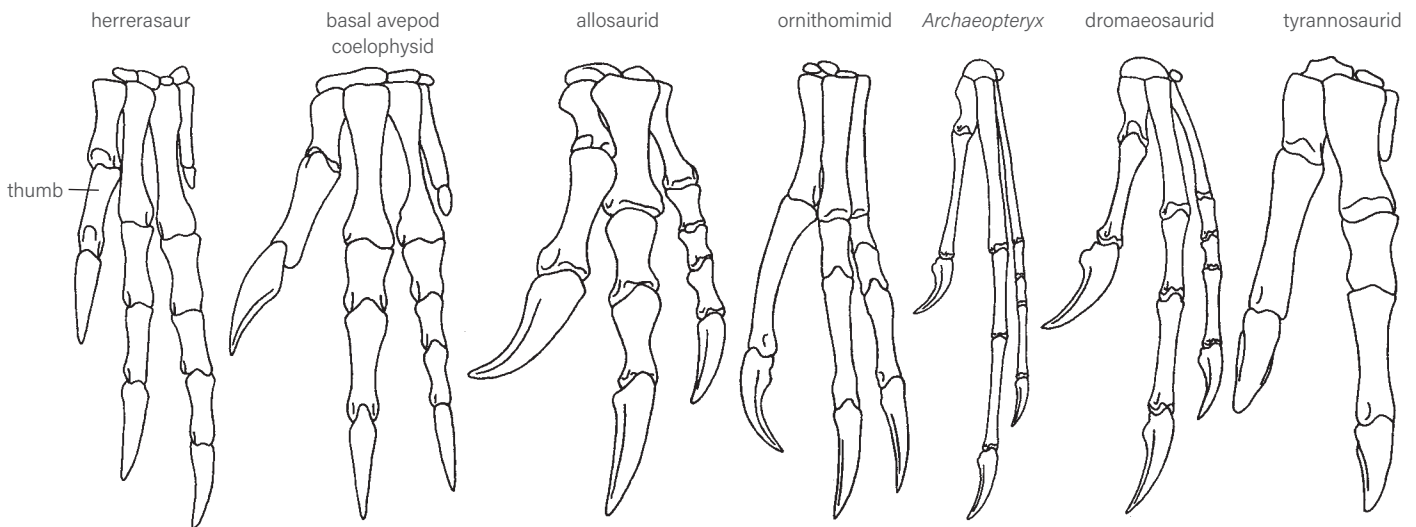


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Predatory dinosaur hands

and the hand was very nearly or completely tridactyl by the avetheropods. Although considerable movement was possible, the dinosaur's fingers were not as flexible and supple as those of humans. As some avepods evolved toward the avian condition, finger flexion was further reduced to better support enlarging hand feathers. The fingers were padded by slender pads that bulged some at the joints. Avepod arms underwent a wide array of radical evolutionary changes in differing clades. Four times among predaceous nonaveairfoilans, in ceratosaurs–abelisaurids, carcharodontosaurids, *Gualicho*, and tyrannosaurids, the arms became reduced down to limited if any functionality. In each case, the nature of the alterations was very distinctive in accord with the evolutionary derivation of the group, with the fingers being reduced to two in *Gualicho* and tyrannosaurs. Severe arm reduction is also typical of neoflightless birds. Also sporting short arms were alvarezsaurids, but in this case they were constructed like those of body builders, probably for digging, with the thumb a massive digit tipped with a big broad claw. The other fingers were very atrophied to the point of being of limited or no use, in some only two fingers were left, and in others essentially only the thumb was left, making them the only known one-fingered dinosaurs. The arms of the nonpredaceous ornithomimosaurids and therizinosaurs became long, large clawed, and adapted for feeding or defense. The real upscaling of dinosaur arms occurred in aveairfoilans, as they were enlarged for climbing and increasingly adapted for flight, until the hand was the fused, flattened, clawless primary feathers support of birds. Pterosaur and bat wrists and hands could hardly be more different, including super elongated fingers to support their wing membranes, which are also attached to the legs.

In the hindlimb the ilium plate of the upper pelvis started out small in basal dinosauriforms, so their thigh muscles were rather narrow. The plate got somewhat

larger and the thigh correspondingly broader in the early theropods and avepods and continued to expand in size until it was large in most averostrans, increasing the breadth, bulk, and power of the thigh muscles in the manner inherited by birds. Among the biggest plates seen were on the extra-fast ornithomimids and tyrannosaurs, and also are seen in birds that spend a lot of time on the ground. The upper edge of the ilium was and is a major visible contour in living dinosaurs. Also expanding the size of the leg muscles was a large, forward-projecting cnemial crest at the knee end of the tibia. This crest helps anchor the big, bulging drumstick of muscles ensheathing the upper shank, which many enjoy when consuming fowl. This big bundle of muscles operates the nearly muscle-free feet via tendons.

It is difficult to restore the precise posture of dinosaur limbs because in life the joints were formed by thick cartilage pads similar to those found on store-bought chickens, which are immature. That dinosaurs normally retained thick cartilage pads in their limb joints throughout their entire lives, no matter how fast or big they became, is a poorly understood difference between them and adult birds and mammals, which have well-ossified limb joints. The manner in which dinosaurs grew up and matured may explain the divergence. In terms of locomotory performance, cartilage joints do not seem to have done dinosaurs any more harm than they do big running birds that still have cartilage joints when fully grown but not yet mature, and they may have had advantages in distributing weight and stress loads. The poor ossification of dinosaur limb joints hinders restoring their posture; even so, some basics can be determined.

The dinosaurian cylindrical hip socket did not allow the legs to sprawl out to the sides in most dinosaurs. As a result, the limbs were close to vertical in the fore-and-aft

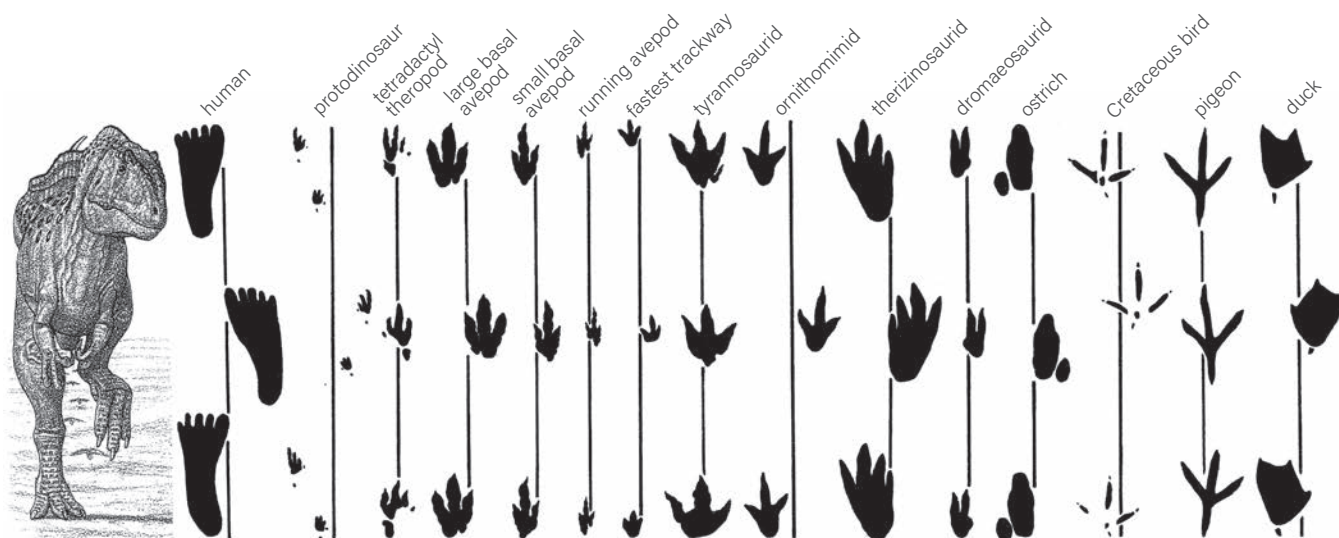
plane. The correspondingly narrow-gauge fossil trackways record the hindprints falling on the midline or very close to it, like in birds and erect-limbed mammals, humans included. Pterosaurs with ball-and-socket hip joints were more variable in limb posture as their trackways affirm; bats are sprawlers. This does not, however, mean that the erect legs of dinosaur-birds work in a perfectly vertical plane; that happens in few if any animals. The femur is somewhat everted outward, especially when swinging forward to clear the gut, all the more so when the abdomen was filled with a recent big kill. The knee was correspondingly bowed out somewhat, the opposite of humans in which it is bowed in a dash—we do not have bellies in front of our knees to clear. The shank sloped inward some to the slightly inward-bent ankle, and the upper foot was vertical or a little sloped outward in fore or aft view.

There was a notable exception to strictly erect avepoid legs. The small, early microraptorine dromaeosaurs sported extra wings on their hindlimbs that, in order to work, required the legs to splay horizontally out to the sides. To accommodate that, the femoral head was rounded and the hip socket partly closed off and more upwardly oriented than in the rest of the dinosaurs. This reversion to the protodinosaur condition allowed the legs to operate in both the vertical and horizontal planes and in between. With no other dinosaurs having leg wings, this was not to be repeated.

In the fore-and-aft plane all predatory dinosaurs, like most terrestrial tetrapods, have had strongly flexed hip, knee, and ankle joints that provided the springlike limb action needed to achieve a full run, in which all feet were off the ground at some point in each complete step cycle. In addition, the ankle remained highly flexible, allowing the long foot to push the dinosaur into a ballistic stride. This was true of even the most gigantic 10 tonne avepods; they did not have the columnar limbs of sauropods or elephants that prevent them from running, rather, their limbs were

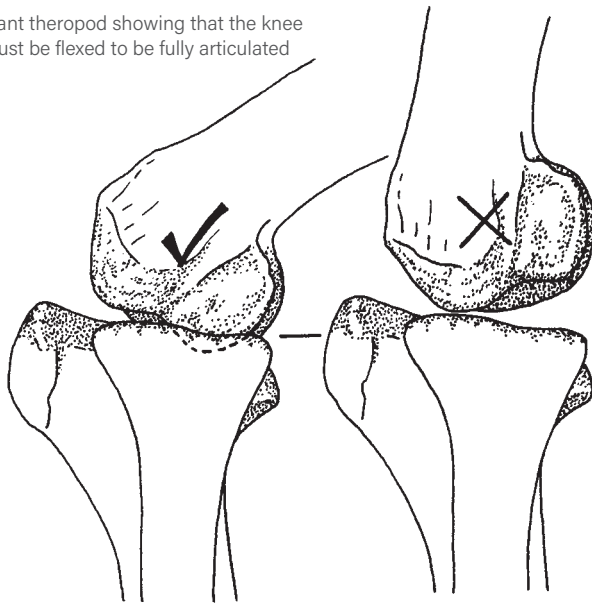
similar to the fairly flexed limbs of giant running rhinos. The knee joints of dinosaurs with flexed limbs were not fully articulated if they were straightened. Humans have vertical legs with straight knees because our vertical bodies place the center of gravity in line with the hip socket. In bipedal dinosaurs, because the head and body were held horizontally and were well forward of the hips, the center of gravity was ahead of the hip socket even with the long tail acting as a counterbalance, so the femur had to slope strongly forward to place the feet beneath the center of gravity. As a result, the theropod femur did not retract much past vertical at the end of the limb stroke even when running at top speed, unlike mammals, including humans, in which the femur swing further aft. This arrangement is taken to an extreme in short-tailed birds, whose femur is nearly horizontal when they are walking in order to place the knees and feet far enough forward; when running, the femur of birds swings more strongly backward, but not to full vertical, to fully utilize the power of the big thigh muscles. The theropod knee could be nearly folded up. Like the elbow, the door-hinge-like roller ankle had nearly 180° of motion from folded to straight. Mesozoic trackways show avepods sometimes walking pigeon toed, sometimes not. The walking gait of the narrow-bodied beasts would have been smoothly striding. The exception would seem to be the fat-bellied therizinosaur, but their trackways show the same narrow-gauge gait as the other theropods rather than the extremely pigeon-toed waddling of plump-bodied geese. There is no anatomical reason to think any dinosaur hopped, and not a single of the enormous sample of trackways shows otherwise.

As per the dinosaur-avian norm, theropod feet are digitigrade like cats and dogs, with the ankle held clear of the ground while the entire weight-bearing toes are pressed to the ground. In plantigrades, as per pterosaurs, bats, bears, and people, the entire foot up to the ankle rests flat; in

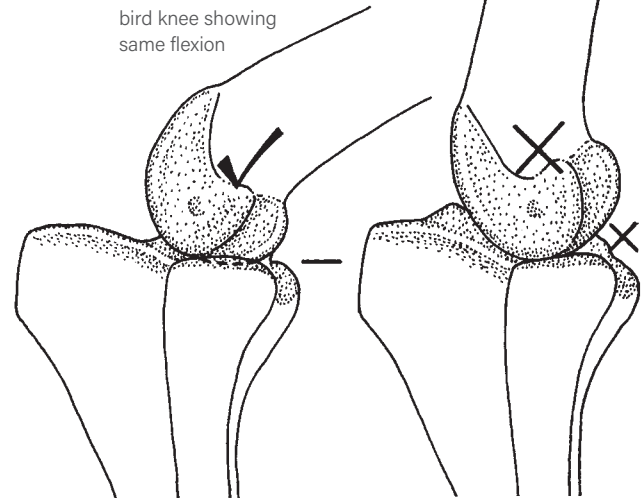


Predatory dinosaur and other trackways

giant theropod showing that the knee must be flexed to be fully articulated



Knee flexion



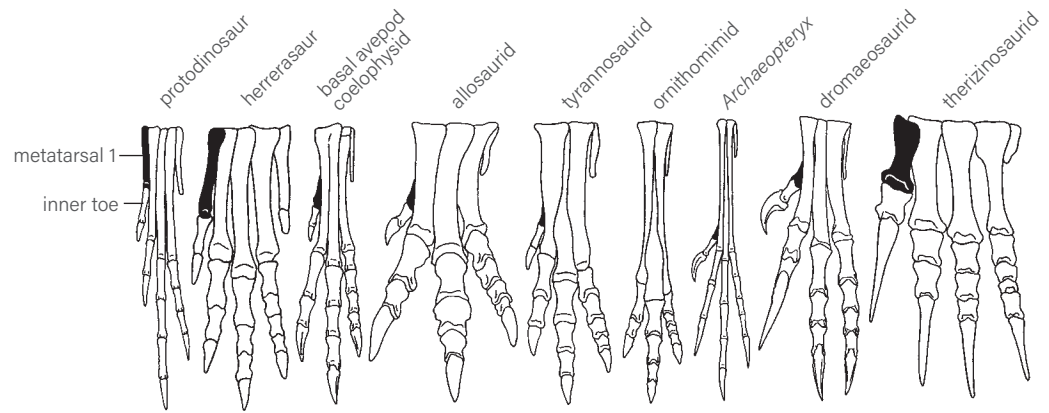
unguligrades only the tips of the toes make ground contact, as in horses and deer. The ostrich is an odd bird in that only the front sections of the toes are on the ground. The load-bearing toes, four in protodinosauroids and first theropods and therizinosaurs, three in most dinosaurs, two in sickle-clawed deinonychosaurs, are underlain by modest padding, which became relatively broader as did the toe bones with greater size and with larger padding under the main base of the foot. The details of this padding are regularly recorded, with some distortion, in fossil footprints. The three central toes of avepods are usually, but not always, not widely divergent until birds, when they splay out much more. In the standard tridactyl and less common bidactyl avepods, the inner toe is clear of the ground or close to it. Usually it subparallels the other toes, and it can be wondered why the hallux was retained, it not appearing to have much if any of a function. It obviously did have functions in peculiar *Balaur*, being enlarged and hyperextendable, bearing a big claw as a weapon, and perhaps being used for climbing. In more arboreal and aerial airfoilans, the hallux became more reversible and distally placed for climbing and perching as well as handling prey items. In some birds the hallux is fully reversed and all the way down the foot, giving it full contact with the ground as well as excellent perching purchase. Even more extreme are those birds that have also reversed the fourth toes, such as roadrunners and woodpeckers: these are sort of tetradactyl. At the opposite extreme are those avepods, often fleet runners, that have entirely lost the inner toe; these include the ornithomimids and their mimics the ratites. These are the most truly tridactyl avepods, matched in this particular point by the big ornithopod dinosaurs and three-toed perrisodactyl ungulates like rhinos. With just two toes, ostriches are closet to two- and one-toed ungulates. The second toes became weaponized in deinonychosaurs, which

may or may not include *Balaur*, and a few birds with an enlarged claw, the saber claw of the cassowary being the premiere living example of that. Paid very little attention is the outermost toe, five, which is reduced to a mere short splint immediately below the ankle, which was retained in Mesozoic avepods other than some birds to the end of the period despite it having no apparent use. Perhaps it provided some leverage to the foot-extending muscles in the drumstick. The little bone is lost in most birds, perhaps to save as much extraneous weight as possible among the fliers—in contrast, the outer toe of early pterosaurs is a long multisection splint that helps support the trailing edge of the membrane between the legs; in the rest of the pterosaurs it too is reduced to a splint of obscure function if any. Pterosaurs had four complete toes, bats keep all five.

The speed at which a fossil trackway was laid down can be approximated—with emphasis on the approximated—by correlating the stride length of the trackway with the length of the articulated leg from the hip joint to the base of the foot. The latter can be estimated from the length of the foot, which is four to one in a surprising array of animals—humans and theropods of all sizes and most types included. Mammals and birds of all sizes tend to walk at speeds around 3–7 km/h (average 3 mph). Note that squirrels will bound rapidly, halt for a moment, then bound some more, stop, and so on. Humans and their dogs typically move at a similar overall pace, as do elephants. This consistency is because the cost of locomotion per given distance scales closely to available aerobic power as size increases, so being big does not provide a major advantage. A typical walking speed recorded by trackways of tridactyl dinosaurs is around 5–7 km/h (4 mph).

