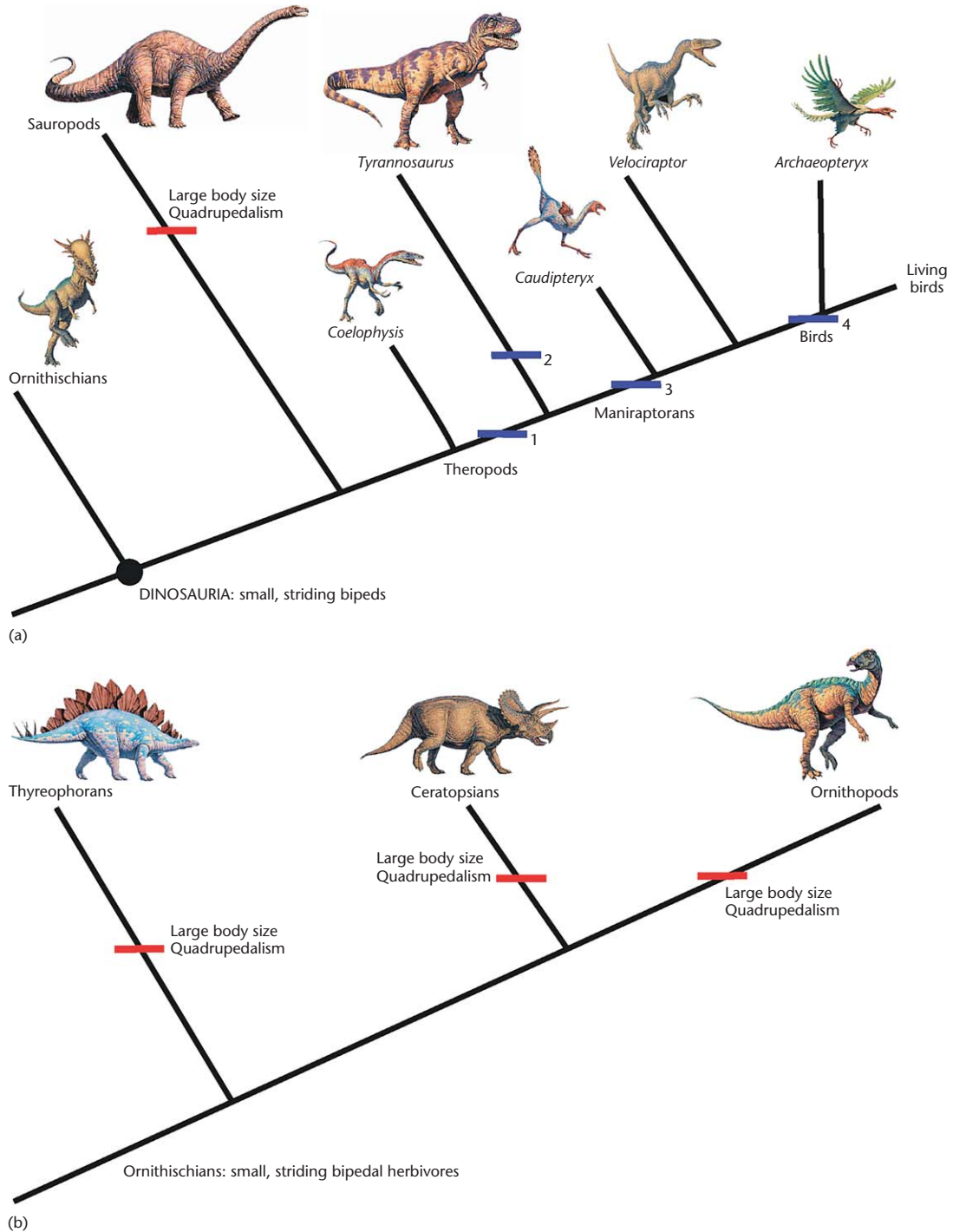


Figure 2 Evolution of dinosaur locomotion. Broad changes in locomotor function are plotted on to these 'phylogenies' of dinosaurs. (a) Dinosaur phylogeny showing the divergence of dinosaurs into ornithischians, sauropods and theropods, and a few key changes within these lineages. In theropods, '1' indicates the origin of feathers, a furcula (wishbone), and other preflight specializations; '2' indicates the secondary increase of size in tyrannosaurs and a concomitant reduction of running ability; '3' indicates the evolution of more preflight features (elongate feathers and large sternum or breastbone), a more crouched pose, and a reduction of body size; and '4' indicates the origin of true powered flight in birds, and subsequent elaborations of terrestrial and aerial locomotion. (b) Ornithischian phylogeny focusing on the three or more independent origins of large size and quadrupedalism. All colour dinosaur illustrations are from Joe Tucciarone (<http://members.aol.com/Dinoplanet/dinosaur.html>), used with permission.

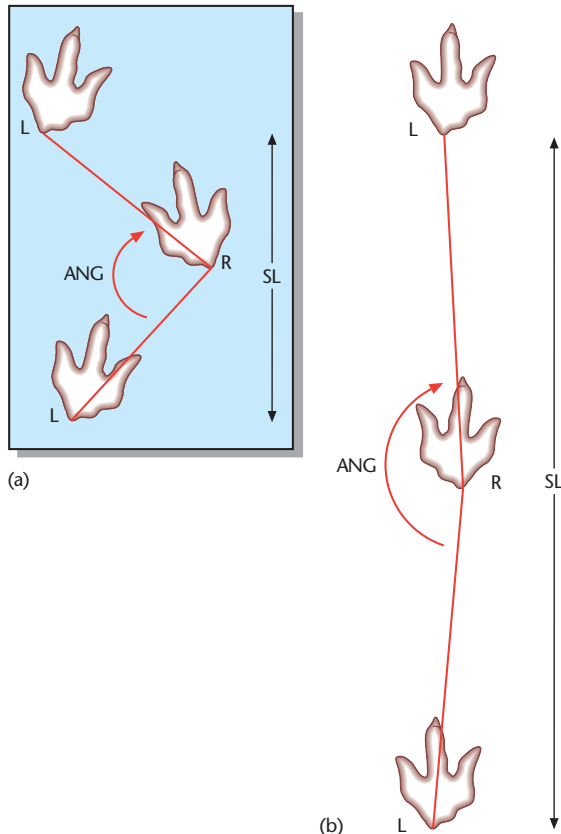


Figure 3 Trackway evidence for walking and perhaps running. A 163-million-year-old trackway of a medium-sized theropod (carnivorous) dinosaur from England, from Day *J et al.* (2002). *Nature* 415: 494–495. The animal was walking slowly (a), then sped up perhaps to a run (b), and then later slowed down. Left (L) and right (R) footprints can be seen, and the stride length (SL) and angulation (ANG) can be measured. Notice how the SL and ANG increase in the faster tracks in (b). This might have been a running gait, but was not an extraordinarily fast one, and is not the fastest one known (see **Table 1**; this trackway is from the second theropod in that list).

Like most aspects of dinosaur palaeontology, the study of dinosaur locomotion went through a renaissance in the late 1960s–1970s. A more mammal or bird-like model of dinosaur locomotion gained dominance. Specializations of dinosaur anatomy became interpreted as evidence for an active lifestyle or even ‘endothermy’ (‘warm-bloodedness’). In some cases, this revision was taken to a ‘supercharged mammal’ extreme, arguing that dinosaurs were as fast as or faster than many mammals or birds regardless of their size. Soon, huge dinosaurs appeared in movies running quickly to chase humans, the *Jurassic Park* films being the obvious example. Some palaeontologists continued to cite evidence that seemed to support this notion.

