CONTENTS

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 in addition to avepods, it is a good scientific bet that dinosaur insulation evolved once, in which case they were all protofeathers. The absence to date of protofeathers in Triassic and Early Jurassic protodinosaurs and basal dinosaurs is the kind of negative evidence that is no more meaningful than their lack of fossil scales, the kind that 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 in the visually striking tail bristles of psittacosaurs. 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. The display-to-insulation hypothesis is supported by the fibers and feathers on some flightless dinosaurs such as heterodontosaurs functioning as both prominent display organs on some parts of the body and insulation cover on others.

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 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. There is no known method to restore the specific colors of scales, although differing degrees of shading can be assayed, and there is evidence that some dinosaurs were countershaded, being darker on top than below. 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. Archosaurs of all sizes may have used specific color displays for intraspecific communication or for startling predators. Crests, frills, skin folds, 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. Dinosaur eyes may have been solid black or brightly colored, like those of many reptiles and birds.

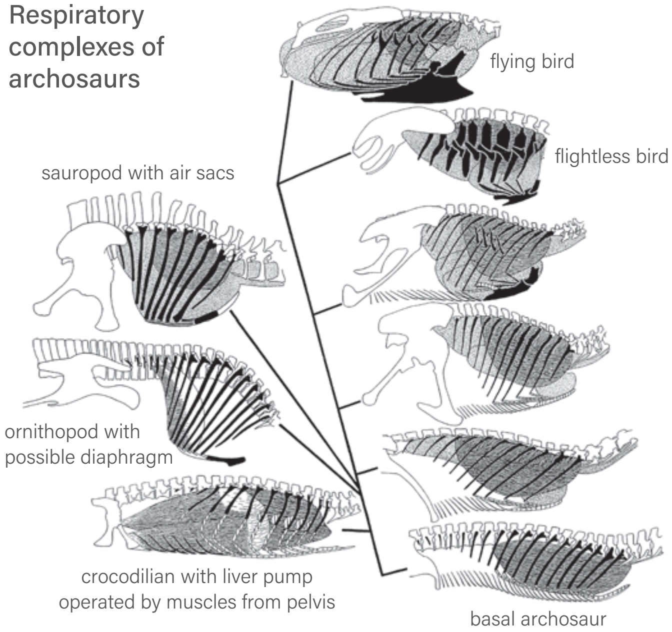
RESPIRATION AND CIRCULATION

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. Crocodilian 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 crocodilians, 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



Respiratory complexes of archosaurs

living tetrapods but among different ornithischian groups. It is not possible to determine the complexity of their lungs; it can only be said that if ornithischians had high aerobic capacity, then their lungs should have been internally intricate. Because no ornithischian shows evidence of pneumatic bones, it can be assumed that they retained high-volume lungs that were either dead-end or had minor extensions similar to those in some reptiles, although airflow may have been partly unidirectional. Nor were their ribs highly mobile—in ankylosaurs most of the ribs were actually fused to the vertebrae. The belly ribs of ceratopsids were packed tightly together and attached to the pelvis, so they could not move either. It can be speculated that in most ornithischians abdominal muscles anchored on the ventral pelvis were used to push the viscera forward, expelling stale air from the lungs; when the muscles were relaxed the lungs expanded. One group of ornithischians had a different arrangement. In ornithopods there was a large rib-free lumbar region with a steeply plunging rib cage immediately ahead. This is so similar to the mammalian lumbar region that it is probable that a diaphragm, perhaps muscular, had evolved in the group. Peculiar among ornithischians are the heterodontosaurs, which had larger than usual, elongated sternals connected to the ribs by robustly constructed sternal ribs, and oddest of all, gastralia not otherwise seen in the Ornithischia. Presumably this means heterodontosaur breathing was distinct from that of other ornithischians, but exactly how is a mystery.

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 and 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 uncinate processes that form a series along the side of the rib cage. Each uncinate process acts as a lever for the muscles that operate the rib the process is attached to. 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 equaling 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 avepod 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 it reached 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 some flightless birds—the extra-long belly ribs of birds with big abdominal air sacs are absent in theropods. In many aveairfoilan 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 uncinate 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 avepod 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.