Perhaps the fastest of dinosaurs are ostriches, which are credited with speeds of over 60 km/h (over 40mph); among Mesozoic avepods this may have been approached

Predatory dinosaur feet



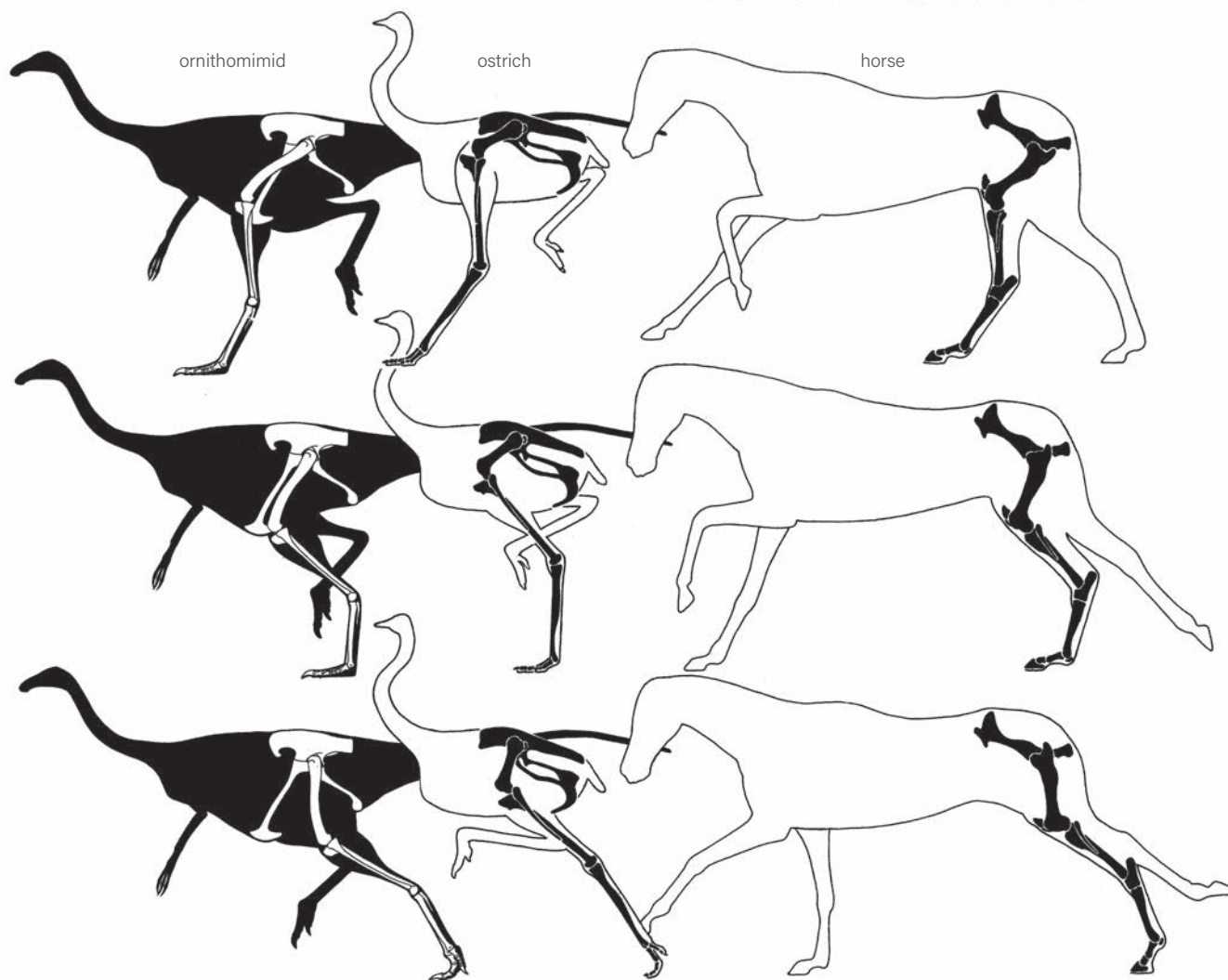
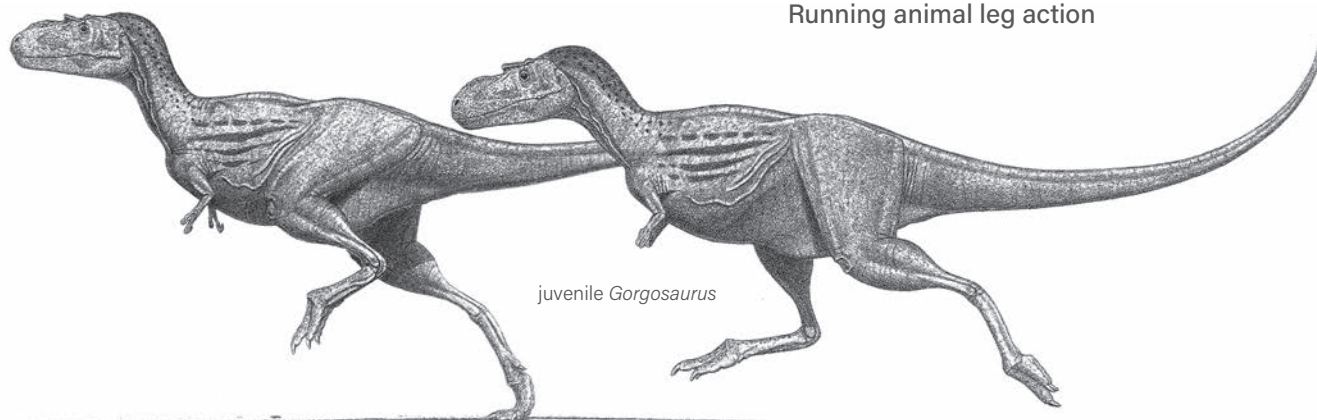
or matched by the nonpredatory ornithomimids. Also looking swift were small troodonts, perhaps as much to escape being prey as to catch it, and insectivorous alvarezosaurs for defense. On the offense were smaller and juvenile tyrannosaurids, built for high speed. About a third or more of the mass of running animals like ostriches consists of leg muscles. Adult animals do not spend much time using these to burn lots of energy per unit time and exhausting themselves running about without a compelling reason, so fossil speed trackways are not surprisingly scarce. The highest Cretaceous dinosaur land speed calculated so far is in the area of 40–50 km/h (~30 mph), made by a 100 kg (200 lb) probable avepod. It is not a surprise that small- and medium-sized dinosaurs with long, slender, flexed legs were able to run at speeds comparable to those of similar-sized ground birds and galloping mammals. Difficulties arise when trying to estimate the top speeds of flexed-limbed dinosaurs weighing many tonnes. Computer analysis has calculated that *Tyrannosaurus* could reach a top speed ranging from no better than that of a similar-sized elephant, 25 km/h (15 mph), up to the 40 km/h of a sprinting athlete. Because big-hipped, birdlike *Tyrannosaurus* was much better adapted for running than are elephants, and even by large avepod standards is exceptionally speed adapted with its enormous pelvis and running birdlike limbs, it is unlikely that it was similarly slow as proboscideans. Its anatomy is more in line with it being twice as fast or so as elephants, able to approach or match galloping rhinos and nonthoroughbred horses. Lesser tyrannosaurids may have been a dash swifter than *Tyrannosaurus*; other less speed adapted comparably titanic-sized avepods were likely to have been somewhat slower. Computer analyses are of at best limited use because they are hard pressed to fully simulate important aspects of animal locomotion, including the energy storage of prestretched elastic leg tendons and the resonant springlike effect of the torso and tail. If the latter proves true, then other giant running dinosaurs may have used special adaptations to move faster than our computer models are indicating. If marine mammals were known only from fossils, it would be logically concluded that being high metabolic rate endotherms none would have been able to hold their

breaths long enough to dive very deep into high-pressure water that would certainly kill them, and computer simulations would be cited as confirmation of that probable fact. Yet some whales and seals can dive thousands of meters because of soft tissue physiological adaptations not preserved in fossils. The core and unavoidable problem with simulations is that they are simulating a simulation, not observing the actual performance of a living animal, so the results are no better than what was put into them and may not reproduce the actual parameters of a living creature. The outcomes can never be scientifically tested and verified.

Avepods pursuing or fleeing not only needed to run, they needed to be able to maneuver, whether when moving or fighting in place. A way to improve turning performance is to be more compact fore and aft, which lowers the distal inertial mass, like a spinning skater pulling in their arms to increase the revolutions per minute. Most predatory dinosaurs were fairly elongated, limiting turn ability. Tyrannosaurids' shorter trunks and tails combined with their reduced arms would have enhanced turning during their assaults on their prey. Ornithomimids had a similar trunk and tail form to enhance their knack for dodging their tyrannosaurid attackers. The very short tails of oviraptorosaurs and most therizinosaurids would have been good for defensive agility. Another way to better turning is to pull the tail up when turning, somewhat like pulling in the arms. All long-tailed theropods could do that, the deinonychosaurs best of all because of their extra-mobile tail bases. Deinonychosaurs could additionally use the combination of a stiffened distal tail with a flexible base to quickly use the appendage as a dynamic stabilizer and turn inducer when maneuvering on the ground or in the air, like pterosaurs with similar tails. Also boosting agility would have been arm and tail feather arrays that could be used as turn-inducing airfoils when at speed.

Ratites are competent swimmers, more so than most mammals, which lacking pneumatic bodies are nearly awash when swimming and therefore have to work to keep their nostrils above the water. Having similar birdy limbs, and most being pneumatically buoyant like their

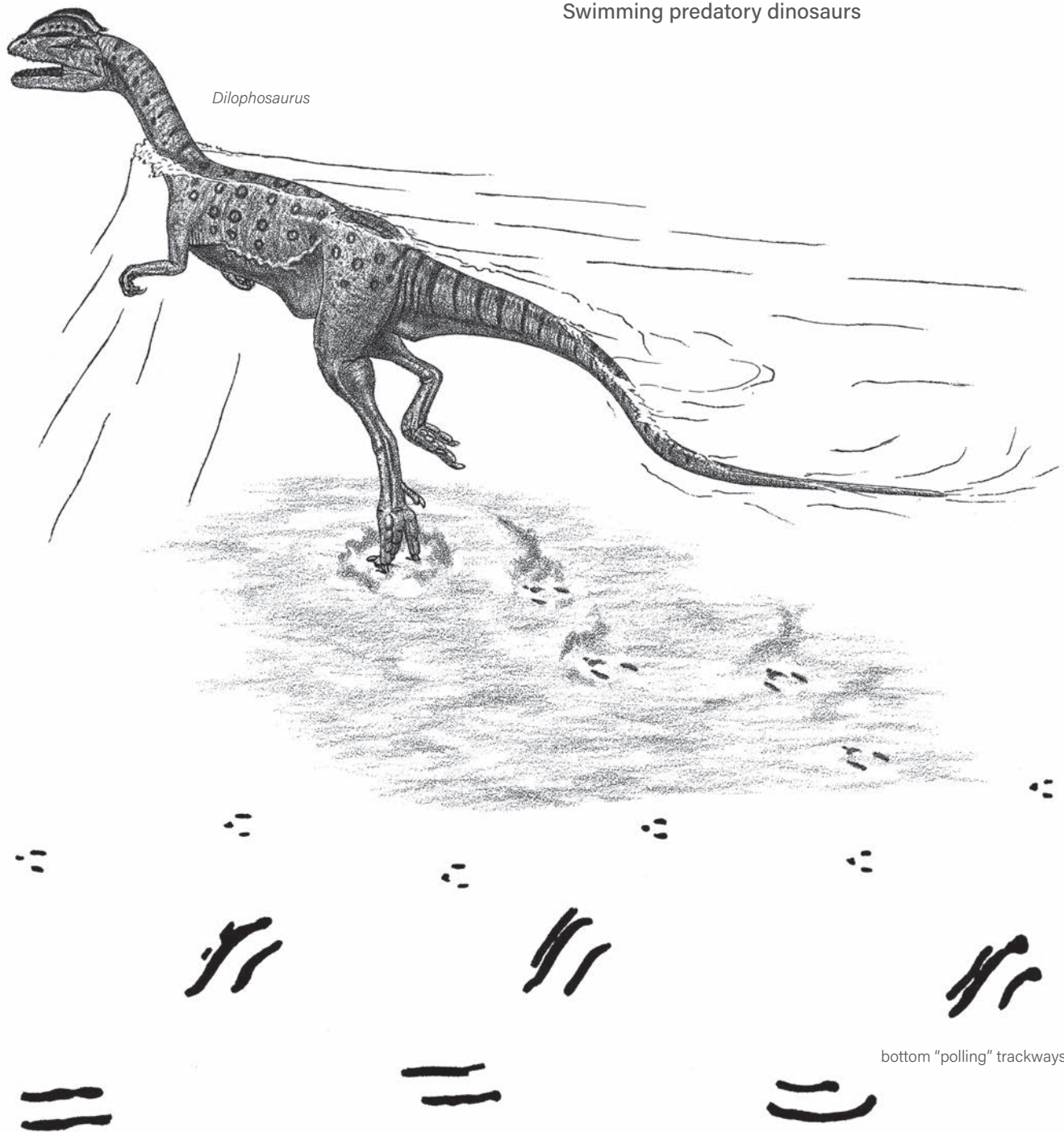
Running animal leg action



avian relations, all predatory dinosaurs were comparably adept in water. Perhaps even more adept were those with long, proximally deep tails able to add a sculling propulsion—*Ceratosaurus* appears exceptional in this regard—which excludes the slender, stiffer-tailed deinonychosaurs and the short-tailed therizinosaurs and oviraptorosaurs,

which like surface-swimming birds relied on the legs alone. Water-tolerant dinosaurs is supported by a number of examples of tridactyl-footed trackways that appear to record the animals polling along the bottom of waters shallow enough for them to reach bottom. Being such good swimmers, predatory dinosaurs could readily cross broad

Swimming predatory dinosaurs



watercourses, all the way to marine islands that they could see in the distance. Spinosaurus have been presented as specialist swimmers in the crocodilian pattern, in part because they were less buoyant than the avepods norm. But they were not nonpneumatic, so they could not have been as deep diving as crocs.

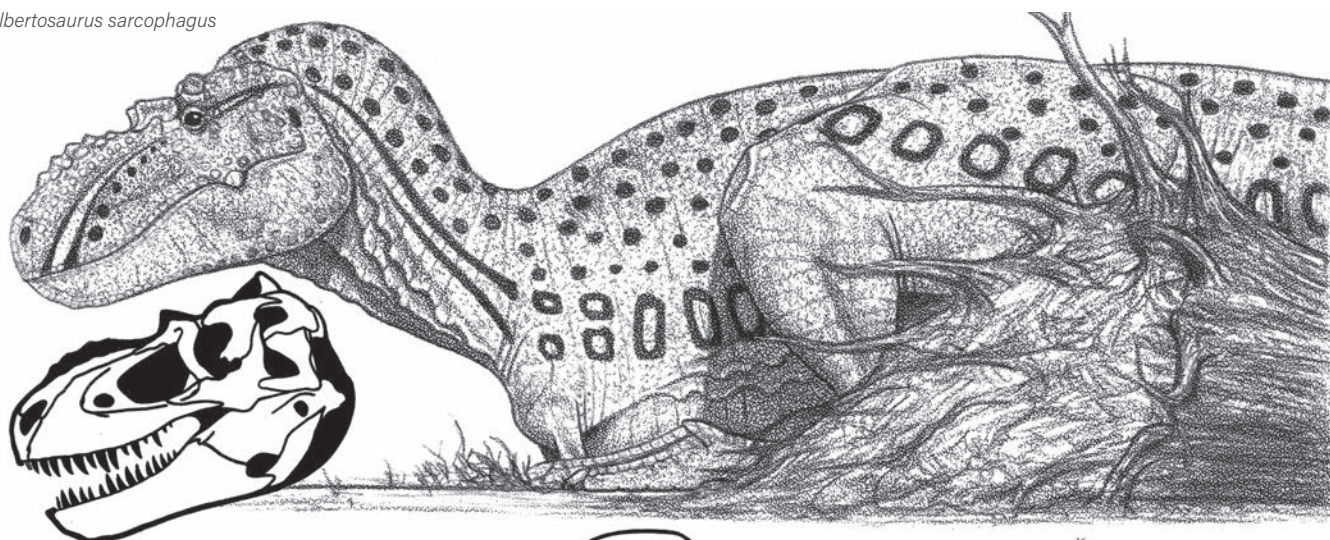
One anatomical item most predaceous dinosaurs did not have was substantial fat deposits, pursuit hunters needing to remain lean to maximize speed and agility. A possible exception would have been theropods living in climates featuring cold winters, to provide some insulation and

help thermally tide over the season—although finding herbivores to kill or scavenge in winters that often weaken or dispatch plant eaters is not necessarily difficult. The slow herbivorous therizinosaurs were candidates for carrying more fat.

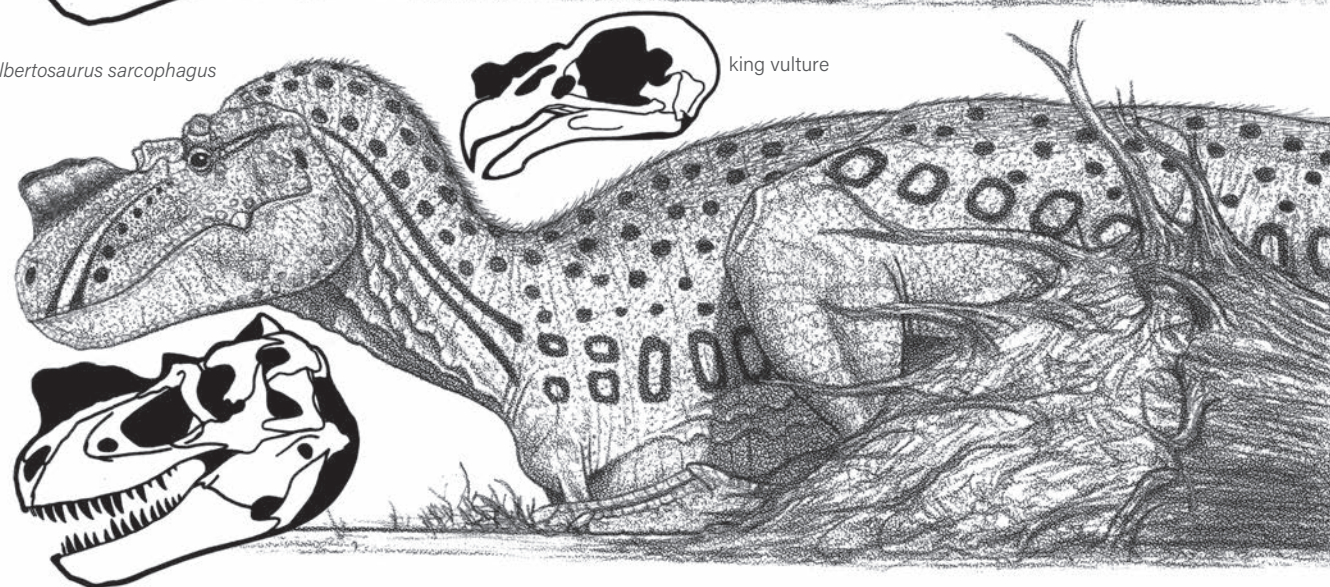
SKIN, FEATHERS, AND COLOR

Most dinosaurs are known from their bones alone, but we know a surprising amount about dinosaur body coverings from a rapidly growing collection of fossils that

Albertosaurus sarcophagus



Albertosaurus sarcophagus



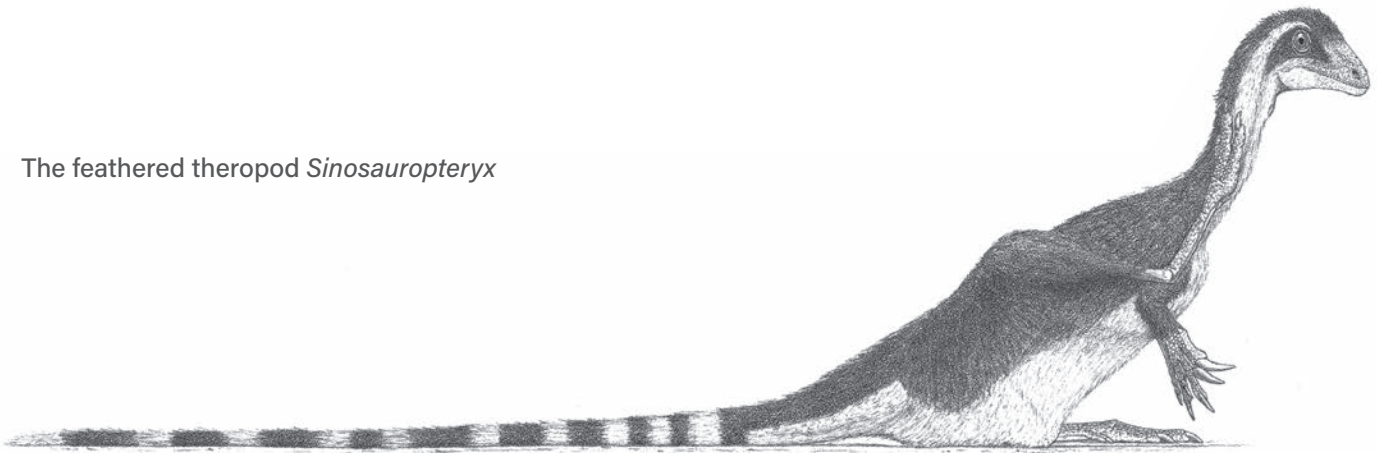
Appearance alternatives

record their integument. It has long been known that large, and some small, dinosaurs were covered with mosaic-patterned scales. These can be preserved as impressions in the sediments before the skin rotted away, but in numerous cases traces of keratin are still preserved. Footprints sometimes preserved the shape of the bottom scales as well as the foot pads. Lizard-like overlapping scales were not common among dinosaurs, although scales like those on the tops of some bird feet may have been present in birdlike dinosaurs. Dinosaur mosaic scales were commonly semihexagonal in shape, with larger scales surrounded by a ring of smaller scales, forming rosettes that were themselves set in a sea of small scales. These scales were often flat, but some were more topographic, ranging from small beads on up. Because dinosaur scales were usually not large, they tend to disappear from visual resolution when viewed from a dozen feet or more away. However, in some cases the center scale in a rosette was a large, projecting, subconical scale; these were often

arranged in irregular rows. On a given dinosaur the size and pattern of the scales varied depending on their location: those low on the body were often smaller than those higher up.