Today our view of dinosaur locomotion falls between the ‘sluggish reptile’ and ‘supercharged mammal’ extremes. Biomechanics has shown that some of the more extreme activities previously attributed to dinosaurs, such as

extremely fast running by larger dinosaurs, are not feasible given what we know or can infer about dinosaur anatomy and physics (**Figure 4**). None the less, trackways and anatomical data have revealed that dinosaurs were far from being ‘lazy lizards’ (**Figure 3**). Smaller dinosaurs could run relatively quickly, and most moved in ways similar to living birds or mammals. The most revolutionary advance has been the acceptance that birds evolved from small, bipedal, nonflying dinosaurs.

Dinosaur anatomy and trackways reveal some characteristics that are ‘ancestral’ (primitive) for reptiles, such as large tail muscles that propelled the thigh through wide arcs during locomotion. Other features were unique to extinct dinosaurs, such as the strange, superficially bird-like pelvic bones of ornithischian dinosaurs. Still others were ‘derived’ (specialized) conditions inherited by birds (**Figure 2**), such as the bipedal stance and erect posture primitive for all dinosaurs. In some cases, dinosaurs show ‘convergent evolution’ with mammals or other animals, including other groups of dinosaurs. The ornithischian and sauropodomorph dinosaurs came from bipedal ancestors, but both reverted to quadrupedalism as their size increased. Mammals and dinosaurs (including their bird descendants) are alike in that they use an erect posture and parasagittal gait (swinging the limbs close to the body rather than sprawling). Specific examples of contemporary thought about dinosaur locomotion follows.

Current Conclusions and Debates

Dinosaur speeds and gaits

How fast could certain dinosaurs move? What was the fastest ‘gait’ (locomotor mechanism such as walking or running) they could use? **Table 1** shows estimates for speeds of several dinosaurs based on fossil trackways. Alexander (1989) and Thulborn (1990) (see Further Reading) explain in more detail how these estimates are made. Briefly, the footprint length is used to estimate the hip height of an animal (usually as footprint length times four, which is a fairly reasonable number for many dinosaurs). The hip height and stride length, or distance between two successive falls of the same foot, are used in an equation to calculate speed:

$$\text{Speed} = 0.25(\text{acceleration due to gravity})^{0.5}(\text{stride length})^{1.67}(\text{hip height})^{-1.17}$$

This speed is in metres per second, and because there is no sound reason to suspect that Earth’s gravity was any different in the Mesozoic, gravity can be set at 9.81 m s^{-2} . The speed estimation equation was obtained by measuring the speeds, stride lengths and hip heights of many walking and running extant animals; hence it should have a complete enough sample size to provide rough estimates of dinosaur speeds, but no better than rough estimates.