Long-necked sauropod respiration (*Giraffatitan*)

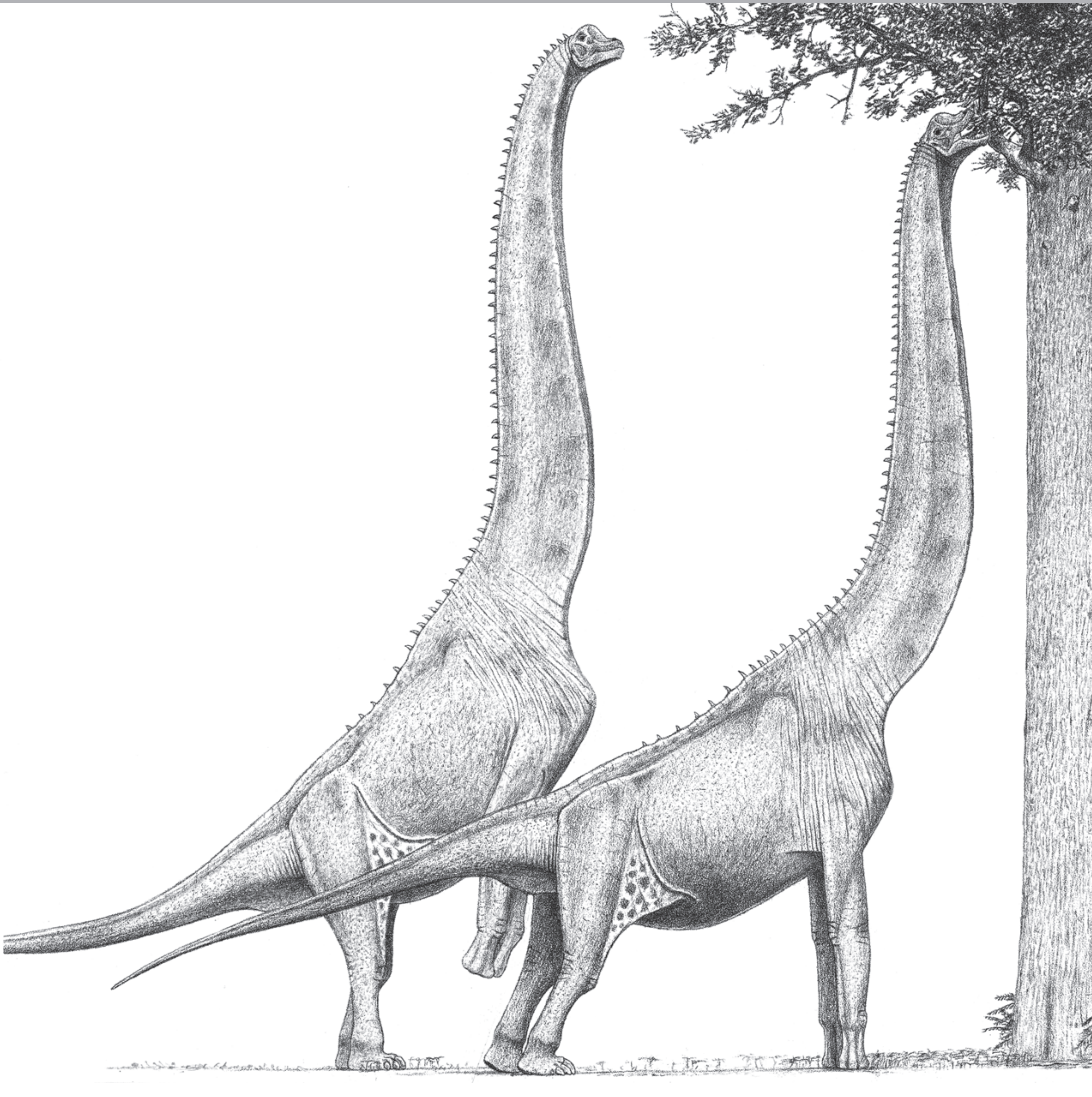
Sauropods show strong evidence that they, too, independently evolved a complex air-sac system. The vertebrae were usually highly pneumatic. Also, all the ribs were hinge jointed, even the belly ribs, which one would expect to instead be solidly anchored in order to better support the big belly. A corrugated rib cage ceiling favors rigid lungs. Most researchers agree that the air sac–filled vertebrae and mobile belly ribs of sauropods are strong signs that they had an air sac–driven respiratory complex that probably involved unidirectional airflow and approached, but did not fully match, the sophistication and efficiency of those of birds. Because sauropods lacked gastralia, the air sacs should have been limited to the rib cage. Sauropods pose an interesting respiratory problem because most of them had to breathe through very long tracheae, which created a large respiratory dead space that had to be overcome with each breath. This is paralleled in long-necked birds such as swans, which have a looped trachea in their chest, so an extra-long trachea does not critically inhibit breathing. Presumably the great air capacity of the air sacs helped sauropods completely flush the lungs with fresh air during each breath.