Dinosaurian soft crests, combs, dewlaps, wattles, and other soft display organs may have been more widespread than we realize. In particular, on some snouts, such as those of tyrannosaurs, the nasal bones bore a long, narrow midline rugosity that is usually restored as being somewhat further enlarged by a shallow, hard keratin sheath. The king vulture also has a modest nasal rugosity, which anchors a very prominent fleshy caruncle. It cannot be ruled out that the dinopredators with similar snout tops had comparable features. A throat pouch has been found under the jaws of an ornithomimosaur theropod, and these may have been more widespread. Bony armor was very scarce on dinopredators, they doing the attacking that drove other dinosaurs to be armored. Plates were covered with hard keratin. The exception was *Ceratosaurus*, which sported a midline

The feathered theropod *Sinosauropteryx*



dorsal row of small bony adornments; these would have been ensheathed by keratin.

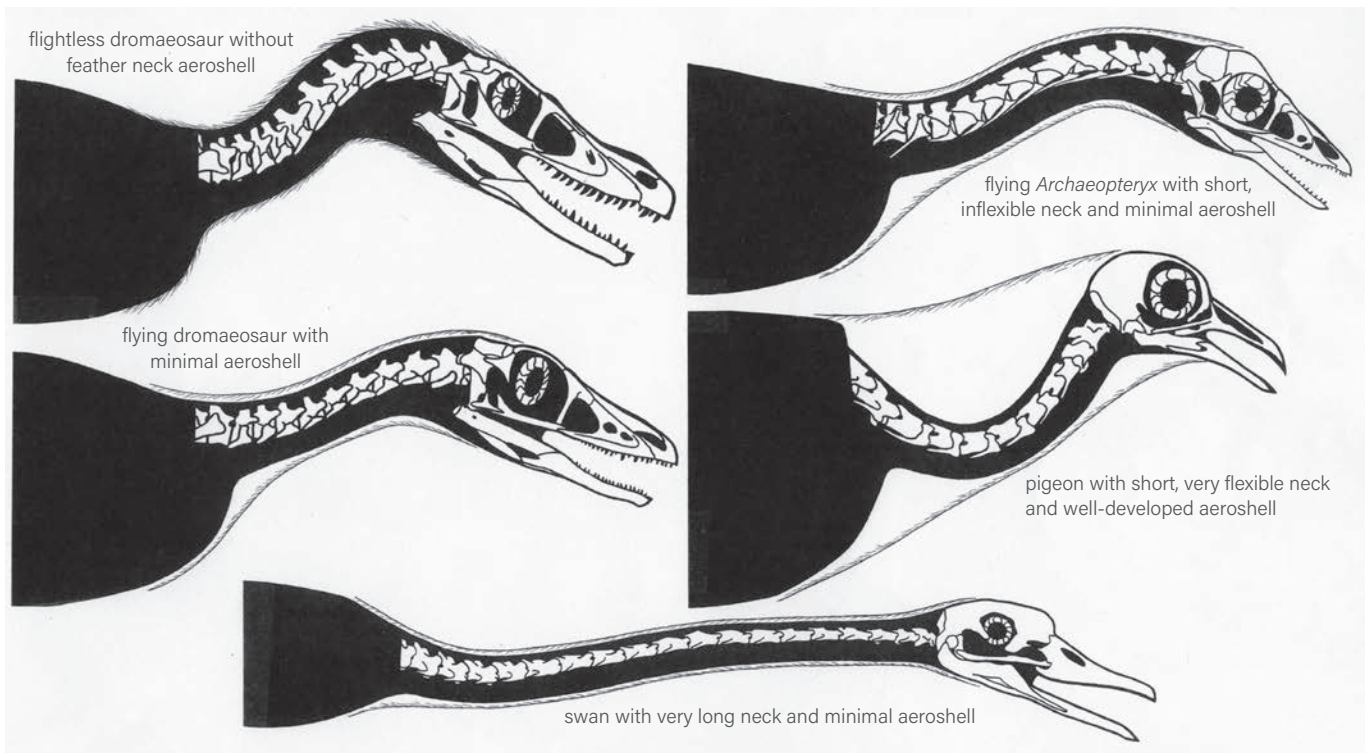
Feathers have long been known on the fossils of birds preserved in fine-grained lake or lagoon bottom sediments, including winged *Archaeopteryx*. After a fossil drought that lasted until the end of the last century, over the last three decades a growing array of small avepod dinosaurs flightless and winged have been found covered with bristle protofeathers or fully developed pennaceous feathers in the Chinese Yixian–Jiufotang beds. Some researchers have claimed that the simpler bristles are really degraded internal collagen fibers. This idea is untenable for a number of reasons, including the discovery of pigmentation—either visible to the naked eye or in microscopic capsules—in the fibers that allows their actual color to be approximated. Some small, nonflying theropods also had scales at least on the tail and perhaps legs. This suggests that the body covering of small dinosaurs was variable—ostriches lack feathers on the legs, and a number of mammals from a small bat through a number of suids as well as humans, rhinos, and elephants are essentially naked.

Ironically, some paleoartists are going too far with feathering dinosaurs, giving many the fully developed aershells in which contour feathers streamline the head, neck, and body of most flying birds. But most Mesozoic dinosaurs did not fly, and like those birds whose ancestors lost flight long ago, flightless dinosaurs would have had shaggier, irregular coats for purposes of insulation and display. Also, modern birds have the hyperflexible necks that allow many but not all fliers to strongly U-curve the neck to the point that the head and heavily feathered neck aerodynamically merge with the body. Dinosaurs and even early flying dinobirds like *Archaeopteryx* and microraptors could not do this, so their less-flexible necks stuck out ahead of the shoulders like those of a number of modern long-necked flying birds.

Because fibers covered basal ornithischians as well as avepods, it is a good scientific bet that dinosaur insulation evolved once, in which case the filaments were all protofeathers. The absence to date of protofeathers in Triassic

and Early Jurassic protodinosaur and basal dinosaurs is the kind of negative evidence that is no more meaningful than their lack of fossil scales; this absence of evidence long led to the denial of insulation in any dinosaurs and is likely but not certainly to be settled by the eventual discovery of insulation in basal examples. However, it cannot be ruled out that insulation evolved more than once in dinosaurs. A question is why dinofur and feathers appeared in the first place. The first few bristles must have been too sparse to provide insulation, so their initial appearance should have been for nonthermoregulatory reasons. One highly plausible selective factor was display. As the bristles increased in number and density to improve their display effect, they became thick enough to help retain the heat generated by the increasingly energetic archosaurs.

A number of researchers argue that the pigment organelles of feathers preserve well and their shape varies according to color, so they are being used to restore the actual colors of feathered dinosaurs. Although some researchers have challenged the reliability of this method, it appears to be largely sound, so this book uses the colors determined by this technique—doing so maximizes the probability of achieving correct coloration, whereas not doing so essentially ensures incorrect results. It appears that the feathers of some dinosaurs were, as might be expected, iridescent, using refraction rather than pigmentation to achieve certain color effects. The hypothesis offered by some researchers, that the differing scale patterns on a particular dinosaur species correspond to differences in coloration, is plausible, but some reptiles are uniformly colored regardless of variations in scales. Dinosaur scales were better suited to carry bold and colorful patterns like those of reptiles, birds, tigers, and giraffes than is the dull gray, nonscaly skin of big mammals, and the color vision of dinosaurs may have encouraged the evolution of colors for display and camouflage. Dinosaurs adapted to living in forested areas may have been prone to using greens as stealth coloring. On the other hand, big reptiles and birds tend to be earth tinged despite their color vision. Small dinosaurs are the best candidates for bright and/or bold



color patterns like those of many but not all small lizards and birds. On yet another hand, because humans lack vision in the ultraviolet range, we miss seeing a lot of the coloration of many animals, so a number of reptiles and especially birds that look drab to us—including genders that look bland and much the same—feature dramatic ultraviolet color patterns, often for sexual purposes. Predaceous dinosaurs of all sizes may have used specific color displays for intraspecific communication or for startling predators. Crests and taller neural spines would be natural bases for vivid, even iridescent, display colors, especially in the breeding season. Because dinosaur eyes were bird- or reptile-like, not mammal-like, they lacked white surrounding the iris. Flesh-eating dinosaurs' eyes may have been solid black or brightly colored, like those of many reptiles and birds.

A number of birds are ensconced in poisonous feathers containing neurotoxins—in a few body tissues may be contaminated. These toxins can afflict those that touch the birds, or worse, consume them; the noxious birds are themselves immune to the chemicals. The origin of these poisons appears to be the bird's diets, including insects. The toxicity probably deters predation while suppressing parasites. Some small-feathered Mesozoic archosaurs that hunted insects may well have been similarly toxic.

RESPIRATION AND CIRCULATION

The hearts of turtles, lizards, and snakes are three-chambered organs incapable of generating high blood pressures. The lungs, although large, are internally simple structures

with limited ability to absorb oxygen and exhaust carbon dioxide and are operated by rib action. Even so, at least some lizards apparently have unidirectional airflow in much of their lungs, which aids oxygen extraction. Crocodylian hearts are incipiently four chambered but are still low pressure. Their lungs are internally dead end, but they too seem to have unidirectional airflow, and the method by which they are ventilated is sophisticated. Muscles attached to the pelvis pull on the liver, which spans the full height and breadth of the rib cage, to expand the lungs. This action is facilitated by an unusually smooth ceiling of the rib cage that allows the liver to easily glide back and forth, the presence of a rib-free lumbar region immediately ahead of the pelvis, and, at least in advanced crocodylians, a very unusual mobile pubis in the pelvis that enhances the action of the muscles attached to it.

Birds and mammals have fully developed four-chambered, double-pump hearts able to propel blood in large volumes at high pressures. Mammals retain fairly large dead-end lungs, but they are internally very intricate, greatly expanding the gas-exchange surface area, and so are efficient despite the absence of one-way airflow. The lungs are operated by a combination of rib action and the vertical, muscular diaphragm. The presence of the diaphragm is indicated by the existence of a well-developed, rib-free lumbar region, preceded by a steeply plunging border to the rib cage on which the vertical diaphragm is stretched.

It is widely agreed that all dinosaurs probably had fully four-chambered, high-capacity, high-pressure hearts. Their respiratory complexes appear to have been much more diverse.

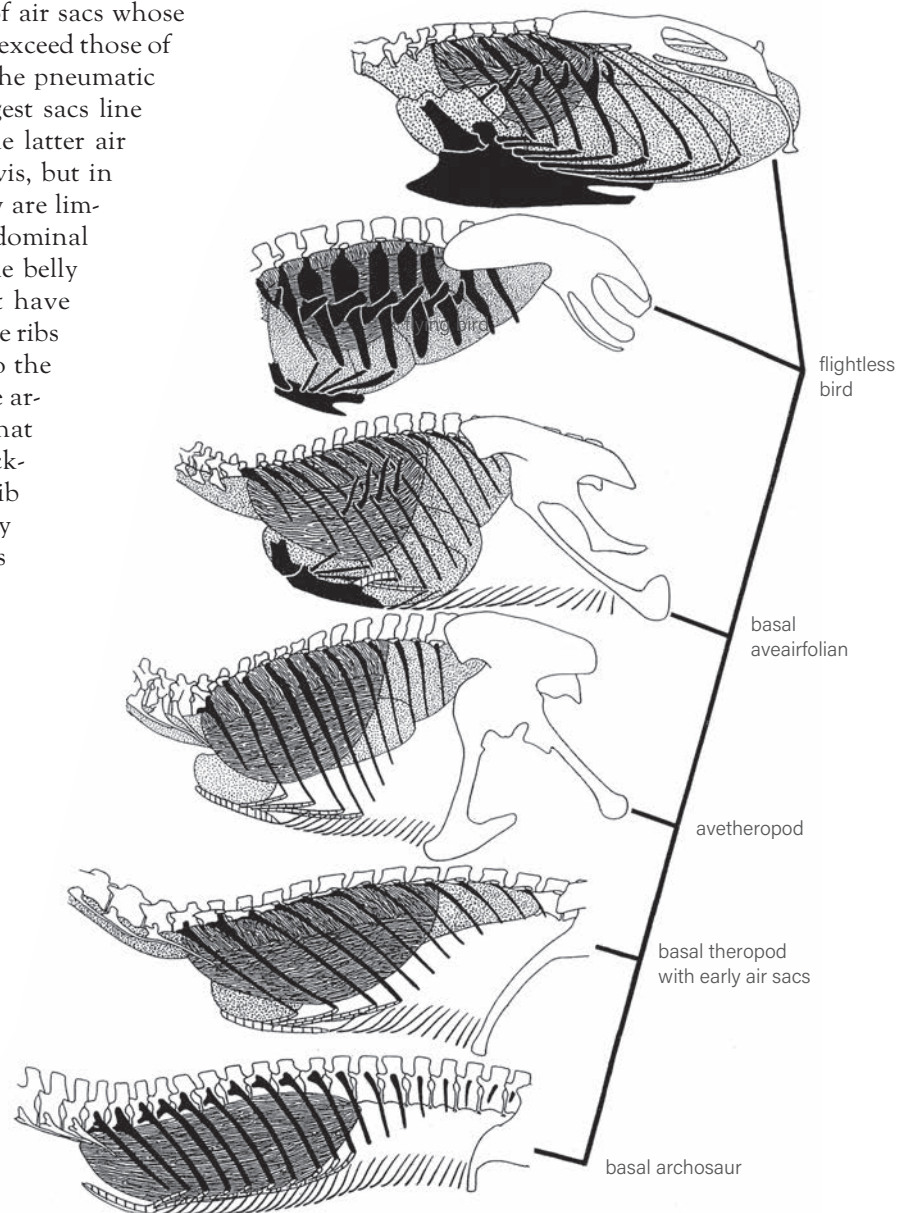
It is difficult to reconstruct the respiratory systems of ornithischians because they left no living descendants and because their rib cages differ not only from those of all living tetrapods but among different ornithischian groups—the absence of skeletal pneumaticity shows they did not have birdlike breathing, and their lungs were probably dead end, perhaps similar to mammals.

Restoring the respiratory complexes of saurischians, especially theropods, is much more straightforward because birds are living members of the group and retain the basic theropod system. Birds have the most complex and efficient respiratory system of any vertebrate. Because the lungs are rather small, the chest ribs that encase them are fairly short, but the lungs are internally intricate so they have a very large gas-exchange area. The lungs are also rather stiff and set deeply up into the strongly corrugated ceiling of the rib cage. The lungs do not dead end; instead, they are connected to a large complex of air sacs whose flexibility and, especially, volume greatly exceed those of the lungs. Some of the air sacs invade the pneumatic vertebrae and other bones, but the largest sacs line the sides of the trunk; in most birds the latter air sacs extend all the way back to the pelvis, but in some, especially flightless examples, they are limited to the rib cage. The chest and abdominal sacs are operated in part by the ribs; the belly ribs tend to be extra long in birds that have well-developed abdominal air sacs. All the ribs are highly mobile because they attach to the trunk vertebrae via well-developed hinge articulations. The hinging is oriented so that the ribs swing outward as they swing backward, inflating the air sacs within the rib cage and then deflating the sacs as they swing forward and inward. In most birds the movement of the ribs is enhanced by ossified uncinuate processes that form a series along the side of the rib cage. Each uncinuate process acts as a lever for the muscles that operate the rib to which the process is attached. In most birds the big sternal plate also helps ventilate the air sacs. The sternum is attached to the ribs via ossified sternal ribs that allow the plate to act as a bellows on the ventral air sacs.

In those birds with short sternums, the flightless ratites, and in active juveniles, the sternum is a less important part of the ventilation system.

The system is set up in such a manner that most of the fresh inhaled air does not pass through the gas-exchange portion of the lungs but instead goes first to the air sacs, from where it is injected through the entire lungs in one direction on its way out. Because this unidirectional airflow eliminates the stale air that remains in dead-end lungs at the end of each breath and allows the blood and airflow to work in opposite, countercurrent directions that maximize gas exchange, the system is very efficient. Some birds can sustain cruising flight at levels higher than Mount Everest and equalling those of jet airliners.