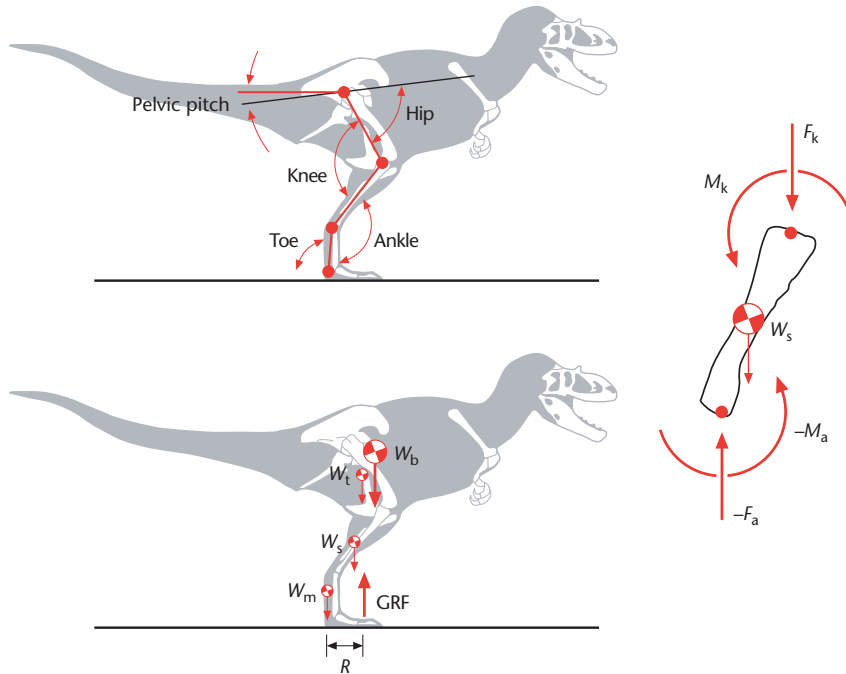


Figure 4 Biomechanics of dinosaur locomotion (from Hutchinson and Garcia, 2002). (a) A tyrannosaur is shown at the midpoint of support during running, in a pose with particular pelvic, hip, knee, ankle and toe angles. (b) In any pose one can calculate the forces (F) and moments (M ; rotational forces equal to a force F times a moment arm R). The weights of the body segments directed downwards (W) and the ground reaction force (GRF) pushing up against the foot are included, for example. To support its body while running at 20 m s^{-1} (72 kph) in the pose shown, a *Tyrannosaurus* would have needed about 86% of its body mass as leg muscles. This is far more than the body could have contained; thus, large tyrannosaurs and other large dinosaurs presumably had to move more slowly, perhaps $5\text{--}11 \text{ m s}^{-1}$ at most (18–40 kph), and used a more upright pose, not such a crouched pose.

Table 1 Trackway data for dinosaurs, using the formula of Alexander to estimate speeds (1989; see text)

Dinosaur Group	Footprint length	Stride length	Hip height	Estimated speed	Kph
<i>‘Running’ dinosaurs:</i>					
Theropod	0.28	4.92	1.12	9.8	35
Ornithopod	0.86	9.25	3.44	7.6	27
Theropod	0.29	5.66	1.16	11.9	43
Theropod	0.48	5.65	1.92	6.6	24
<i>Walking dinosaurs:</i>					
Sauropod	0.76	2.5	3.04	1.0	4
Sauropod	0.38	1.6	1.52	1.1	4
Theropod	0.53	3	2.12	2.0	7
Ornithopod	0.30	1.6	1.20	1.9	7

All measurements are in metres except that speed is listed in metres per second, and then kilometres per hour (kph) in the last column. Note that these are very rough estimates with a wide potential error. From: Thulborn (1990); Irby GV (1996) Paleontological evidence for running dinosaurs worldwide. *Museum of Northern Arizona Bulletin* 60: 109–112; and Day J *et al.* (2002; see Figure 3 caption).

Although trackway speed estimates have been formulated with equations based on measurement of living animals and their speeds, as mentioned above these equations can be off by a factor of two or so. Researchers are working on how to refine these techniques to obtain better

speed estimates for living and extinct animals’ tracks. Because it is often difficult to determine exactly what species of dinosaur made a given trackway, it is hard to say exactly which dinosaurs could run, particularly the larger ones. Whether some large dinosaurs could jump, gallop, rear up

on two legs, or perform other seemingly strenuous activities are interesting questions that are not yet resolved.

Many smaller dinosaurs were competent bipedal runners. Fossilized trackways of smaller dinosaurs suggest that some smaller dinosaurs, even up to 1–2 tonnes of body mass, could run at least as fast as the fastest humans (perhaps over 10 m s^{-1} ; 22 mph or 36 kph). However, these speed estimates are notoriously imprecise and must be taken as rough approximations. None the less, the available trackway data (Table 1) demonstrate that small- to medium-sized bipedal dinosaurs could run fairly quickly in absolute terms. Such trackways have step lengths that are very long relative to the length of the footprints – too long to have been made by slower walkers (Figure 3). This concurs with the anatomical evidence: smaller dinosaurs have relatively longer, more slender limbs that seem well suited for taking quick, long steps.