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.

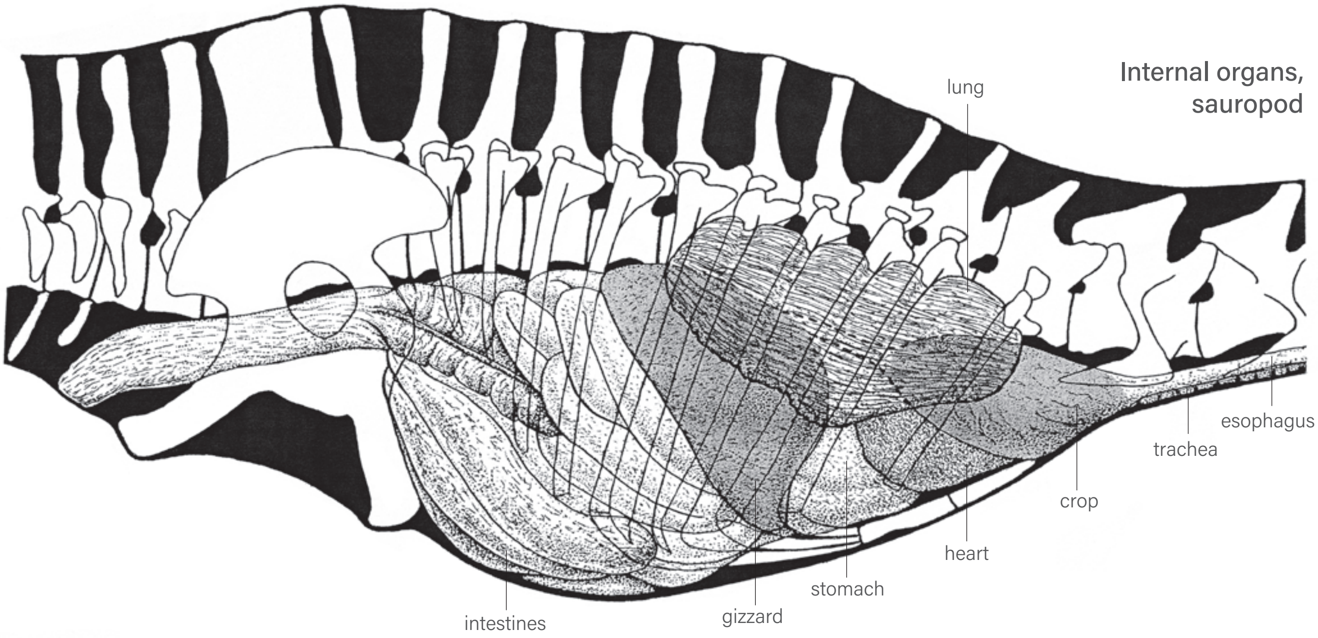
DIGESTIVE TRACTS

In a number of dinosaur fossils from a number of groups, gastroliths, or gizzard stones, are preserved within the rib cage, often as bundles of stones. In some dinosaur formations large numbers of polished stones are present even though geological forces that could explain their presence are absent. This evidence indicates that many dinosaurs, herbivores especially, utilized stone-rolling gizzards. But not all; a number of articulated skeletons show no sign of their presence, and they have not yet been found in blade-toothed predatory dinosaurs.