Neither the first theropods nor prosauropods show clear evidence that they possessed air sacs, and aside from their lungs therefore being dead-end organs or close to it, little is known about their respiration. In the first avepoid



Respiratory complexes of archosaurs

theropods some of the vertebrae were pneumatic, indicating the presence of air sacs. Also, the hinge jointing of the ribs increased, indicating that they were probably helping to ventilate the lungs by inflating and deflating trunk air sacs. As theropods evolved, the hinge jointing of the ribs further increased, as did the invasion of the vertebrae by air sacs until reaching the hips. Also, the chest ribs began to shorten, probably because the lungs, set up into a corrugated ceiling of ribs, were becoming smaller and stiffer as the air sacs did more of the work. By this stage the air-sac complex was probably approaching the avian condition, and airflow in the lungs should have been largely unidirectional. The sternum was still small, but the gastralia may have been used to help ventilate the ventral

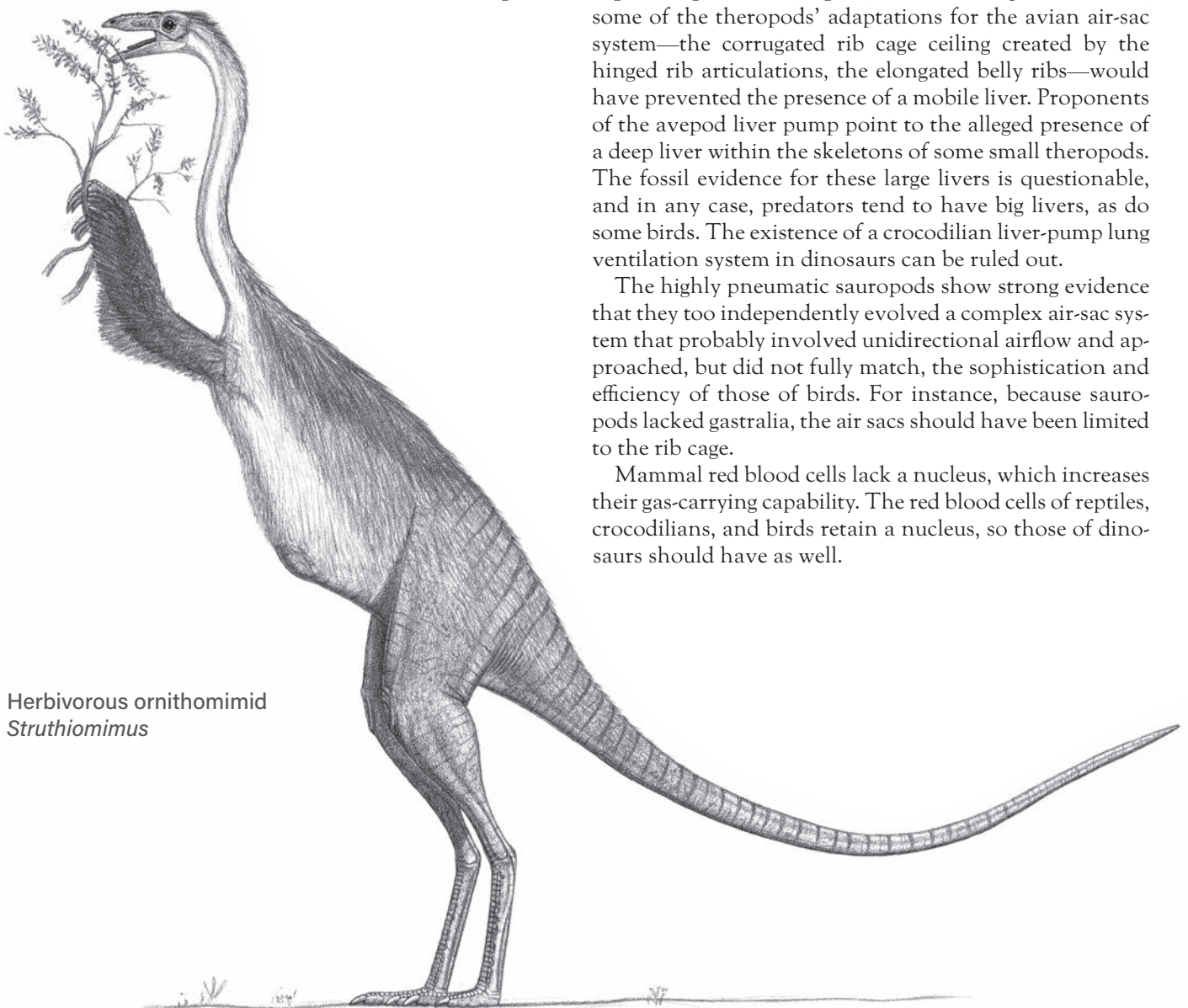
belly air sacs. Alternatively, the air sacs were limited to the rib cage as they are in at least some flightless

birds—the extra-long belly ribs of birds with big abdominal air sacs are absent in theropods. In many avian theropods the ossified sternum was as large as it is in ratites and juvenile birds and was attached to the ribs via ossified sternal ribs, so the sternal plate was combining with the gastralia to inflate and deflate the air sacs. Also, ossified uncinat processes are often present, indicating that the bellows-like action of the rib cage was also improved. At this stage the respiratory complex was probably about as well developed as it is in some modern birds.

The very few researchers who think birds are not dinosaurs deny that theropods breathed like birds. Some propose that theropod dinosaurs had a crocodilian liver-pump system. Aside from theropods not being close relatives of crocodilians, they lacked the anatomical specializations that make the liver-pump system possible—a smooth rib cage ceiling, a lumbar region, and a mobile pubis. Instead, some of the theropods' adaptations for the avian air-sac system—the corrugated rib cage ceiling created by the hinged rib articulations, the elongated belly ribs—would have prevented the presence of a mobile liver. Proponents of the avian liver pump point to the alleged presence of a deep liver within the skeletons of some small theropods. The fossil evidence for these large livers is questionable, and in any case, predators tend to have big livers, as do some birds. The existence of a crocodilian liver-pump lung ventilation system in dinosaurs can be ruled out.

The highly pneumatic sauropods show strong evidence that they too independently evolved a complex air-sac system that probably involved unidirectional airflow and approached, but did not fully match, the sophistication and efficiency of those of birds. For instance, because sauropods lacked gastralia, the air sacs should have been limited to the rib cage.

Mammal red blood cells lack a nucleus, which increases their gas-carrying capability. The red blood cells of reptiles, crocodilians, and birds retain a nucleus, so those of dinosaurs should have as well.



Herbivorous ornithomimid
Struthiomimus

DIGESTIVE TRACTS

In a number of avepods specimens, gastroliths, or gizzard stones, are preserved within the rib cage, often as stone bundles. This does not appear to be a general dinopredator attribute, stone bundles having not been turning up in the articulated ribcages of flesh eaters prior to aveairfoilans. They do appear in the herbivorous elaphrosaurs, ornithomimids, and oviraptorosaurs and the protobird anchiornids. The stones could be used directly to help mash and grind up plant materials as they were squeezed and manipulated by powerful gizzard muscles and/or to help mix the foodstuffs up like agitator balls in spray paint cans.

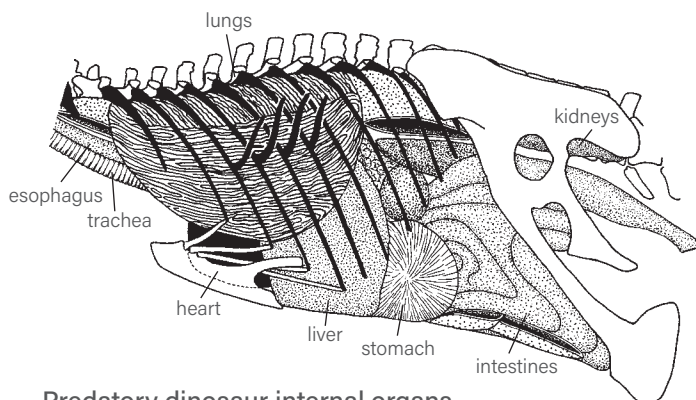
The digestive tracts of meat, fish, and insect consuming dinosaurs were relatively short, simple systems that quickly processed the easily digested chunks of flesh bolted down whole or in substantial pieces after the simple puncturing and scissoring action of the serrated teeth. Coprolites attributable to large theropods often contain large amounts of undigested bone, confirming the rapid passage of food through the tract. A few preserved remains indicate that nonvolant predatory dinosaurs retained a somewhat larger digestive tract than do birds with their overall lighter complexes, starting with a large crop. Most of the herbivorous avepods did not have tooth batteries or saw-edged beaks to chew with; their mouths merely cut off bits of vegetation to be quickly swallowed. Not being highly sophisticated herbivores, ornithomimid and oviraptorosaur abdomens were not highly capacious. Ratites carry a combination of gastroliths, gut flora, ingested fodder, and feces amounting to about a tenth of body mass, and such was probably true of the similar-grade omni/herbivorous ornithomimids and oviraptorosaurs. It was the therizinosauroids among avepods that went for high-capacity digestive complexes that broke down tough plant material, presumably via fermentation accomplished by gut bacteria. In most herbivores this occurs in the hindgut. Among such full-blown herbivores, the gut contents can be up to a fifth of total mass. In the highly specialized ruminant ungulates, cattle included, the microbial breakdown begins in the foregut in a special chamber. Hoatzins sport a comparable system in which the crop is used to initiate microbial processing—thus their tag the “stink

bird” is due to the methane they put out. Therizinosauroids may have carried a ruminant-like, possibly smelly digestive complex. The cheeks that appear to have been present on therizinosauroids should have allowed them to mash food a little with their modestly developed dental batteries before swallowing. Hoatzins are unusual among avepods in doing a little chewing with their gently serrated beaks.

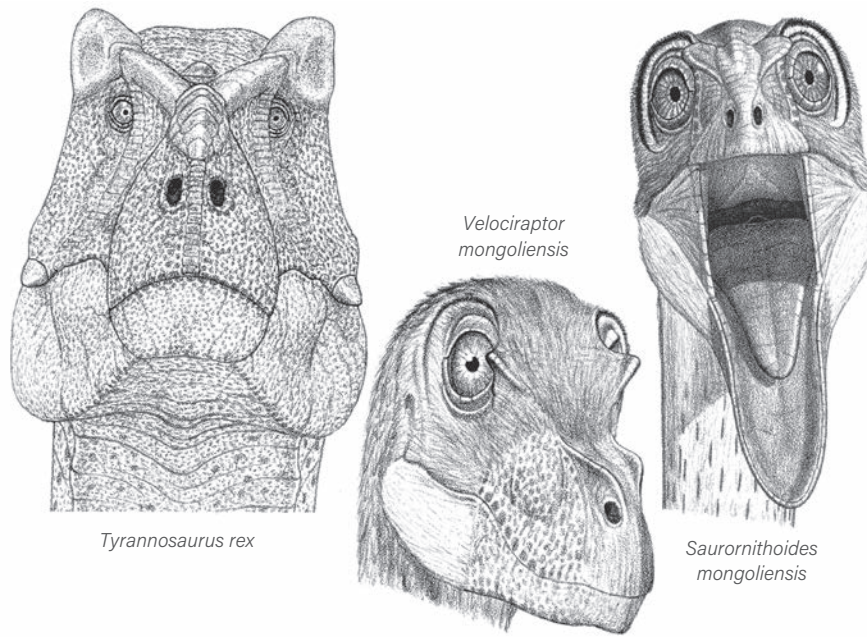
SENSES

The large eyes and well-developed optical lobes characteristic of most dinosaurs indicate that vision was usually their primary sensory system, as it is in nearly all birds. Reptiles and birds have full color vision extending into the ultraviolet range, so dinosaurs very probably did too. The comparatively poorly developed color vision of most mammals is a heritage of the nocturnal habits of early mammals, which reduced vision in the group to such a degree that eyesight is often not the most important of the senses. Reptile eyesight is about as good as that of well-sighted mammals, and birds tend to have very high-resolution vision, both because their eyes tend to be larger than those of reptiles and mammals of similar body size and because they have higher densities of light-detecting cones and rods than do mammals. The cones and rods are also spread at a high density over a larger area of the retina than in mammals, in which high-density light cells are more concentrated at the fovea (so our sharp field of vision covers just a few degrees). Some birds have a secondary fovea. Day-loving raptors can see about three times better than people, and their sharp field of vision is much more extensive, so birds do not have to point their eye at an object as precisely as mammals to focus on it. Birds can also focus over larger ranges, 20 diopters compared with 13 diopters in young adult humans. The vision of the bigger-eyed predatory dinosaurs may have rivaled this level of performance. The dinosaurs’ big eyes have been cited as evidence for both daylight and nighttime habits. Large eyes are compatible with either lifestyle—it is the (in this case unknowable) structure of the retina and pupil that determines the type of light sensitivity.

Birds’ eyes are so large relative to the head that they are nearly or entirely fixed in the skull, so looking at specific items requires turning the entire head. The same was likely to have been true of smaller-headed avepods. Theropods with larger heads should have had more mobile eyeballs that could scan for objects without rotating the entire cranium. The eyes of most dinosaurs faced to the sides, maximizing the area of visual coverage at the expense of the binocular view directly ahead. Some birds and mammals—primates most of all—have forward-facing eyes with overlapping fields of vision, and in at least some cases, vision includes a binocular, stereo effect that provides depth perception. Tyrannosaurid, ornithomimid, and many aveairfoilan theropods had partly forward-facing eyes with overlapping vision fields. Whether vision was truly stereo in any or all of these dinosaurs is not certain; it is possible



Predatory dinosaur internal organs



Predatory dinosaurs with forward facing eyes

that the forward-facing eyes were an incidental but perhaps beneficial side effect of the expansion of the back of the skull to accommodate larger jaw muscles in tyrannosaurs, *Tyrannosaurus* most of all.

Most birds have a poorly developed sense of smell, the result of the lack of utility of this sense for flying animals as well the lack of space in heads whose snouts have been reduced to save weight. Exceptions are some vultures, which use smell to detect rotting carcasses hidden by deep vegetation, and grub-hunting kiwis. As nonfliers with large snouts, many reptiles and mammals have very well-developed olfaction, sometimes to the degree that it is a primary sensory system, canids being a well-known example. Dinosaurs often had extremely well-developed, voluminous nasal passages with abundant room at the back for large areas of olfactory tissues. In many dinosaur brains the olfactory lobes were large, verifying their effective sense of smell. Herbivorous dinosaurs probably had to be approached from downwind to avoid their sensing and fleeing from an attack. Among predatory dinosaurs, tyrannosaurs and dromaeosaurs had especially excellent olfaction, useful for finding both live prey and carcasses.

Mammals have exceptional hearing, in part because of the presence of large, often movable outer ear pinnae that help catch and direct sounds into the ear opening and especially because of the intricate middle ear made up of three elements that evolved from what were once jaw bones. In some mammals hearing is the most important sense, bats and cetaceans being the premier examples. Reptiles and birds lack fleshy outer ears, and there is only one inner ear bone. The combination of outer and complex inner ears means that mammals can pick up sounds at low volume. Birds partly compensate by having more auditory sensory cells per unit length of the cochlea, so sharpness of hearing and discrimination of frequencies are broadly similar in

birds and mammals. Where mammalian hearing is markedly superior is in high-frequency sound detection. In many reptiles and birds the auditory range is just 1–5 kHz; owls are exceptional in being able to pick up from 250 Hz to 12 kHz, and geckos go as high as 10 kHz. In comparison, humans can hear 20 kHz, dogs up to 60 kHz, and bats 100 kHz. At the other end of the sound spectrum, some birds can detect very low frequencies: 25 Hz in cassowaries, which use this ability to communicate over long distances, and just 2 Hz in pigeons, which may detect approaching storms. It has been suggested that cassowaries use their big, pneumatic head crests to detect low-frequency sounds, but pigeons register even deeper bass sounds without a large organ.

In the absence of fleshy outer and complex inner ears, dinosaur hearing was in the reptilian-avian class, and they could not detect very high frequencies. Nor were the auditory lobes of dinosaur brains especially enlarged, although they were not poorly developed either. Nocturnal, flying, rodent-hunting owls are the only birds that can hear fairly high-frequency sounds, so certainly most and possibly all dinosaurs could not hear them either. Oviraptorosaurs had hollow head crests similar to those of cassowaries, hinting at similar low-frequency sound detection abilities. The big ears of large dinosaurs had the potential to capture very low frequencies, allowing them to communicate over long distances. It is unlikely that hearing was the most important sense in any dinosaur, but it was probably important for detection of prey and predators, and for communication, in all species.

VOCALIZATION

No living reptile has truly sophisticated vocal abilities, which are best developed in crocodylians. Some mammals do, humans most of all. Birds use the syrinx in the chest to

generate sounds; when this scheme evolved among dinosaurs is not yet clear. A number of birds have limited vocal performance, but many have evolved a varied and often very complex vocal repertoire not seen among other vertebrates outside of people. Songbirds sing, and a number of birds are excellent mimics, to the point that some can imitate artificial sounds such as bells and sirens, and parrots can produce understandable humanlike speech. Some birds, swans particularly, possess elongated tracheal loops in the chest that they use to produce high-volume vocalizations. Cassowaries call one another over long ranges with very low-frequency sounds, and so do elephants. Birds possess the intricate voice boxes needed to help form complex vocalizations. Among dinosaur fossils only an ankylosaur skull includes a complete voice box. The complicated structure of the armored dinosaurs' larynx suggests vocal performance at an avian level, perhaps high-end performance, and such may have been true of other dinosaurs, including those predatory. The long trachea of long-necked dinosaurs such as therizinosaurs should have been able to generate powerful low-frequency sounds that could be broadcast over long ranges. Vocalization is conducted through the open mouth rather than through the nasal passages, so complex nasal passages acted as supplementary resonating chambers. It is doubtful that any nonavian

dinosaur had vocal abilities to match the more sophisticated examples seen in the most vocally advanced birds and mammals. Although we will never know what dinosaurs sounded like, and the grand roars of dinosaur movies are not likely, there is little doubt that the Mesozoic forests, prairies, and deserts were filled with their voices.

GENETICS

As more fossils are found in different levels of geological formations, the evidence is growing that dinosaurs enjoyed high rates of speciation that boosted their diversity at any given time. And over time, via a rapid turnover of species, most did not last for more than a few hundred thousand years before being replaced by new species one way or another. The same is true of birds, which have more chromosomes than slower-evolving mammals. Dinosaurs presumably had the same genetic diversity as their direct avian descendants, which may have been a driving force behind their multiplicity.

DISEASE AND PATHOLOGIES

Planet Earth has long been infested with a toxic soup of diseases and other dangers that put dinopredators at high

Predatory dinosaurs in conflict,
Velociraptor and *Saurornithoides*



risk. The disease problem was accentuated by the global greenhouse effect, which maximized the tropical conditions that favored disease organisms, especially bacteria and parasites. Biting insects able to spread assorted diseases were abundant during the Mesozoic; specimens have been found in amber and fine-grained sediments. Reptile and bird immune systems operate somewhat differently from those of mammals; in birds the lymphatic system is particularly important. Presumably the same was true of their dinopredator ancestors. Wild living animals are prone to be loaded with arrays of resident multicellular parasites in the form of arthropods and worms on their skins, amidst their integument, in internal cavities, including, especially, the digestive tract, and within internal tissues. In some cases, these parasites can become debilitating.