Larger dinosaurs were more limited in their scope of potential locomotor activities. It is unlikely that huge dinosaurs such as *Tyrannosaurus*, *Triceratops* and particularly the sauropod dinosaurs could run quickly, if they could run at all. Although there are some striking anatomical similarities between some larger dinosaurs and fairly large, fast-running living animals, biomechanics tells us that very large animals must move relatively slower than their smaller relatives. This is because of ‘scaling’: the changes of biological properties with body mass. The forces that an animal’s muscles can generate to support the body during a given activity increase about 2/3 as fast as body weight increases. The reason for this scaling is that muscle force is dependent on cross-sectional area, which scales as a linear dimension squared. Body weight is a linear dimension cubed; thus area scales as mass^{2/3}. Thus, very large animals are relatively less able to generate the forces needed to support their own weight during movement. They must slow down to avoid falling, straining muscles, or breaking bones and tendons. Eventually, they become unable to use the broad range of locomotor activities that smaller animals can do – elephants do not gallop like racehorses or leap like gazelles.

This principle should apply to dinosaurs. Table 2 shows a few examples of the body masses of living animals and dinosaurs. The larger sauropod dinosaurs, up to perhaps 50–80 tonnes of mass, were surely restricted to slower locomotion, as their trackways record (around $1\text{--}2 \text{ m s}^{-1}$; $\sim 5 \text{ mph}$ or 7 kph). Yet the old idea that sauropods had to be aquatic to support their weight has been overturned by abundant anatomical and trackway evidence.

Tyrannosaurus, *Triceratops* and similar dinosaurs at around 6 tonnes of mass were presumably faster than sauropods (Figure 4), but still not the skilled runners that younger and smaller dinosaurs seem to have been. Because there is no evidence that gravity was appreciably different in the Mesozoic era, we can assume that large dinosaurs were still limited by their size and weight. In contrast, smaller dinosaurs had a wider locomotor repertoire – including

Table 2 Body masses of large extant animals and dinosaurs

Animal	Mass (kg)
Giraffe	1200
Hippopotamus	1600
Rhinoceros	3600
African Elephant	6300
<i>Iguanodon</i>	2500
<i>Triceratops</i>	4000
<i>Tyrannosaurus</i>	7200
<i>Stegosaurus</i>	7900
<i>Diplodocus</i>	13 000

Masses are rounded to the nearest 100 kg and are for a ‘typical’ large adult. Dinosaur masses were estimated with 3D volumetric computer models. From Henderson DM (1999) Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology* 25: 88–106.

flight in certain small, specialized spawn of dinosaurs. Dinosaur anatomy concurs with these conclusions: larger dinosaurs were more bulky and less well built for running than their smaller relatives.

There is no evidence that any extinct dinosaurs hopped. Although some bipedal dinosaurs vaguely resembled kangaroos (long tails and legs), their anatomy is more similar to modern striding bipeds such as humans or birds, rather than hoppers. Furthermore, there are no clear tracks of hopping dinosaurs; all known tracks from the Mesozoic are from striding bipeds. Many living birds do hop, but this is a specialized behaviour that has evolved a few times in recent birds, not a legacy of extinct theropods.

Almost all Mesozoic dinosaurs were land-dwelling, not amphibious or wholly aquatic. Only a few extinct forms (e.g. the loon-like Cretaceous bird *Hesperornis*) show any evidence for good swimming ability. Although some of the earlier depictions of dinosaurs placed them in swamps, lakes and rivers, later and more thorough studies conclusively established that Mesozoic dinosaurs were better suited to life on land. The thousands of tracks known for a wide variety of dinosaurs show that they moved frequently for long distances, and many lived in arid regions. Gut contents of herbivorous dinosaurs and wear patterns on their teeth indicate that these dinosaurs generally ate tough plants on land, not soft aquatic plants. Webbed toes are known in a few extinct birds, but in none of the ‘duckbilled’ ornithischians, which instead had hoof-like claws. Other details of fossil anatomy, such as well-defined joints, hollow bones, long limbs and large muscular attachments, reveal that dinosaur limb structure is similar to many land-dwelling animals, lacking clear specializations for an amphibious lifestyle. While dinosaurs surely did not avoid water, they were not aquatic, like living hippos, ducks, or crocodiles, but were more terrestrial, like living hoofed mammals and ground birds.