The digestive tracts of predatory theropods were relatively short, simple systems that quickly processed the easily digested chunks of flesh bolted down by the simple 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. Some vegetarian theropods used numerous gastroliths in a crop to break up plant material. Like herbivorous birds, most sauropods lacked the ability to chew the plant materials they ingested. The fodder was physically broken down in the gizzard, which often contained stones. Because these are not found in



Giraffatitan brancai

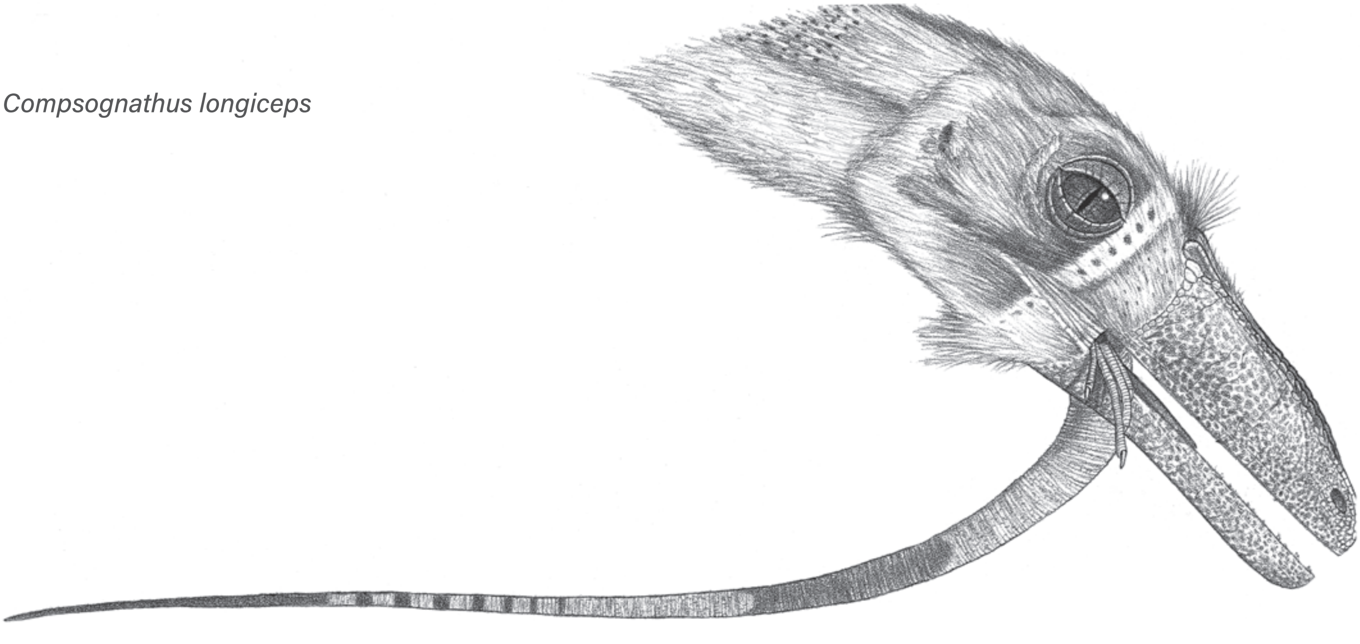


Internal organs, sauropod

large numbers, these sauropods may have used the stones not so much to directly pulp and grind plant material as to stir it up. Sauropods had large rib cages that contained the long, complex digestive tracts needed to ferment and chemically break down leaves and twigs. The system was taken to an extreme in the broad-bellied titanosaurs.

The cheeks that appear to have been present on at least some prosauropods, early sauropods, and therizinosaurs should have allowed them to mash food before swallowing. Food chewing may explain why prosauropods did not have particularly big, fermenting tummies. But it was the ornithischians that fully exploited the cheek-dependent system. After cropping food with their beaks, they could break up plant parts with their dental batteries. As some of the food fell outside the tooth rows, it was held in the elastic cheek pouches until the tongue swept it up for further processing or swallowing. Having taken the evolution of dinosaur dental complexes the furthest, hadrosauriformes had modest-sized abdomens to further process the well-chewed fodder. At the other end of this factor, some ornithischians had relatively weakly developed tooth complexes and used massive digestive tracts contained in enormous bellies to ferment and break down food. In pachycephalosaurs the digestive tract was further expanded by broadening the base of the tail in order to accommodate an enlargement of the intestines behind the pelvis. A few ornithischians supplemented plant processing with dense, food-grinding bundles of gastroliths. In herbivores the ingested fodder,

Compsognathus longiceps



bacterial gut flora, feces, and gizzard stones if present make up 10 to 20 percent of the animal's total mass.