The skeletons of predaceous dinosaurs often preserve pathologies, sometimes numerous in a given individual. Some appear to record internal diseases and disorders. Fused vertebrae are fairly common. Also found are growths that represent benign conditions or cancers. Most pathologies are injuries caused by stress or wounds; the latter often became infected, creating long-term, pus-producing lesions that affected the structure of the bone. Injuries tell us a lot about

the activities of dinosaurs. Some dinosaur skeletons are so afflicted with serious defects that one of them very probably killed the beast, especially if it was immature.

The predaceous dinosaurs are, not surprisingly, especially prone to show signs of combat-related injury that derived from hunting, disputes over carcasses, and intraspecific conflicts, as well as everyday accidents. One *Allosaurus* individual shows evidence of damage to its ribs, tail, shoulder, feet, and toes as well as chronic infections of a foot, finger, and rib. The tail injury, probably caused by a kick or fall, occurred early in life. Some of the injuries, including those to the feet and ribs, look severe enough that they may have limited its activities and contributed to its death. A wound in another *Allosaurus* tail appears to have been inflicted by the spike of a stegosaur. The famous *Tyrannosaurus* “Sue” had problems with its face and tail as well as a neck rib, finger, and fibula. The head and neck wounds appear to have been caused by other *Tyrannosaurus* and in one case had undergone considerable healing. Other researchers have suggested that infections caused some of the injuries. The sickle-claw-bearing toes of dromaeosaurs and troodonts frequently show signs of stress damage. Some fossils show signs of injury from falls.

BEHAVIOR

BRAINS, NERVES, AND INTELLIGENCE

Assessing brain power is complicated because many factors are involved. One that has long been used is the mass of the brain relative to total body mass at a given size. Within the context that brains of a given performance level tend to become smaller relative to the body as size increases—elephant brains are many times absolutely larger than those of people while being many times smaller relative to body weight, and we are overall more intelligent—relatively bigger brains are likely to produce higher cognition. Also important is brain structure, with birds and mammals having more complex schemes, including large forebrains. Adding to the complications is the neural density factor. Reptiles have much lower neural density relative to brain mass than do mammals and birds, and the latter are markedly higher in this regard than mammals. The last point helps explain why birds with absolutely small brains, such as crows and parrots, achieve levels of thinking comparable to those of some far larger-headed primates. Avian brains are also markedly more energy efficient, their neurons requiring less glucose to process information. Big brains packed with lots of neurons can correlate with metabolism in that low-energy animals cannot produce enough metabolic power to operate high-cognition brains, which require a high metabolism. Less clear is whether energetic animals automatically have similarly energetic brains. In

particular, it is not known whether reptilian brains can have high neural densities even if the animals run at high metabolic rates.

The brains of the great majority of dinosaurs were reptilian both in size relative to the body and in structure. There was some variation in size compared with body mass: the giant tyrannosaurids had unusually large brains for dinosaurs of their size and so did the duck-billed hadrosaurs they hunted. However, even the diminutive brains of sauropods and stegosaurs were within the reptilian norm for animals of their great mass.

Taken at face value, the small, fairly simple brains common to most dinosaurs seem to indicate that their behavioral repertoire was limited compared with those of birds and mammals, being more genetically programmed and stereotypical. But if dinosaurs are presumed to have been stable-temperature endotherms via high metabolic rates, then it is possible, albeit by no means certain, that their neural densities were in the mammalian or, since dinosaurs include birds, even in the avian range. This has led to estimates that bigger-brained dinosaurs such as tyrannosaurs were as smart as the cleverest birds, as well as primates other than humans, and may have used simple, crafted nonstone/nonmetal tools. “Crafting” implies modifying an object in some manner to make it usable, rather than just picking up a rock and using it to smash open a hard-shelled item. Crafting can be as simple as stripping leaves and side branches off a twig to make it into a probe or lever. But this is by no means certain when it comes to the

majority of dinosaurs, whose thinking organs were reptilian in form. That the energetic dinosaurs had the low neural densities of reptiles unable to sustain high levels of activity appears unlikely, but their simple brains may have precluded the neural concentrations of birds. It is therefore not possible to reliably assess the intelligence of dinosaurs with reptilian-form brains at this time, and it may never be doable. Even if big theropods were not supersmart, it is pertinent that even small-brained animals can achieve remarkable levels of mental ability. Fish and lizards can retain new information and learn new tasks. Many fish live in organized groups. Crocodylians care for their nests and young. Social insects with tiny neural systems live in organized colonies that rear the young, enslave other insects, and even build large, complex architectural structures. It is not unthinkable that dinosaurs up to the biggest sauropods could use sticks and leafy branches to scratch themselves if they could reach close enough to their bodies with their mouths, use heavy sticks to knock down otherwise unreachable choice food items, or build leafy branch piles over water holes to protect them when not in use, as elephants do.

The major exception to dinosaurian reptile brains appeared in the birdlike *aveairfoilans*. Their brains were proportionally larger, falling into the lower avian zone, as did their complexity. It is possible if not probable that neural densities were approaching if not at the avian level. It may be that the expanded and upgraded brains of *aveairfoilans* evolved at least in part in the context of the initial stages of dinosaurian flight. Presumably the bigger-brained dinosaurs were capable of more sophisticated behavior than other dinosaurs. Use of very simple tools is plausible, all the more so because many small nonavian *avepods* that had supple-fingered hands may have been able to manipulate devices, in addition to using their mouths in ways similar to tool-using birds. On the other hand, use of crafted tools in wild birds is not extensive, and it may well be that no Mesozoic dinosaur did this. If any did, tool utilization may have occurred in the context of prying open hard-shelled food items or probing insect holes in search of prey. The insectivorous *alvarezsaur*s might have been

Possible predatory dinosaur pack trackways



especially prone to the latter, but their stout and powerful arms and hands were much better suited for bursting open insect colonies than holding tools.

The enlarged spinal cavity in the pelvic region of many small-brained dinosaurs was an adaptation to better coordinate the function of the hind limbs and is paralleled in big ground birds.

SOCIAL ACTIVITIES

Land reptiles do not form organized groups. Birds and mammals often do, but many do not. Most big cats, for instance, are solitary, but lions are highly social. Some, but not all, deer form herds.

The presence of a number of individuals of a single species of theropod in association with the skeleton of a potential prey animal has been cited as evidence that dinopredators sometimes killed and fed in packs. It is, however, often difficult to explain why so many theropods happened to die at the same time while feeding on a harmless carcass. It is more probable that the theropod skeletons represent individuals killed by other theropods in disputes over feeding privileges, an event that often occurs when large carnivorous mammals and reptiles compete over a kill.

Trackways are the closest thing we have to motion pictures of the behavior of fossil animals. A significant portion of the trackways of a diverse assortment of predatory dinosaurs are solitary, indicating that the maker was not part of a larger group. There are examples of multiple trackways of dinopredators that lie close together on parallel paths. In some cases, this may be because the track makers were forced to follow the same path along a shoreline even if they were moving independently of one another. But such parallel trackways are common enough to suggest some dinosaurian predators moved in small packs. That said, the big majority of avepod footprints track animals moving on their own as they patrolled or traveled along fresh- and saltwater shorelines.

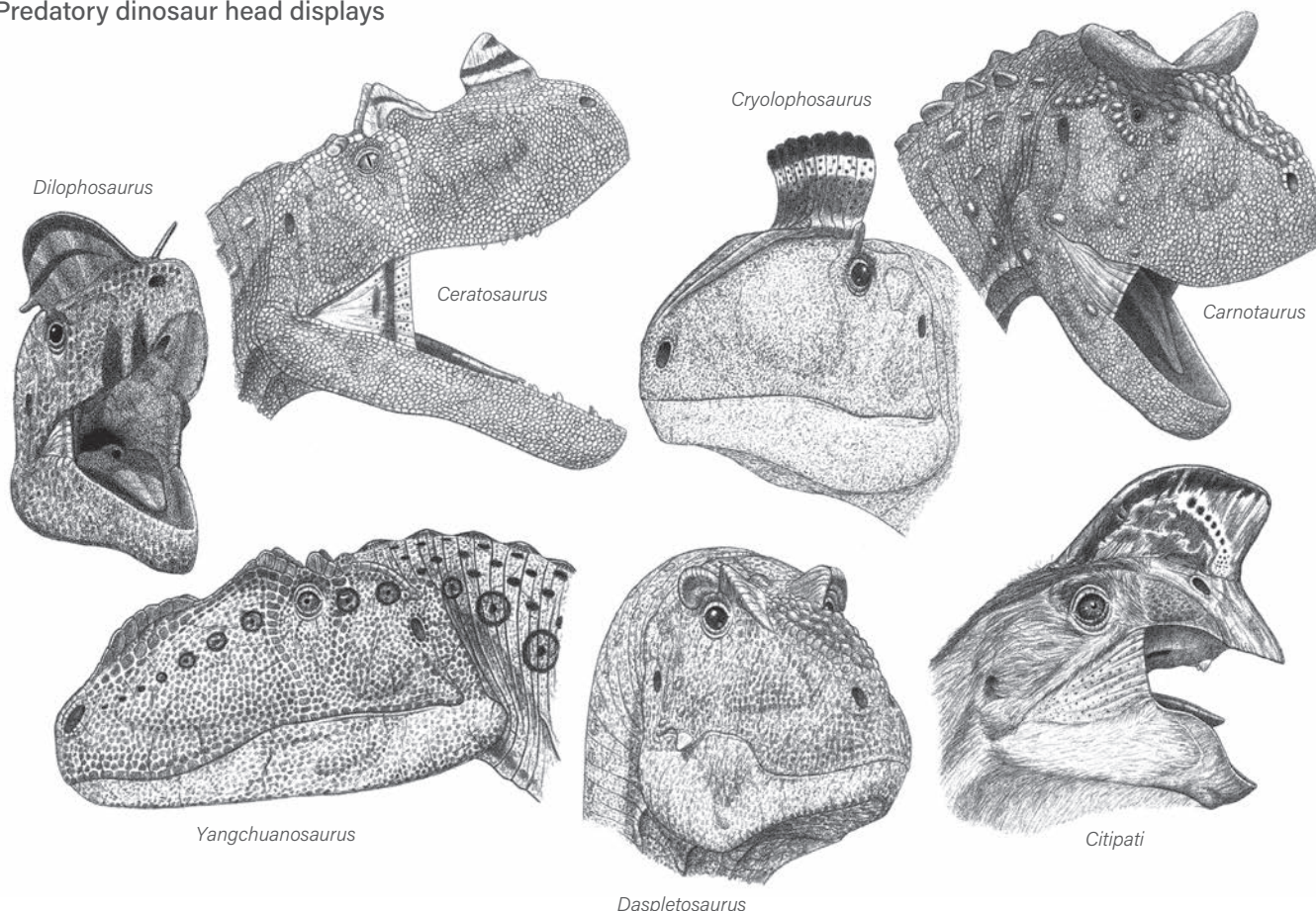
As for the herbivorous avepods, they may have been prone to move in pods, flocks, and herds. Flocking birds

almost always fly in single-species groups. On open ground where a lot of species dwell, herbivores such as wildebeest, zebras, ostriches, elephants, and gazelles often form collective herds, each taxon bringing its own best predator-detection system into the mix. One can imagine therizinosaurs, ornithomimids, and other predator-wary dinosaurs of assorted sizes doing the same, but multispecies bone beds indicating that dinosaurs did this have yet to be uncovered, so perhaps they did not.

REPRODUCTION

It has been suggested that some predatory dinosaur species exhibit robust and gracile morphs that represent the two sexes. It is difficult either to confirm or deny many of these claims because it is possible that the two forms represent different species. Males are often more robust than females, but there are exceptions. Female raptors are usually larger than the males, for instance, and the same is true of some whales. Attempts to use the depth of the chevron bones beneath the base of the tail to distinguish males from females have failed because the two factors are not consistent in modern reptiles. Head-crested oviraptorosaurs may be males if they are not mature individuals of both sexes. On the other hand, among cassowaries it is the females that have somewhat larger crests. This is

Predatory dinosaur head displays



atypical for crested birds, in which males have markedly larger display structures; that male cassowaries do a lot of the parenting may have something to do with their crest dimensions. The robust form of *Tyrannosaurus* has been tentatively identified as the female based on the inner bone tissues associated with egg production in birds, but the distribution of the stout and gracile morphs of this genus over stratigraphic time is more compatible with different species than with sexes. What is more suggestive of boys and girls is variation in size of the orbital bosses of *Tyrannosaurus* at a given geological level, although ontogeny may also be a factor. While preparing these guides, I realized that a pair of fairly complete *Allosaurus* skulls from the same quarry share features indicating they are a distinct species, yet they come in two forms, a deep and a shallow overall shape, providing perhaps the best evidence of dinosaurian gender identity yet observed.

Reptiles and some birds and mammals, including humans, achieve sexual maturity before reaching adult size, but most mammals and extant birds do not. Females that are producing eggs deposit special calcium-rich tissues on the inner surface of their hollow bones. The presence of this tissue has been used to show that a number of dinosaurs began to reproduce while still immature in terms of growth. The presence of still-growing aveairfoils brooding their nests confirms this pattern. Most or all predatory dinosaurs probably became reproductive before reaching full adult size.

The marvelous array of head and body crests, hornlets, bosses, and feathers evolved by assorted predatory dinosaurs shows that many were under strong sexual selective pressure to develop distinctive display organs and weapons to identify themselves to other members of their species and to succeed in sexual competition. The organs we find preserved record only a portion of these visual devices—those consisting of soft tissues and color patterns are largely lost. How these organs were used varied widely. Females used display organs to signal males of the species that they were suitable and fertile mates. Males used them both to intimidate male rivals and to attract and inseminate females.

Healthy animals in their reproductive prime are generally able to dedicate more resources to growing superior-quality displays better able to attract similar quality mates. Many dinosaurs probably engaged in intricate ritual display movements and vocalizations during competition and courtship, using display organs when they had them; these behavioral displays have been lost to time. The head and body display surfaces of many dinosaurs were oriented to the sides, so they had to turn themselves to best flaunt their display. This orientation was true of the avepods with the paired crests atop their snouts, which were popular, for reasons not known, in the Jurassic in podokesauroids, basal averostrans, and early tyrannosauroids. These crests did not make it into the Cretaceous as far as is known. The transversely flattened ceratosaur nasal horn was another

side view display organ, as were the hornlets and bosses common among a variety of big avepods. Large subtriangular hornlets above the orbits were a frequent feature, continuing into most tyrannosaurids. Then, just before the final extinction, the very similar *Tarbosaurus* and *Tyrannosaurus* entirely dropped the hornlets in favor of the bosses just aft of them. Why is unknown. In *Tyrannosaurus*, the earliest of the known species, *T. imperator*, bore distinctive long and rather low rugose spindle bosses, followed by the newly recognized and prominent upright discs of *T. rex*, which lived alongside *T. regina*, sporting its own boss form in a classic species identification pattern not yet seen in the rest of Theropoda. The transverse head crest of *Cryolophosaurus*, and the stout sideways projecting horns and domes of some abelisaurids, provided unusual frontal displays.

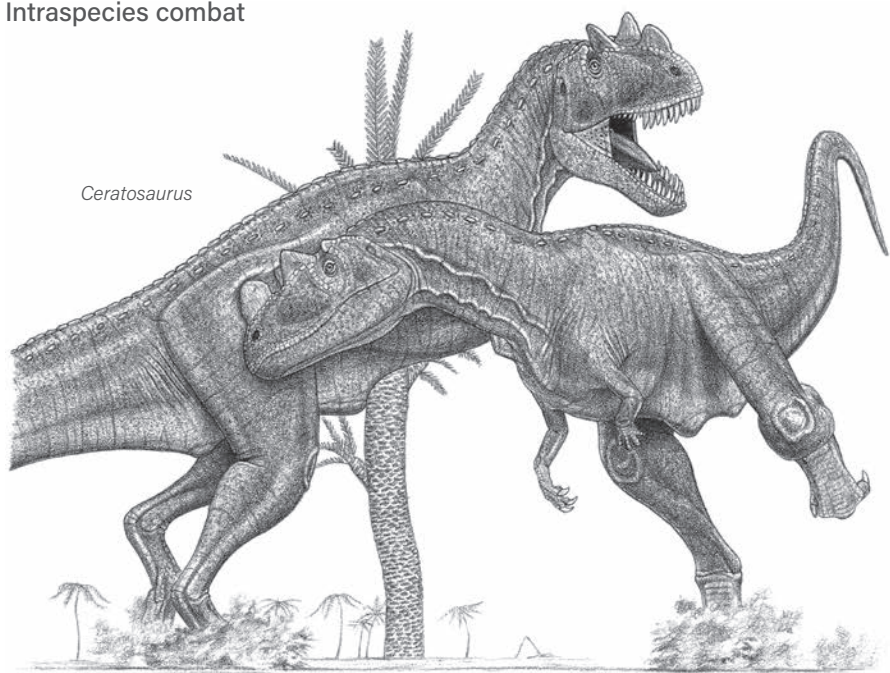
Many birds, including flightless examples that still have large arm-borne feathers, use their arm and tail arrays for intraspecific display, and such would have been probable in basal aveairfoils. Those with the capability to fly, as per archaeopterygians and microraptorines, could have done so while on the wing, twirling in the air as they showed off to one another. Simply fluffing up and bristling head and body feathers would have been a common means of close-up display.

While intraspecific competition is often fairly pacific to avoid casualties, it can be forceful and even violent in animals that bear weapons. Male hippos and lions suffer high injury and mortality from members of their own species, and the same may have been true of predatory theropods as males battled with sharp teeth and claws, as evidenced by the large number of wounds inflicted by such on theropod skulls.

In reptiles and birds, the penis and the testes are internal, and this was the condition in dinosaurs. Most birds lack a penis, but whether any more basal dinosaurs shared this characteristic is unknown. Presumably copulation was a quick process that occurred with the female lowering her shoulders and swinging her tail aside to provide clearance for the male, which reared behind her on two legs or even one leg while placing his hands on her back to steady them.