Locomotor evolution

The first dinosaurs were small, erect, bipedal (moving on two legs) animals that rarely, if ever, moved on all fours. The closest cousins to dinosaurs (*Lagosuchus* or *Marasuchus* and *Lewisuchus* or *Pseudolagosuchus*), which have small forelimbs, long hindlimbs and hinge-like joints, much like the earliest dinosaurs, offer anatomical support for this idea. Furthermore, most fossil dinosaur tracks from the first dinosaurs were made by striding bipedal animals.

As later dinosaurs increased in body size, some of them reverted to a quadrupedal stance. This happened in the common ancestor of all enormous ‘sauropod’ dinosaurs such as *Apatosaurus* and *Brachiosaurus*, as well as in at least three independent lineages of ‘ornithischian’ dinosaurs: the armoured ‘thyreophorans’, the horned ‘ceratopsians’, and the duckbilled ‘ornithopods’ (Figure 2).

Anatomical and trackway evidence signals that large size and obligate or facultative quadrupedalism coevolved in herbivorous ornithischian and sauropod ancestors. Early members of these lineages were smaller and predominantly bipedal; then, as size increased more quadrupedal specializations evolved. This pattern is matched by evidence from quadrupedal tracks. The ornithopods such as *Tenontosaurus* seem to have retained some bipedal abilities, judging from their short forelimbs and some bipedal trackways; yet anatomical evidence (hoof-like hands) and other trackways show that ornithopods used quadrupedalism as well.

All ‘theropod’ (carnivorous) dinosaurs retained the ancestral condition of striding bipedalism, and birds inherited this condition from their theropod forebears. Although a few tracks of theropod dinosaurs standing or moving slowly on four limbs have been tentatively identified, there are hundreds of theropod trackways made by bipeds. Likewise, the forelimbs of theropod dinosaurs have no specializations for terrestrial locomotion, and in some cases are vestigial and clearly useless for locomotion (e.g. *Tyrannosaurus*, *Caudipteryx*, or among birds, ostriches) or specialized for other uses (grasping food items in most theropods, or wings used for flight in birds). Bipedalism is not new to birds; it is an ancient holdover from the ancestors of all dinosaurs, preserved in theropod dinosaurs and their avian descendants. Birds have retained many other ancient traits that early dinosaurs had, such as hollow bones and three main digits on the feet.

Dinosaur locomotion evolved: early dinosaurs moved differently from later lineages. Although the first dinosaurs were competent striding bipeds, and trackway evidence suggests that this basic locomotor mechanism changed little in most bipedal lineages, anatomical evidence indicates that subtle changes in locomotion evolved. In the theropod dinosaurs, for example, bipedalism was maintained, but shortening of the tail, lengthening of the limbs and changes of joint structure, muscle attachments and body mass distribution indicate that the patterns of limb motion in

theropods changed markedly on the line to birds. Early theropods such as *Coelophysus* (Figure 2) moved with a more upright pose, keeping their legs straighter than birds do today. Theropods that were closely related to birds, such as *Caudipteryx* and *Velociraptor*, had shorter tails and longer limbs; hence, perhaps they moved more like birds, with a more crouched pose than their ancestors. This pattern of change seems to have continued gradually even after birds evolved. The earliest birds, such as *Archaeopteryx*, probably moved slightly differently than the birds of today. After the most recent common ancestor of all living birds evolved, birds diverged into many different terrestrial locomotor modes, from the extraordinary running abilities of ostriches and emus to the waddling of penguins.

Flying dinosaurs?