There is no evidence that any dinosaur evolved a highly efficient ruminant-like system in which herbivores chew their own cuds. Such a system works only in animals of medium size in any case, and it was not suitable for the most titanic dinosaurs.

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 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. Our own skew toward color vision is different from that typical of animals, being more oriented to green. 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 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 to 13 diopters in young adult humans. The vision of the bigger-eyed 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 dinosaurs. Dinosaurs 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 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 tyrannosaurids, *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, and it is possible that olfaction was as important as vision in the smaller-eyed ankylosaurs. Among theropods the tyrannosaurs and dromaeosaurs had especially excellent olfaction, useful for finding both live prey and dead 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 basser 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 crocodilians. Some mammals do, humans most of all. A number of birds have limited vocal performance, but many have evolved a varied and often very sophisticated 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 generate 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. The long trachea of long-necked dinosaurs should have been able to generate powerful low-frequency sounds that could be broadcast over long ranges. Vocalization is done through the open mouth rather than through the nasal passages, so complex nasal passages acted as supplementary resonating chambers. This system was taken to an extreme in the large-crested lambeosaurine hadrosaurs with their convoluted nasal tracts. It is doubtful that any nonavian dinosaur had vocal abilities to match the more sophisticated examples seen in the most vocally sophisticated 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.

DISEASES AND PATHOLOGIES

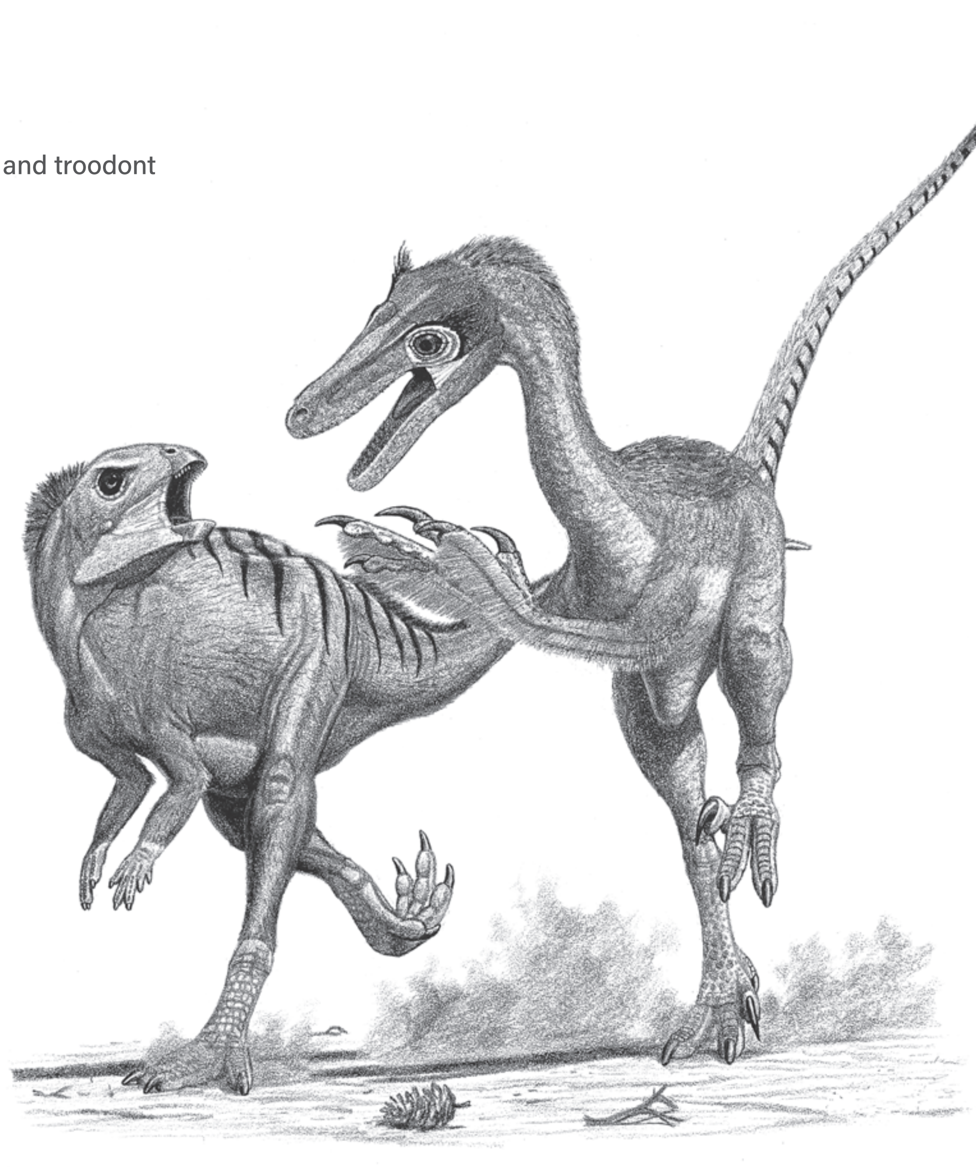
Planet Earth was infested with a toxic soup of diseases and other dangers that put all dinosaurs at high risk. The disease problem was accentuated by the global greenhouse effect, which maximized the tropical conditions that favored disease organisms, especially bacteria and parasites. Biting insects able to spread assorted diseases were abundant during the Mesozoic; fossils 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 dinosaur ancestors.