At least some dinosaurs from theropods to sauropods to ornithomimids produced hard-shelled eggs like those of birds rather than the softer-shelled eggs of reptiles, including crocodylians, and mammals. The evolution of calcified shells may have precluded live birth, which is fairly common among reptiles and is absent in birds. On the other hand, eggs of prosauropods and protoceratopsids appear to have been soft shelled, indicating that there was considerable variation in the feature in dinosaurs, perhaps even within subgroups. If so, that could help explain why remains of dinosaur eggs are surprisingly scarce through much of the Mesozoic. Even so, a growing collection of eggs and nests is now known for a variety of Late Jurassic and Cretaceous dinosaurs great and small. Firmly identifying the producer of a given type of egg requires the presence of intact eggs within the articulated trunk skeleton

Intraspecies combat



Ceratosaurus



Daspletosaurus

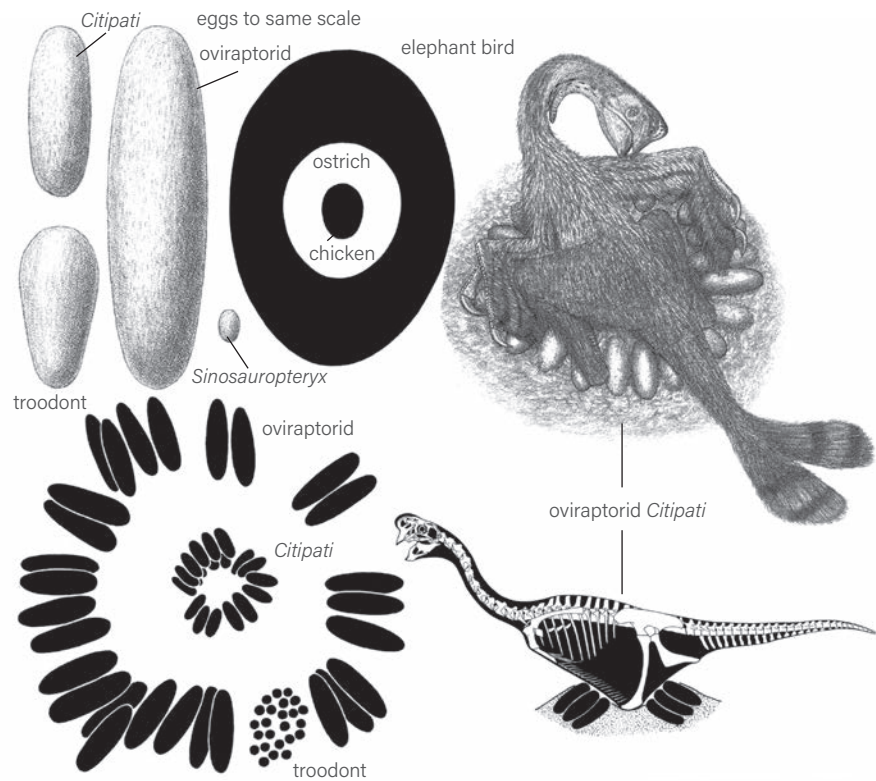
or identifiable embryo skeletons within the eggs, as well as adults found atop their nests in brooding posture. Because each dinosaur group produced distinctive types of eggshells and shapes, the differences can be used to further identify their origin, although the producers of many types remain obscure. While the eggs of some herbivorous dinosaurs were near-perfect spheres, as far as is known those of the meat eaters were elongated, very much so in oviraptorosaurs, and strongly tapered in troodonts. The surface texture of the egg was crenulated in some and bumpy in others. The arrangement of eggs within dinosaur bodies

and in their nests shows that they were formed and deposited in pairs as in reptiles, rather than singly as in birds. Even small reptiles lay small eggs relative to the size of the parent's body, whereas birds lay proportionally larger eggs. The eggs of small dinosaurs are intermediate in size between those of reptiles and birds. It is interesting that no known Mesozoic dinosaur eggs matches the size of the gigantic 12 kg (25 lb) eggs laid by the flightless elephant birds, which, as big as they got at nearly 400 kg (800 lb), was dwarfed by many dinosaurs. The largest Mesozoic dinosaur eggs discovered so far weighed 5 kg (11 lb) and probably belonged to 1-tonne-plus oviraptors.

Two basic reproductive stratagems are known as r-strategy and K-strategy: K-strategists are slow breeders that produce few young; r-strategists produce large numbers of offspring that offset high losses of juveniles. Rapid reproduction has an advantage. Producing large numbers of young allows a species to quickly expand its population when conditions are suitable, so r-strategists are "weed species" able to rapidly colonize new territories or promptly recover their population after it has crashed for one reason or another. As far as we know, predatory dinosaurs of all sizes were r-strategists that typically laid large numbers of eggs in the breeding season, although dinosaurs isolated on predator-free islands might have been slow breeders. This reproductive strategy may explain why dinosaurs laid smaller eggs than birds, most of which produce a modest number of eggs and provide the chicks with considerable parental attention.

One r-strategist bird group is the big modern ratites, which produce numerous eggs. This is in contrast to the big island ratites that laid only one to a few oversized eggs a year because the young were not at risk of being snarfed up by predators, until humans liquidated the populations just a thousand years ago in part by eating the giant eggs. Elephant-sized avepods were very different in this respect from same-sized mammals, which are K-strategists that produce few calves, which then receive extensive care over a span of years. Nor did any dinosaur nurse its young via milk-producing mammary glands. It is possible

Predatory dinosaur eggs and nests to same scales (shaded larger scale)



that some dinosaurs produced a “milk”-like substance in the digestive tract that was regurgitated to their young, as pigeons do, but there is no direct evidence of this.

It was long tacitly assumed that, like most reptiles, dinosaurs paid little or no attention to their eggs after burying them. A few lizards do stay with the nest, and pythons actually incubate their eggs with muscle heat. Crocodylians often guard their nests and hatchlings. All birds lavish attention on their eggs. Nearly all incubate the eggs with body heat; the exception is megapode fowl that warm eggs in mounds that generate heat via fermenting vegetation. The fowl carefully regulate the temperature of the nest by adding and removing vegetation to and from the mound. But when megapode chicks hatch, they are so well developed that the precocial juveniles quickly take off and survive on their own. The newly hatched chicks of ratites are also precocial, but they remain under the guardianship of adults that guide them to food sources and protect them from attack. Most bird chicks are altricial: they are so poorly developed when they break out of the egg that they have to be kept warm and fed by adults.

A spate of recent discoveries has revealed that the manner in which dinosaurs deposited eggs and then dealt with them and the offspring varied widely and was both similar to and distinctive from this behavior in living tetrapods.

Laying many eggs each breeding season helped overwhelm the ability of the local predators, including other avepods, to find and eat all the eggs and emerging hatchlings, although a fossil shows a large snake feeding on a just-emerged hatchling. Some dinosaur eggs whose makers have yet to be identified were buried in a manner that

implies they were not brooded. Not clear is if any parents stayed close to their nests to guard the eggs; currently there is no evidence that predaceous dinosaurs built heat-generating mounds, although some of the herbivorous variety did. Some prehatchling reptiles in mass nests start vocalizing to better coordinate their synchronous emergence, even though doing so risks attracting egg and hatchling eaters. On the positive side, hatchling chirping can inspire guarding parents to open up the nest and help release its chicks.

Because smaller dinosaurs did not face the problem of accidentally crushing their offspring, they had the potential to be more intensely parental. The best evidence for dinosaur brooding and incubating is provided by the bird-like aveairfoilan theropods, especially oviraptors. The large number of eggs, up to a few dozen in some cases, could not have been produced by a single female, so the nests were probably communal. The big ratites also nest communally, and the resulting brood is therefore that of multiple parents cared for by the locally dominant couple. Oviraptors laid their elongated eggs in two-layered rings with an open center. Laid flat, the eggs were partly buried and partly exposed. Because eggs left open to the elements would die from exposure or predation, eggs were not left exposed unless they were intended to be protected and incubated by adults. A number of oviraptor nests have been found with an adult in classic avian brooding posture atop the eggs, the legs tucked up alongside the hips, the arms spread over the eggs. The egg-free area in the center of the ring allowed the downward-projecting pubis of the deep pelvis to rest between the eggs without crushing them;

flatter-bellied birds do not need this space between their eggs. Presumably the arm and other feathers of oviraptorosaurs completely covered the eggs to protect them from inclement conditions and to retain the incubator's body heat. It is thought that brooding oviraptors were killed in place by sandstorms or more likely dune slides. The giant eggs appear to be of the type laid by oviraptors, and they too are laid in rings, in their case of enormous dimensions (up to 3 m, or 10 ft, across). These are the largest incubated nests known and were apparently brooded by oviraptors weighing a tonne or two—brooding by such big parents was made possible by the body being supported by the pubis between the eggs, rather than the entire body bearing down on the eggs. It may be that these are the biggest nests that are practical for brooding, and that prevented adult oviraptors from becoming even larger. In troodont nests the less-elongated eggs were laid subvertically in a partial spiral ring, again with the center open to accommodate the brooder's pelvis. The size of the adult troodonts found in brooding posture atop their nests is as small as 0.5 kg (1 lb). The half-buried, half-incubated nesting habits of *aveairfoilians* ideally represent the near-avian arrangement expected in the dinosaurs closest to birds. This scheme was retained in basal birds including enantiornithines, even those that were strongly arboreal. Egg brooding without external heat did not appear until more modern avians, in the Late Cretaceous, and nesting up in vegetation possibly not until the Cenozoic. Megapode fowl have undergone a reversal by incubating eggs in fermenting vegetation mound nests that they carefully maintain at the proper temperature. We humans tend to presume that it was females that did most or all of the brooding, but in birds, including ratites, males often do a lot of the egg and nestling warming, and male cassowaries do all of it.

A problem that all embryos that develop in hard-shelled eggs face is getting out of that shell when the time is right. The effort to do so is all the harder when the egg is large and the shell correspondingly thick. Fortunately, some of the shell is absorbed and used to help build the skeleton of the growing creature. Baby birds use an "egg tooth" to

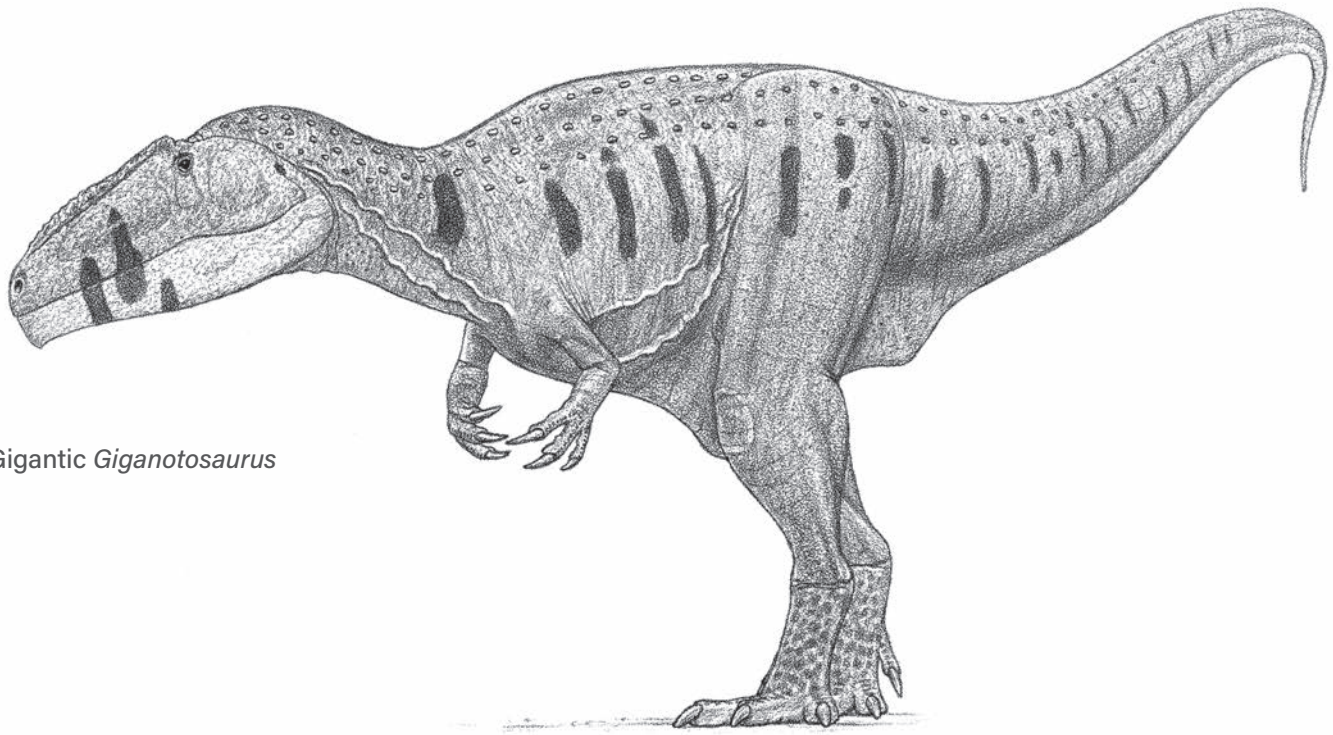
achieve the breakout, and such is likely among the Mesozoic relations. While fossil evidence is not on hand, it is likely that the hatchlings of the carnivorous dinosaurs were precocial, being immediately ready to leave the nest and feed themselves like the chicks of ratites and many fowl. Parental care probably ranged from nonexistent as it is for modern megapode fowl chicks to extensive in dinosaurs; in a number of cases it probably exceeded that seen in reptiles or even crocodylians, rivaling that of birds. Upon hatching the babies of adults over half a tonne were probably on their own, the size disparity rendering parental care impractical. Juvenile tyrannosaurids were unusual in having elongated snouts, the opposite of the short faces of juveniles cared for by their parents. This suggests that growing tyrannosaurids hunted independently of the adults, who may have seen the youngsters as potential meals. Suggestions that the gracile juvenile tyrannosaurids hunted prey for their parents are implausible; when food is exchanged between juveniles and adults, it is the latter who feed the former. Collective trackways clearly indicative of dinosaur packs or flocks incorporating potential parents and offspring are not known. Dinosaurs of a few hundred kilograms on down that tended to their nests are the best candidates for parenting. The nonpredatory elaphosaurs, medium-sized therizinosaurs, oviraptors, and especially the ratite-like ornithomimosaur were most likely to have practiced the scheme of precocial chicks following their adults as the former feed themselves. If so, it is very possible that males did much or most of the caretaking in some taxa. When broods were large, they would have consisted of juveniles of assorted parents, cared for by a locally dominant couple ready to defend the chicks while leading them to suitable food sources. It is possible that no Mesozoic avepods brought food to helpless altricial nestlings that could not leave their nests.

What no dinosaur did was lavish its offspring with the intensive, often long-term parenting typical of many mammals. And because dinosaurs did not nurse, it is likely that most of them could grow up on their own normally or even if something happened to the grown-ups.

GROWTH

All land reptiles grow slowly. This is true even of giant tortoises and big, energetic (by reptilian standards) monitors. Land reptiles can grow most quickly only in perpetually hot equatorial climates, and even then they are hard pressed to reach a tonne. Aquatic reptiles can grow more rapidly, probably because the low energy cost of swimming allows them the freedom to acquire the large amounts of food needed to put on bulk. But even crocodylians, including the extinct giants that reached nearly 10 tonnes, do not grow as fast as many land mammals. Mature reptiles tend to continue to grow slowly throughout their lives.

Some marsupials and large primates, including humans, grow no faster or only a little faster than the fastest-growing land reptiles. Other mammals, including other marsupials and a number of placentals, grow at a modest pace. Still others grow very rapidly; horses are fully grown in less than two years, and aquatic whales can reach 50 to 100 tonnes in just a few decades. Bull elephants take about 30 years to mature. All living birds grow rapidly; this is especially true of altricial species and the big ratites. No extant bird takes more than a year to grow up, but some of the recently extinct giant island ratites may have taken a few years to complete growth. The secret to fast growth appears



Gigantic *Gigantotyrannus*

to be having an aerobic capacity high enough to allow the growing juvenile, or its adult food provider, to gather the large amounts of food needed to sustain rapid growth.

High mortality rates from predation, disease, and accidents make it statistically improbable that unarmored, nonaquatic animals will live very long lives, so they are under pressure to grow rapidly. On the other hand, starting to reproduce while still growing tends to slow down the growth process as energy and nutritional resources are diverted to produce offspring. Few mammals and no living birds begin to breed before they reach adult size. No bird continues to grow once it is mature, nor do most mammals; however, some marsupials and elephants never quite cease growing.

At the microscopic scale the bone matrix is influenced by the speed of growth, and the bone matrix of dinosaurs tended to be more similar to that of birds and mammals, which grows at a faster pace than that of reptiles. Bone ring counts are being used to estimate the growth rate and life span of an increasing number of extinct dinosaurs, but this technique can be problematic because some living birds lay down more than one ring in a year, so ring counts can overestimate age and understate growth rate. There is also the problem of animals that do not lay down growth rings; it is probable that they grow rapidly, but exactly how fast is difficult to pin down. There are additional statistical issues because as animals grow, the innermost growth rings tend to be destroyed, leading to difficulties in estimating the

number of missing age markers. Almost all dinosaurs sampled so far appear to have grown at least somewhat faster than land reptiles. A possible exception is a very small, bird-like troodontid theropod whose bone rings seem to have been laid down multiple times in a year, perhaps because it was reproducing while growing. Most small dinosaurs fall along the lower end of the mammalian zone of growth, perhaps because they were reproducing while immature. Big dinosaur predators appear to have grown as fast as similar-sized land mammals, albeit with considerable variation between types. Tyrannosaurids appear to have been on the faster growth rate side of things, with *Tyrannosaurus* reaching final size in about two decades—note that a *Jurassic Park* scenario flaw as glaring as it usually goes unnoticed is the presence of gargantuan artificially bred dinosaurs so soon after the initiation of the paleo theme park project.

The cessation of significant growth of the outer surface of many adult dinosaur bones indicates that most but not all species did not grow throughout life. Medium-sized and large mammals and birds live for only a few years or decades: elephants live about half a century and giant whales can last longer, with the sluggish right whales making it well over 100 years. There is no evidence that dinosaurs lived longer than mammals or birds of similar size. Living in the fast lane, tyrannosaurs combined their rapid growth with rather short life spans of 20 to 30 years. Other giant avepods, such as *Gigantotyrannus*, did not grow as extremely fast and lived longer, up to half a century.

ENERGETICS

Vertebrates can utilize two forms of power production. One is aerobiosis, the direct use of oxygen taken in from the lungs to power muscles and other functions. Like air-breathing engines, this system has the advantage of producing power indefinitely but is limited in its maximum power output. An animal that is walking at a modest speed for a long distance, for instance, is exercising aerobically. The other is anaerobiosis, in which chemical reactions that do not immediately require oxygen are used to power muscles. Rather like rockets that do not need to take in air, this system has the advantage of being able to generate about 10 times more power per unit of tissue and time. But it cannot be sustained for an extended period and produces toxins that can lead to serious illness if sustained at too high a rate for too long, which is tens of minutes. Anaerobiosis also builds up an oxygen debt that has to be paid back during a period of recovery. Any fairly fast animal that is running, swimming, or power flying near its top speed is exercising anaerobically.

Most fish and all amphibians and reptiles have low resting bradymetabolic rates and low aerobic capacity. They are therefore bradyenergetic, and even the most energetic reptiles, including the most aerobically capable monitor lizards, are unable to sustain truly high levels of activity for extended periods. Many bradyenergetic animals are, however, able to achieve very high levels of anaerobic burst activity, such as when a monitor lizard or crocodylian suddenly dashes toward and captures prey. Because bradyenergetic animals do not have high metabolic rates, they are largely dependent on external heat sources, primarily the ambient temperature and the sun, for their body heat, so they are ectothermic. As a consequence, bradyenergetic animals tend to experience large fluctuations in body temperature, rendering them heterothermic. The temperature at which reptiles normally operate varies widely depending on their normal habitat. Some are adapted to function optimally at modest temperatures of 12°C (52°F). Those living in hot climates are optimized to function at temperatures of 38°C (100°F) or higher, so it is incorrect to generalize reptiles as “cold blooded.” In general, the higher the body temperature is, the more active an animal can be, but even warm reptiles have limited activity potential.