Birds, the living descendants of extinct dinosaurs, evolved flight. Although there is no trackway evidence that demonstrates this, the anatomical evidence speaks clearly. Feathers first appeared in nonflying dinosaurs; hence, they were originally not crucial for locomotion. Certain close relatives of birds within the theropod dinosaur group evolved the ‘furcula’ (wishbone), large ‘sternum’ (breastbone), and longer arms with reconfigured joints that allowed them to flap their arms much like a flying bird does. What this motion was used for prior to the evolution of flight is controversial (e.g. gliding from the trees down or from the ground up; or part of a ‘predatory strike’ used to grab prey; or climbing; or even wing-assisted running), but some key components of the ‘modern’ bird flight stroke evolved out of the context of flight.

Birds coopted feathers for use in flight. Feathers, like many other features, evolved in a stepwise pattern within theropod dinosaurs, especially the ‘maniraptorans’ (*Velociraptor*, *Caudipteryx*, birds, and their most bird-like relatives). A decrease in body size and an increase in relative wing and forelimb muscle size allowed the most recent ancestor of all flying birds, and its descendants such as *Archaeopteryx* and the predecessors to living birds, to generate the thrust and lift needed to remain aloft. This novelty opened new evolutionary possibilities for birds that thousands of the species enjoy today, but many components that allow flight were assembled and modified in theropod dinosaurs well before the origin of birds and their flight. Indeed, very recent fossil finds suggest that perhaps some dinosaurs very closely related to birds (such as the feathered maniraptoran *Microraptor*) might have flown or glided, but this is controversial.

Flight performance continued to evolve long after the origin of flight. Terrestrial locomotion evolved along many paths in dinosaurs before and after the origin of birds, but flight also evolved within birds after the first birds took to the skies. Some modifications of the flight apparatus, such as an increase in muscle size and leverage, evolved within

birds and likely improved flight performance. The flight acrobatics of the living swallows, swifts and hummingbirds, or the underwater flight of penguins, are extreme examples of this evolutionary divergence. These marvels were not possible in early extinct birds such as *Archaeopteryx*, which were probably poor fliers by comparison.

Problems for Future Work

The ultimate goal of research on dinosaur locomotion is to be able to reconstruct the precise motions of a given dinosaur in any activity, based on solid methods and evidence with minimal assumptions. Reconstructing how that locomotor pattern evolved along dinosaur lineages could be extrapolated from such studies of multiple animals. Yet despite the wealth of trackway and anatomical evidence available, we do not know how any one extinct dinosaur moved. There are too many unknown factors, such as body mass, muscle anatomy, nervous control and physiology for us to reliably animate any extinct dinosaur based on actual or inferred data. Although animations of dinosaurs in movies and elsewhere may seem convincing, they generally assume more than they demonstrate. Analogies with living animals are limited, and difficult to test even indirectly. More information on how living animals move, and biomechanical studies that model the locomotor dynamics of dinosaurs, will surely shed more light on this issue. More complex questions, such as how dinosaurs changed gait from walking to running, could also be addressed.

Because we know little about the exact movements that dinosaurs made, it is hard to reconstruct how the terrestrial and aerial locomotion of birds evolved. Anatomical features allow some simple inferences to be made, when reasonable links between anatomy and locomotor function are known. In order to piece together the sequence of assembly and modification of bird locomotion, we need stronger integration of many lines of evidence in a phylogenetic context.

Likewise, many dinosaurs evolved unique features separately from birds that must have been significant for their

locomotion. Ornithischian dinosaurs had modified pelvic bones that are vaguely similar to bird hips; the significance of this anatomy for their locomotor function remains somewhat unclear. Again, much more can be learned from biomechanics, anatomy, trackways and evolution.

How did locomotion develop in dinosaurs from hatchlings to adults? Some studies suggest that small hatchlings of some quadrupedal dinosaurs such as ornithomorphs were initially bipedal, and then attained their more quadrupedal stance later in life. How transitions like this occurred during the growth of an individual remains poorly understood, and could have implications for dinosaur ecology, parental care and evolution.

While these obstacles are considerable, the questions are still interesting and could provide general insights into locomotor function in animals in general. Integrative approaches combining methods and evidence from anatomy, trackways and biomechanics or computer modelling should resolve some pieces of these mysteries, continuing to shed light on the ways in which dinosaurs moved.

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