Dinosaur skeletons often preserve numerous pathologies. 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 theropods are, not surprisingly, especially prone to show signs of combat-related injury. 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. The sickle claw–bearing toes of dromaeosaurs and troodonts frequently show signs of stress damage.

Among herbivorous dinosaurs, stegosaur tail spikes are often damaged or even broken and then healed, verification that they were used for combat. The horn of a *Triceratops* was bitten off by a *Tyrannosaurus*, according to the tooth marks, and then healed during the following years, indicating that the prey survived face-to-face combat with the great predator. Whether the predator survived the combat is unknown. Healed bite marks in the tails of sauropods and duck-billed hadrosaurs indicate that they too survived attacks by allosaurs and tyrannosaurs, respectively. Sauropods, despite or perhaps because of their size and slow speeds, show relatively little evidence of injury.

Parkosaurus and troodont



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 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 to 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 to 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 such 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. Crocodilians 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 aveairfoilan theropods. 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 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 alvarezsaurs might have been 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. The great length of some dinosaurs posed a potential problem in terms of the time it took for electrochemical impulses to travel along the nerves. In the biggest sauropods, a command to the end of the tail and the response back could have had to travel as much as 75 m (250 ft) or more. Synaptic gaps where chemical reactions transmit information slow down the impulses, so this problem could have been minimized by growing individual nerve cords as long as possible.

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.

That dinosaurs often formed social groups is supported by some single-species bone beds that do not appear to have been death traps that slowly accrued fossils over time, or perhaps resulted from droughts that compelled numerous individuals to gather at a water source where they starved to death as the vegetation ran out. Some accumulations appear to have been the result of sudden events caused by volcanic ashfalls, flash floods, drownings when many dinosaurs crossed fast-flowing streams, or dune slides. Such bone beds, which in some cases suggest the existence of very large herds, usually consist of herbivorous dinosaurs.

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 predatory dinosaurs 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 reptiles and mammals 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 dinosaurs are

Trackways of a herd of sauropods

solitary, indicating that the maker was not part of a larger group. It is also very common for multiple trackways of a variety of dinosaur species to 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 many times the parallel trackways are crisscrossed by the trackways of other dinosaurs that appear to have been free to travel in other directions. The large number of parallel trackways is therefore evidence that many species of predatory and herbivorous dinosaurs of all sizes often formed collectives that moved as pods, flocks, packs, and herds.