Most mammals and birds have high resting tachymetabolic rates and high aerobic capacity. They are therefore tachyenergetic and are able to sustain high levels of activity for extended periods. The ability to better exploit oxygen for power over time is probably the chief advantage of being tachyenergetic. Tachyenergetic animals also use anaerobic power to briefly achieve the highest levels of athletic performance, but they do not need to rely on this as much as reptiles, are not at risk of serious self-injury, and can recover more quickly. Because tachyenergetic animals have high metabolic rates, they produce most of their

body heat internally, so they are endothermic. As a consequence, tachyenergetic animals can achieve more stable body temperatures. Some, like humans, are fully homeothermic, maintaining a nearly constant body temperature at all times when healthy. Many birds and mammals, however, allow their body temperatures to fluctuate to varying degrees, for reasons ranging from going into some degree of torpor to storing excess heat on hot days, on a daily or seasonal basis. So they are semiheterothermic or semihomeothermic depending on the degree of temperature variation. The ability to keep the body at or near its optimal temperature is another advantage of having a high metabolic rate. Normal body temperatures range from 30°C to 44°C (86°F–105°F), with birds always at least at 38°C. High levels of energy production are also necessary to do the cardiac work that creates the high blood pressures needed to be a tall animal.

Typically, mammals and birds have resting metabolic rates and aerobic capacities about 10 times higher than those of reptiles, and differences in energy budgets are even higher. However, there is substantial variation from these norms in tachyenergetic animals. Some mammals, among them monotremes, some marsupials, hedgehogs, armadillos, sloths, and manatees, have modest levels of energy consumption and aerobic performance, in some cases not much higher than those seen in the most energetic reptiles. In general, marsupials are somewhat less energetic than their placental counterparts, so kangaroos are about a third more energy efficient than deer. Among birds, the big ratites are about as energy efficient as similar-sized marsupials. At the other extreme, some small birds share with similarly tiny mammals extremely high levels of oxygen consumption even when their small body size is taken into account.

Widely different energy systems have evolved because they permit a given species to succeed in its particular habitat and lifestyle. Reptiles enjoy the advantage of being energy efficient, allowing them to survive and thrive on limited resources. Tachyenergetic animals are able to sustain much higher levels of activity that can be used to acquire even more energy, which can then be dedicated to the key factor in evolutionary success, reproduction. Tachyenergy has allowed mammals and birds to become the dominant large land animals from the tropics to the poles. But reptiles remain very numerous and successful in the tropics and, to a lesser extent, in the temperate zones.

As diverse as the energy systems of vertebrates are, there appear to be things that they cannot do. All insects have low, reptile-like resting metabolic rates. When flying, larger insects use oxygen at very high rates similar to those of birds and bats. Insects can therefore achieve extremely high maximal/minimal metabolic ratios, allowing them to be both energy efficient and aerobically capable. Insects

can do this because they have a dispersed system of tracheae that oxygenate their muscles. No vertebrate has both a very high aerobic capacity and a very low resting metabolism, probably because the centralized respiratory–circulatory system requires that the internal organs work hard even when resting in tachyenergetic vertebrates. An insect-like metabolic arrangement should not, therefore, be applied to dinosaurs. However, it is unlikely that all the energy systems that have evolved in land vertebrates have survived until today, so the possibility that some or all dinosaurs were energetically exotic needs to be considered.

The general assumption until the 1960s was that dinosaur energetics was largely reptilian, but most researchers now agree that their power production and thermoregulation were closer to those of birds and mammals. It is also widely agreed that because dinosaurs were such a large group of diverse forms, there was considerable variation in their energetics, as there is in birds and especially mammals.

Reptiles' nonerect, sprawling legs are suitable for the slow walking speeds of 1–2 km/h (0.5–1 mph) that their low aerobic capacity can power over extended periods. Sprawling limbs also allow reptiles to easily drop onto their belly and rest if they become exhausted. No living bradyenergetic animal has erect legs. Walking is always energy expensive—it is up to a dozen times more costly than swimming the same distance—so only aerobically capable animals can easily walk faster than 3 km/h. The long, erect legs of dinosaurs matched those of birds and mammals and favored the high walking speeds of 3–10 km/h (2–6 mph) that only tachyenergetic animals can sustain for hours at a time. The speed at which an animal of a given size is moving can be approximately estimated from the length of its stride—an animal that is walking slowly steps with shorter strides than it does when it picks up the pace. The trackways of tridactyl dinosaurs show that they normally walked at speeds of 4–7 km/h (average 4 mph), much faster than the slow speeds recorded in the trackways of prehistoric reptiles. Dinosaur legs and the trackways they made both indicate that the dinosaurs' sustained aerobic capacity well exceeded the reptilian maximum. That meant that they could forage over much longer ranges and areas than carnivores with reptilian energetics. They also had the potential to migrate, but big cats, canids, and hyenas tend not to do so, finding it more selectively advantageous to stay in place and go after the local herbivores and any that are passing by on their arduous migrations.

Even the fastest reptiles have slender leg muscles because their low-capacity respirocirculatory systems cannot supply enough oxygen to a larger set of locomotory muscles. Mammals and birds tend to have large leg muscles that propel them at a fast pace over long distances. As a result, mammals and birds have a large pelvis that supports a broad set of thigh muscles. It is interesting that protodinosaur and first theropods had a short pelvis that could have anchored only a narrow thigh, yet their legs are long

and erect. Such a combination does not exist in any modern animal. This suggests that the small-hipped dinosaurs had an extinct metabolic system, probably intermediate between those of reptiles and mammals. All other avepods had the large hips able to support the large thigh muscles typical of more aerobically capable animals.

That many dinosaurs, therizinosaurs most of all among avepods, could hold their brains far above the level of their hearts indicates that they had the high levels of power production seen in similarly tall birds and mammals.

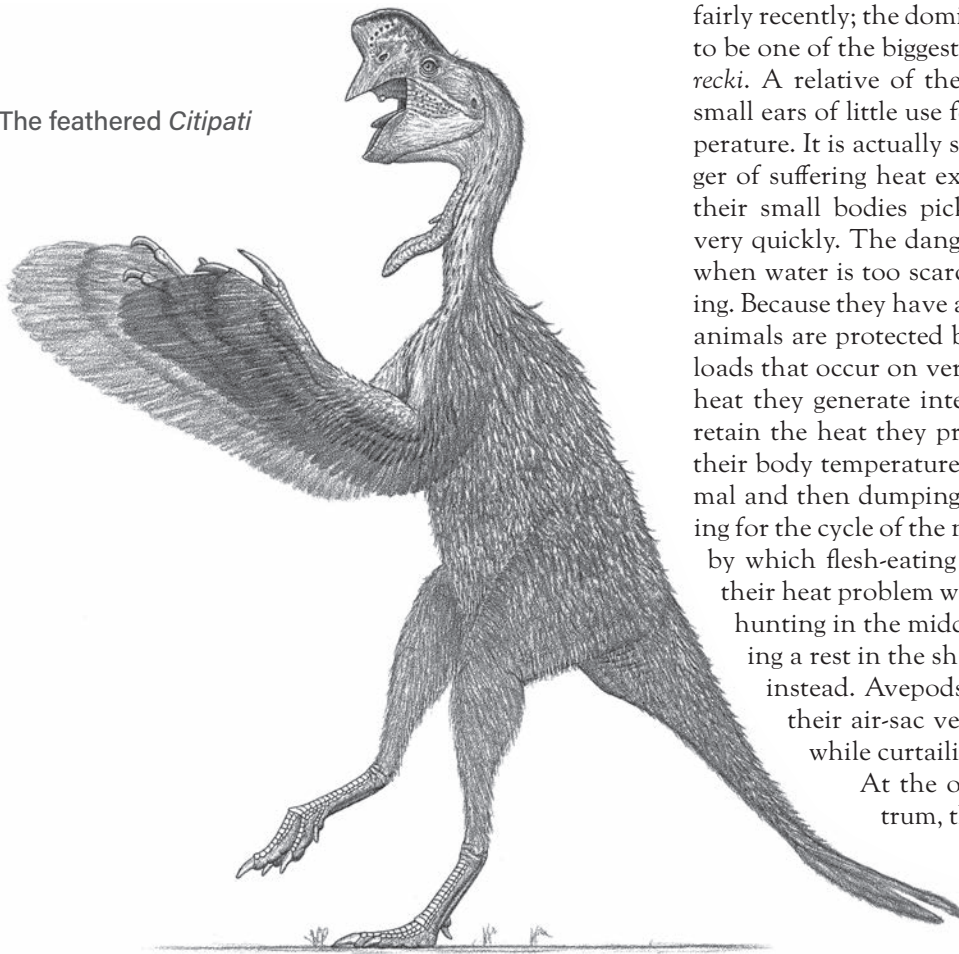
If we turn to breathing, an intermediate metabolism is compatible with the unsophisticated lungs that protodinosaur and basal dinopredators appear to have had. The increasingly highly efficient birdlike air-sac-ventilated respiratory complex of avepod theropods is widely understood as being evidence that elevated levels of oxygen consumption were further evolving in these dinosaurs.

Many birds and mammals have large nasal passages that contain respiratory turbinals. These are used to process exhaled air in a manner that helps retain heat and water that would otherwise be lost during the high levels of respiration associated with high metabolic rates. Because they breathe more slowly, reptiles do not need or have respiratory turbinals. Some researchers point to the lack of preserved turbinals in dinosaur nasal passages, and the small dimensions of some of the passages, as evidence that dinosaurs had the low respiration rates of bradyenergetic reptiles. However, some birds and mammals lack well-developed respiratory turbinals, and in a number of birds they are completely cartilaginous and leave no bony traces. Some birds do not even breathe primarily through their nasal passages: California condors, for example, have tiny nostrils. The space available for turbinals has been underestimated in some dinosaurs, including the usually big-snouted dinopredators. Overall, the turbinal evidence does not seem to be definitive.

The presence of a blanket of hollow fibers in a growing array of small dinosaurs is strong evidence of elevated metabolic rates. Such insulation hinders the intake of environmental heat too much to allow ectotherms to quickly warm themselves and is never found adorning bradyenergetic animals. The evolution of insulation early in the group indicates that high metabolic rates also evolved near the beginning of the group or in their ancestors. The uninsulated skin of many dinosaurs is compatible with high metabolic rates, as in mammalian giants, many suids, human children, and even small naked tropical bats. The tropical climate most dinosaurs lived in reduced the need for insulation, and the bulk of large dinosaurs eliminated any need for it.

The low exercise capacity of land reptiles appears to prevent them from being active enough to gather enough food to grow rapidly. In an expression of the principle that it takes money to make money, tachyenergetic animals are able to eat the large amounts of food needed to produce the power needed to gather the additional large

The feathered *Citipati*



amounts of food needed to grow rapidly. Tachyenergetic juveniles either gather the food themselves or are fed by their parents. That the predatory dinosaurs, large and small, usually grew at rates faster than those seen in land reptiles of similar size indicates that the former had higher aerobic capacity and energy budgets.

A hot topic has been the concern by many that giant dinosaurs would have overheated in the Mesozoic greenhouse if they had avian- or mammalian-like levels of energy production. However, the largest animals dwelling in the modern tropics, including deserts, are big birds and mammals. And consider that there are no reptiles over a tonne dwelling in the balmy tropics. Further consider that some of the largest elephants—similar in mass to the greatest avepods—live in the Namib Desert of the Skeleton Coast of southwestern Africa, where they often have to tolerate extreme heat and sun without the benefit of shade. It is widely thought that elephants use their ears to keep themselves cool when it is really hot, something dinosaurs could not do. However, elephants flap their ears only when the ambient temperature is below that of their bodies. When the air is as warm as the body, heat can no longer flow out, and flapping the ears actually picks up heat when the air is warmer than the body. Nor was the big-eared African elephant the main savanna elephant until

fairly recently; the dominant open-area proboscidean used to be one of the biggest land mammals ever, *Palaeoloxodon recki*. A relative of the Asian elephant, it probably had small ears of little use for shedding body heat at any temperature. It is actually small animals that are most in danger of suffering heat exhaustion and heat stroke because their small bodies pick up heat from the environment very quickly. The danger is especially acute in a drought, when water is too scarce to be used for evaporative cooling. Because they have a low surface area/mass ratio, large animals are protected by their bulk against the high heat loads that occur on very hot days, and they can store the heat they generate internally. Large birds and mammals retain the heat they produce during the day by allowing their body temperature to climb a few degrees above normal and then dumping it into the cool night sky, preparing for the cycle of the next day. A basic behavioral means by which flesh-eating dinosaurs would have minimized their heat problem would have been by simply avoiding hunting in the middle of hot, sunny days, instead taking a rest in the shade or a bath in water, if available, instead. Avepods of all sizes have been able to use their air-sac ventilation system to help keep cool while curtailing water loss.

At the other end of the temperature spectrum, the presence of a diverse array of dinosaurs in temperate polar regions and highlands that are known to have experienced freezing conditions during the winter, and were not particularly warm even in the summer, provides additional evidence that dinosaurs were better able to generate internal heat than reptiles, which were scarce or totally absent in the same habitats. It was not practical for land-walking dinosaurs to migrate far enough toward the equator to escape the cold; it would have cost too much in time and energy, and in some locations, oceans barred movement toward warmer climes. A point that is unknown is whether large polar and high-altitude dinosaurs retained bare skin, in which case they would have needed high internal heat production to ward off frostbite, or whether they were heavily insulated, which also supports tachyendothermy. That the largest known, over a tonne, Early Cretaceous tyrannosauroid living at chilling high altitudes was well feathered hints at possibilities. The largest known polar avepods were Late Cretaceous tyrannosaurids over two tonnes, but the status of their skin remains unknown. The discovery of probable dinosaur burrows in then-polar Australia suggests that some small dinosaurs did hibernate through the winter in a manner similar to bears. While many if not all the burrows were dug by herbivores, the cold-evading flesh eaters may have evicted them on occasion to squat on the property.

Bone isotopes have been used to help assess the metabolism of dinosaurs. These can be used to examine the



Alaskan *Nansaurus*

Mongolian *Therizinosaurus* vs. *Tarbosaurus*



Winter scenes

temperature fluctuations that a bone experienced during life. If the bones show evidence of strong temperature differences, then the animal was heterothermic on either a daily or seasonal basis. In this case the animal could have been either a bradyenergetic ectotherm or a tachyenergetic endotherm that hibernated in the winter. The results indicate that most dinosaurs, large and small, were more homeothermic, and therefore more tachyenergetic and endothermic, than crocodylians from the same formations.

Bone biomolecules too are being used to restore the metabolic rates of dinosaurs. This effort is in its early stages, and it is not clear that the sample of living and fossil animals of known metabolic levels is yet sufficient to establish the reliability of the method. Also, the sample of dinosaurs is too limited to allow high confidence in the results to date, which is all the more true because the estimates for dinosaurs appear inconsistent in peculiar ways. While the one armored ankylosaur is attributed with a high energy budget that appears excessive for such a relatively slow-moving creature with weak dentition, the sole armored stegosaur is recovered well down in the reptilian range, which looks both too low for an animal with long, erect legs and fairly fast growth and too different from the other armored dinosaur. Also problematic is that reptilian energetics are assigned to the hadrosaur and the ceratopsid examined, not the higher levels expected in animals with such fast food processing and growth and with the large leg muscles and fast-walking pace expected in tachyenergetic endotherms. Also of note is the low metabolism of the giant flying marine pterosaur. The initial biomolecule results indicating that the earliest dinosaurs were endotherms, with avepods big and small remaining so, await further analysis.

Because the most basal and largest of living birds, the ratites, have energy budgets similar to those of marsupials, it is probable that most or all of their Mesozoic relatives did not exceed this limit. This fits with some bone isotope data that seem to indicate that dinosaurs had moderately high levels of food consumption, somewhat lower than seen in most placentals of the same size. Possible exceptions include polar dinosaurs that remained active in the winter and needed to produce lots of warmth. At the opposite end of the spectrum, early dinosaurs, and awkward therizinosaurs, probably had modest energy budgets like those of the less-energetic mammals. It is likely that dinosaurs, like birds, were less prone to controlling their body temperatures as precisely as do many mammals. This is in accord with their tendency to lay down bone rings. Because they lived on a largely hot planet, it is probable that most dinosaurs had high body temperatures of 38°C (100°F) or more to be able to resist overheating. The possible exception was again high-latitude dinosaurs, which may have adopted slightly lower operating temperatures and saved some energy, especially if they were active during the winter. Some researchers have characterized

dinosaurs as mesotherms, intermediate between reptiles on the one hand and mammals and birds on the other. But because some mammals and birds themselves are metabolic intermediates, and dinosaurs were probably diverse in their energetics, with some in the avian–mammalian zone, it is not appropriate to tag dinosaurs with a uniform, intermediary label.

Until the 1960s it was widely assumed that high metabolic rates and/or endothermy were an atypical specialization among animals, being limited to mammals and birds, and perhaps to some therapsid ancestors of mammals and the flying pterosaurs. The hypothesis was that being tachyenergetic and endothermic is too energy expensive and inefficient for most creatures and evolved only in special circumstances, such as the presence of live birth and lactation or powered flight. Energy efficiency should be the preferred status of animals, as it reduces their need to gather food in the first place. Since then it has been realized that varying forms of tachyenergy definitely are or probably were present in large flying insects, some tuna and lamnid sharks, some basal Paleozoic reptiles, some marine turtles and the oceangoing plesiosaurs, ichthyosaurs, and mosasaurs, brooding pythons, basal archosaurs, basal crocodylians, pterosaurs, all dinosaurs including birds, some pelycosaur, therapsids, and mammals. Energy-expensive elevated metabolic rates and body temperatures appear to be a widespread adaptation that has evolved multiple times in animals of the water, land, and air. This should not be surprising in that being highly energetic allows animals to do things that bradyenergetic ectotherms cannot do, and DNA selection acts to exploit available lifestyles that allow reproductive success without a priori caring whether it is done energy efficiently or not. Whatever works, works. So many animals do live on low, energy-efficient budgets, while others follow the scheme of using more energy to acquire yet more energy that can be dedicated to reproducing the species.

A long-term debate asks what specifically it is that leads animals to be tachyenergetic and endothermic. One hypothesis proposes that it is habitat expansion, that animals able to keep their bodies warm when it is cold outside are better or exclusively able to survive in chilly places—near the poles, at high altitudes, in deep waters—or during frosty nights. The other proffers that only tachyenergetic animals with high aerobic capacity can achieve high levels of sustained activity regardless of the ambient temperature, whether at sea level in the tropical daylight or during polar winter nights, and that ability is critical to going high energy. Certainly the first hypothesis is true, but it is also true that all of the many animal groups that feature high energy budgets and warmer-than-ambient body temperatures also thrive in warm and even hot climes, where they beat out the bradyenergetic creatures in activity levels. So both hypotheses are operative, and which is more so depends on the biocircumstances—including being really big on land.