The degree of organizational sophistication of herbivorous dinosaur groups was likely variable. That of the big dinosaurs was probably similar to that in fish schools and less developed than that in organized mammal herds. Suggestions that the trackways of sauropods show that the juveniles were ringed by protective parents have not been borne out, and it is unlikely that very large dinosaurs directly cared for and protected offspring that were so tiny when they came out of their eggs or nests. Trackways never show very large adults and their very small offspring moving together, which makes sense because the former would have accidentally stomped on the latter, which would not have been able to keep up with their parents. When adult plant eaters were less enormous, perhaps a half tonne or less, then having their juveniles alongside would have been practical, as with ratites and their chicks. 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 hadrosaurs, ornithomimids, and ornithopods 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. Nor is it likely that theropod packs employed tactics as advanced as those attributed to canid packs or lion prides.

REPRODUCTION

It has been suggested that some dinosaur species exhibit robust and gracile morphs that represent the two sexes. It is difficult to either 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. Heterodontosaurs appear to come both with small tusks and without, and the former may be the males. Head-crested oviraptorosaurs and dome-headed pachycephalosaurs 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 atypical for crested birds, in which males have markedly larger display structures. 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

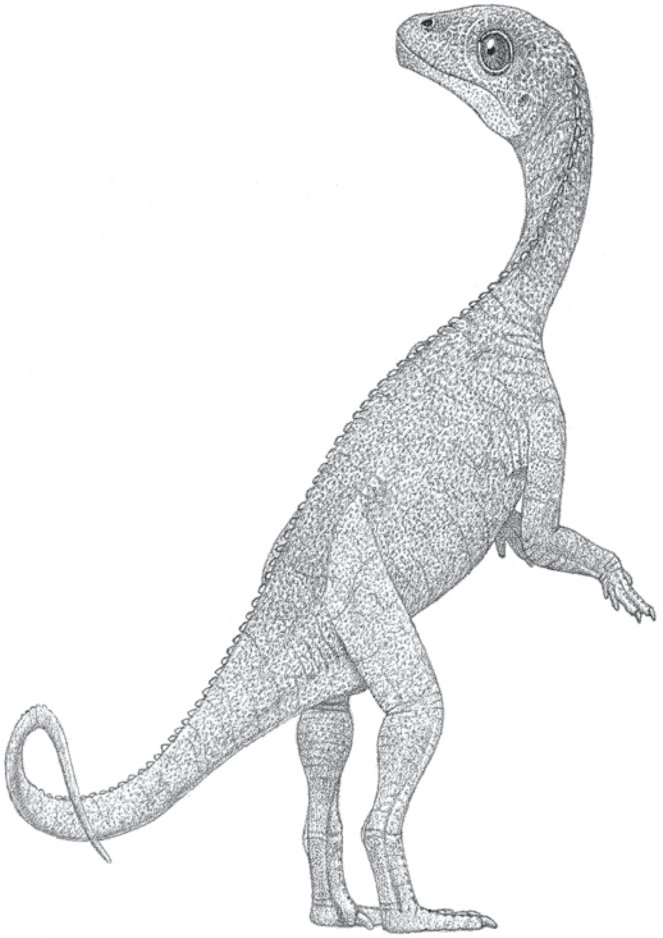
Hypacrosaurus stebingeri nest

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 this book, 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 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 dinosaurs brooding their nests confirms this pattern. Most dinosaurs probably became reproductive before maturing. Exceptions may have been ceratopsids and hadrosaurs, whose display organs did not become completely developed until they approached adult proportions.

The marvelous array of head and body crests, frills, horns, hornlets, spikes, spines, tail clubs, bristles, and feathers evolved by assorted 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 that are better able to attract mates in similarly fine condition. Use of display organs in sexual attraction and competition can be a relatively peaceful affair, and this system was taken to its dinosaurian height among the hadrosaurs with their spectacular head crests. Many dinosaurs probably engaged in intricate ritual display movements and vocalizations during competition and courtship that 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. The ceratopsians, whose head frills were most prominent in front view with the frill tilted up, were a major exception. The domes adorning pachycephalosaur heads were at least as prominent in front as in side view and may also have been tilted forward to intimidate opponents. Among the predatory avepods, the transverse head crest of *Cryolophosaurus* and the horns and domes of some abelisaurs provided unusual frontal displays. The same was true of the crest of the rather small-headed brachylophosaur hadrosaurs.