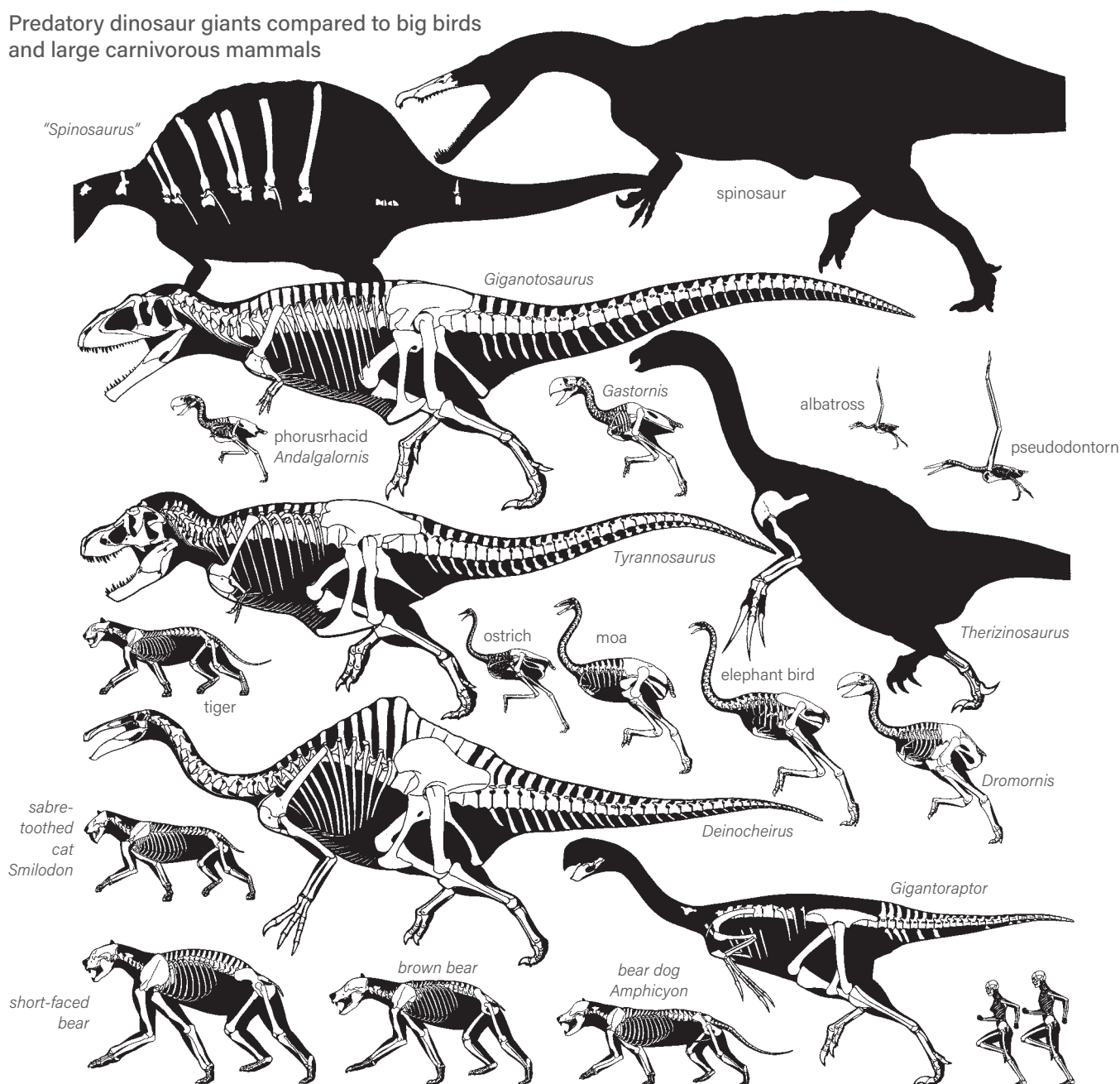
GIGANTISM

Although dinosaurs evolved from small protodinosaur, and many were small—birds included—dinosaurs are famous for their tendency to develop gigantic forms. The average mammal is the size of a dog, whereas the average fossil dinosaur was bear sized. But those are just averages. Predatory theropods reached as much as 10 plus tonnes, as big as elephants and dwarfing the largest carnivorous mammals by a factor or 10 or more.

Among land animals whose energetics are known, only those that are tachyenergetic have been able to become gigantic on land. The biggest fully terrestrial reptiles, some

oversized tortoises and monitors, have never much exceeded a tonne. Land reptiles are probably not able to grow rapidly enough to reach great size in reasonable time. Other factors may also limit their size. It could be that living at 1 g, the normal force of gravity, without the support of water is possible only among animals that can produce high levels of sustained aerobic power. The inability of the low-power, low-pressure reptilian circulatory system to pump blood far above the level of the heart probably helps limit the size of bradyenergetic land animals. That a number of Mesozoic dinosaurs, including those predaceous,

Predatory dinosaur giants compared to big birds and large carnivorous mammals



exceeded a tonne, as have mammals since then, is compelling evidence that they too had high aerobic power capacity and the correspondingly elevated energy budgets.

The hypothesis that only tachyenergetic animals can grow to enormous dimensions on land is called terramegathery. An alternative concept, gigantothermy, proposes that the metabolic systems of giant reptiles converge with those of giant mammals, resulting in energy efficiency in all giant animals. In this view, giants rely on their great mass, not high levels of heat production, to achieve thermal stability. This idea reflects a misunderstanding of how animal power systems work. A consistently high body temperature does not provide the motive power needed to sustain high levels of activity; it merely allows a tachyenergetic animal, and only an animal with a high aerobic capacity, to sustain high levels of activity around the clock. A gigantic reptile with a high body temperature would still not be able to remain highly athletic for extended periods. Measurements show that the metabolic rates and aerobic capacity of elephants and whales are as high as expected in mammals of their size and are far higher than those of the biggest crocodylians and turtles, which have the low levels of energy production typical of reptiles. Also pushing animals to be big is improved thermoregulation—the high bulk to relatively low surface area ratio making it easier both to retain internal warmth when it is chilly and to keep external heat out and store heat on hot days.

Another subtle reason that dinosaurs, particularly sauropods, could become so enormous has to do with their mode of reproduction. Because big mammals are slow-breeding K-strategists that lavish attention and care on the small number of calves they produce, there always has to be a large population of adults present to raise the next generation. A healthy herd of elephants has about as many breeding adults as it does juveniles, which cannot survive without parental care. Because there always has to be a lot of grown-ups, the size of the adults has to be limited in order to avoid overexploiting their ecosystem's food resources, which will cause the population to collapse. This constraint appears to limit slow-reproducing mammalian

herbivores from exceeding 10–20 tonnes. Flesh eaters live off an even smaller resource base because they prey on the surplus herbivores, and it seems that carnivorous mammals cannot maintain a viable population if they are larger than between 0.5 and 1 tonne.

Because giant dinosaurs were fast-breeding r-strategists that produced large numbers of offspring that could care for themselves, their situation was very different from that of big mammals. A small population of adults, approaching or in the area of the low six figures, was able to produce large numbers of young each year. Even if all adults were killed off on occasion, their eggs and offspring could survive and thrive, keeping the species going over time. Because dinosaurs could get along with smaller populations of adults, the grown-ups were able to grow to enormous dimensions without overexploiting their resource base. This evolutionary scheme allowed plant-eating dinosaurs to grow to over 20 to, perhaps on occasion, 200 tonnes. Because the bulk of the biomass of adult dinoherbivores was tied up in oversized giants, the theropods needed to evolve great size themselves in order to be able to fully access the nutrition tied up in the huge adults—the idea that theropods grew to 6 to 10 tonnes only to “play it safe” by consistently hunting smaller juveniles is not logical—and the fast-breeding and fast-growing, high-energy predators had the ability to reach such tremendous size. The existence of oversized predators in turn may have resulted in a size race in which sauropods evolved great size in part as protection against their enemies, which later encouraged the appearance of supersized theropods that could bring them down.

In the 1800s Edward Cope proposed what has become known as Cope's Rule, the tendency of animal groups to evolve gigantism. The propensity of dinosaurs to take this evolutionary pattern to an extreme means that the Mesozoic saw events on land that are today limited to the oceans. In modern times combat between giants occurs between orcas up to 10 tonnes and whales up to 200. In the dinosaur era it occurred between orca-sized theropods and whale-sized sauropods, hadrosaurs, and ceratopsids.

HUNTING, SCAVENGING, AND DEFENSE

None of the sauropodomorph or ornithischian dinosaurs were archpredators. That does not mean, however, they were purely pacific plant eaters. Ratites are omnivores happy to snatch up small creatures and insects. Even cattle and deer occasionally ingest animal protein and calcium. The dinosaurs least prone to do so would have been those large ornithopod ornithischians with blunt beaks. Most ornithischians, as well as oviraptorosaurs, had sharp beaks, sometimes hooked, and in some cases fangs that would have allowed them to catch and dispatch prey and to scavenge. They would have been suid-like omnivores, including the big-horned ceratopsids that may have competed

with tyrannosaurids for access to carcasses. With their long necks, sauropods, prosauropods, therizinosaurs, ornithomimids, and elaphrosaurs would have had no trouble reaching out and up to pick up small creatures, and dine on dead corpses, to supplement their vegetarian diets. While sauropod heads look small, that is relative to the rest of their bodies. In absolute terms their heads could be quite large, the mouth of *Giraffatitan* was a third of a meter broad and could swallow creatures weighing tens of kilograms—the children in *Jurassic Park* would not have been as safe as they seemed.

Among dinosauriforms, only protodinosaur, herrerasaurs, and theropods—mostly avepods but excluding

nonpredaceous elaphrosaurs, ornithomimosaur, therizinosaurs, oviraptorosaurs, and alvarezsaur—were full-blown flesh and, to a certain extent, bone-craving predaceous carnivores that made a living by eating other vertebrates for their main sustenance. While doing so the only competition they had to deal with were a few terrestrial crocodylians, none of which were giants.

A big difference between Mesozoic and Cenozoic circumstances is the size factor. In the Age of Mammals, the biggest terrestrial carnivores have been one tonners going after 10 to 20 tonners. In the Age of Dinosaurs, it was 5–10 tonne avepods assaulting sauropods of 20 to 200 tonnes, for reasons that were just discussed.

Another contrast between dinosaur and mammal predator–prey affairs is that therian hunting is limited to adults often involved with raising and feeding their innocuous young and to large juveniles in training, whereas the juveniles of predaceous dinosaurs, especially the larger examples, were deadly hunters competing with similar-sized adults of other species while posing a serious threat to prey dinosaurs. This is a fundamental difference—one driven by radically different reproductive adaptations—between the dinosaur-dominated versus mammal-dominated predator–prey faunas of the Mesozoic versus Cenozoic.

Shared with hunting mammals was that most dinosaur habitats and faunas had more than one big predator in each one: *Allosaurus*, *Ceratosaurus*, and *Torvosaurus* in the Morrison; *Giganotosaurus* and *Ekrixinatosaurus* in the Candeleros; *Carcharodontosaurus* and *Rugops* in the Echkar; *Gorgosaurus* and *Daspletosaurus* in Dinosaur Park; *Tarbosaurus* and *Alioramus* in the Nemegt; and *Tyrannosaurus*, *Nanotyrannus*, and *Stygivenator* in the Hell Creek, Lance, and other formations, with *T. rex* and *T. regina* alive at the same time. This is similar to bears, wolves, and cougars in western North America and lions, leopards, cheetahs, hyenas, and hunting dogs in eastern and southern Africa. That the Horseshoe Canyon fauna seems to have featured only *Albertosaurus* seems to have been a rarity.

In a given dinosaur habitat each predator species and individual would tend to concentrate on those prey items best suited for the carnivore's characteristics regarding its size, speed, and killing power and techniques. Giant adults would focus on mega prey, while their juvenile and small theropods would be limited to similarly lesser victims on down to insects no grown-up *Tyrannosaurus* would consider dining upon. Even so, there was lots of dietary overlap. Wolves eat caribou and moose as well as the voles and mice coyotes commonly target. Cape hunting dogs snap up rodents, and their packs bring down big ungulates. It is possible that robust *Daspletosaurus* was more prone to taking on the combative parrot-beaked and horned ceratopsids while its more gracile competitor *Gorgosaurus* went after the more vulnerable duck-billed hadrosaurs, but both probably fed on the other's preference on a common basis. While lithe *Stygivenator*, *Nanotyrannus*, and juvenile *Tyrannosaurus* were all targeting different, smaller prey than the

massive adults of the latter, the bigger arms, less robust teeth, and more gracile legs of *Stygivenator* and *Nanotyrannus* show they were doing so in a different manner from young *Tyrannosaurus* and quite successfully—they outnumbered the fast-growing *Tyrannosaurus* two to one. In some cases what was eating what is more perplexing. *Allosaurus* was generally larger than contemporary *Ceratosaurus*, but the latter had larger teeth so may have been more prone to attack sauropods and stegosaurs than it first appears.

A main means by which Mesozoic predatory dinosaurs small and large and young and old caught prey was by running it down, all examples having the well-muscled, flexed, long-footed, birdy legs needed to run at good speed. And they all had the elevated aerobic exercise capacity and high body temperatures that allowed them to sustain the high speeds to a greater degree than did bradyaerobic reptiles, this being most true in avepods yet more so in the big-hipped averostrans and beyond. Among the big dinosaurian carnivores, it was long-legged, large-hipped, small-armed abelisaur and especially the tyrannosaurids of the Late Cretaceous that went the furthest in regard to the speed pursuit factor. The Cenozoic predatory ground birds of South America could have given their Mesozoic predecessors a run for their money. Few mammal hunters could match or exceed the avepods pace, the exception being cheetahs, which are probably the fastest of land animals to have evolved.

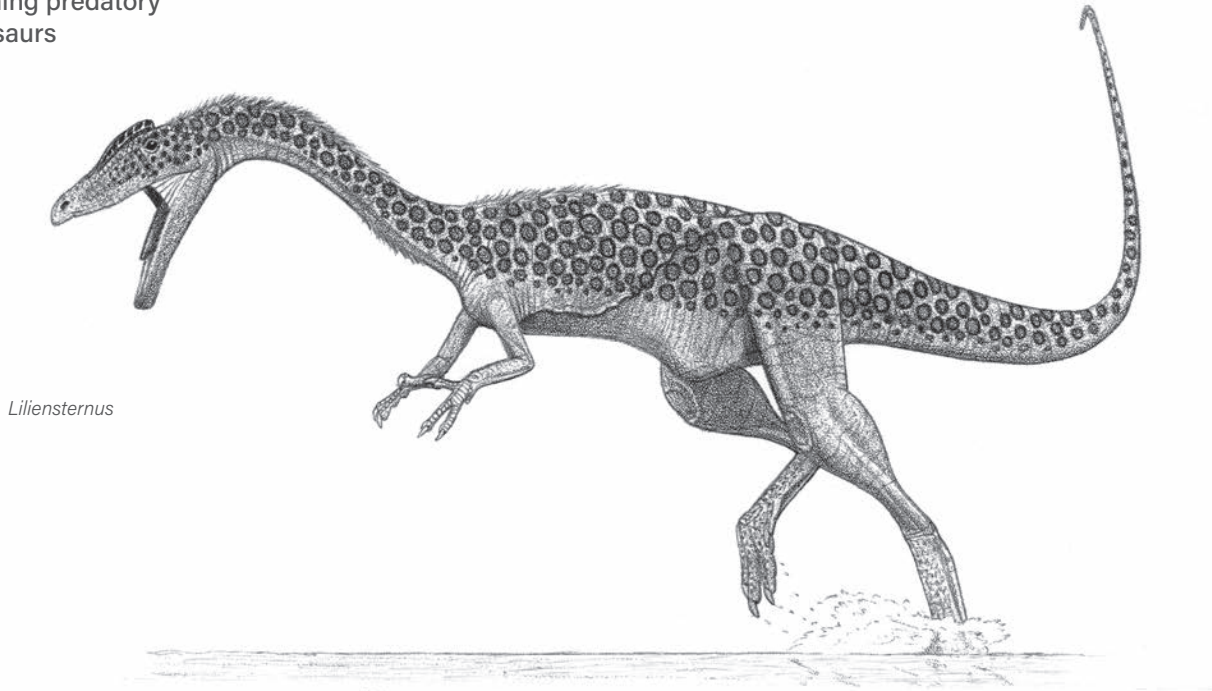
In general, dinosaur hunters were faster than their dinosaur prey. Prosauropods were never speedsters, perhaps even less so were derived therizinosaurs, while heavy limbed sauropods and stegosaurs were limited to an amble about a third as fast as their tormentors. Also not speedy were the armored dinosaurs. Ceratopsians small to gigantic could run, trot, and perhaps gallop at a good clip. At least as fast and often more so among ornithischians were lesothosaurs, heterodontosaurs, pachycephalosaurs, and petite to gigantic ornithopods. Among the latter, the big hadrosaurs with their gracile arms should have been able to outpace the clunkier, heavier-armed iguanodonts. The few prey dinosaurs that were really swift were of course the ratite-like ornithomimids, plus caudipterids, avimimids, and alvarezsaur—but these were all Cretaceous; of them, only the alvarezsaur are known from south of the equator, where they were not commonplace. Back in the Jurassic the nonpredaceous elaphrosaurs were fairly fleet. This situation of most predators being faster than most of the prey is another big difference with the layout of modern land mammals, in which some of the ungulates possess extremely gracile, long, unguligrade limbs that give them nominally greater velocity than the digitigrade and plantigrade carnivores, with ratites also being faster than the latter. In Australia the bounding kangaroos could outpace the marsupial and super lizard hunters until human invaders did the pouched predator in. The hows and whys of the predator–prey speed contest are interesting. When

HUNTING, SCAVENGING, AND DEFENSE

on the hunt, meat eaters have the advantage of carrying small digestive tracts empty of food that are much lighter than the bulky digestive complexes packed with digesting fodder plant consumers have to carry around all the time, even when fleeing for their lives. Swift quadrupedal mammalian herbivores have been able to get around the gut size disadvantage via the adaptation of legs with very willowy unguligrade feet, while the carnivores have to have flatter-footed limbs robust enough to grapple with prey, so they have trouble keeping up with their toe-tip-running targets. That said, there are videos showing brown

bears successfully chasing down large, apparently fit, and fast elk galloping full tilt across fields. Being bipeds that in most cases did not use their hindlimbs to injure prey, theropods and company were free to maximize their legs' running potential. Meanwhile, bipeds have to have toes that lie flat on the ground to avoid tipping over when not standing, so bipedal herbivorous dinosaurs could not go extreme unguligrade. That the nonpredaceous ornithomimids, caudipterids, avimimids, and alvarezsaur had exceptional digitigrade running legs may be due to their not being burdened by capacious fodder-fermenting guts; that

Running predatory dinosaurs



Liliensternus



Andalgornis

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