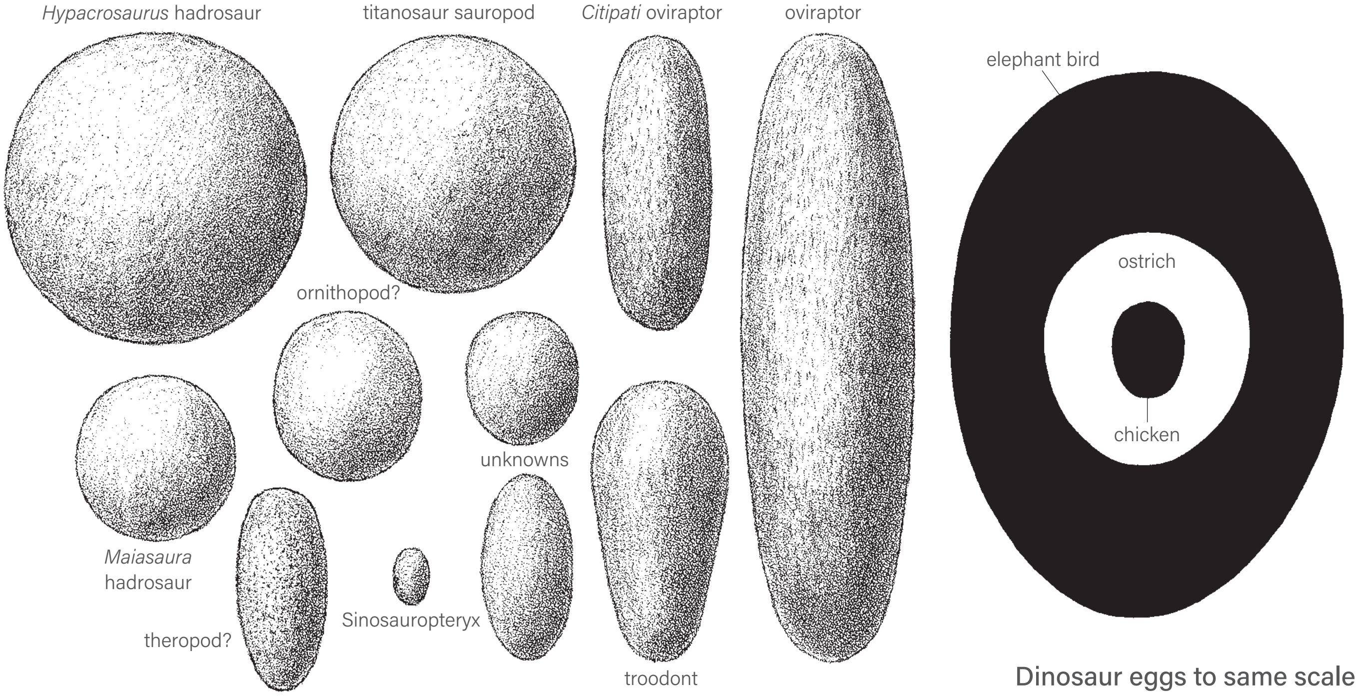
Mussaurus patagonicus hatchling

Intraspecific competition is often forceful and even violent in animals that bear weapons. Sauropods could have reared up and assaulted one another with their thumb claws. The iguanodonts' thumb spikes were potentially even more dangerous intraspecific weapons. Domeheads may have battered each other's broad flanks with their heads. Whether they used their rounded domes to head-butt like bighorn sheep is controversial. Male ankylosaurids are quite likely to have pummeled one another with their tail clubs, and other ankylosaurs probably locked their shoulder spines and engaged in strength-testing shoving matches. Multihorned ceratopsids may have interlocked their horns and done the same. Healed wounds indicate that ceratopsids also used their horns to injure one another. Tusked male heterodontosaurs may have done the same thing. The conceit that males have evolved means to avoid lethally injuring one another in reproductive contests is true in many cases, but not in others. Male hippos and lions suffer high mortality from members of their own species, and the same may have been true of theropods, ceratopsians, and big-thumb-spiked iguanodonts.

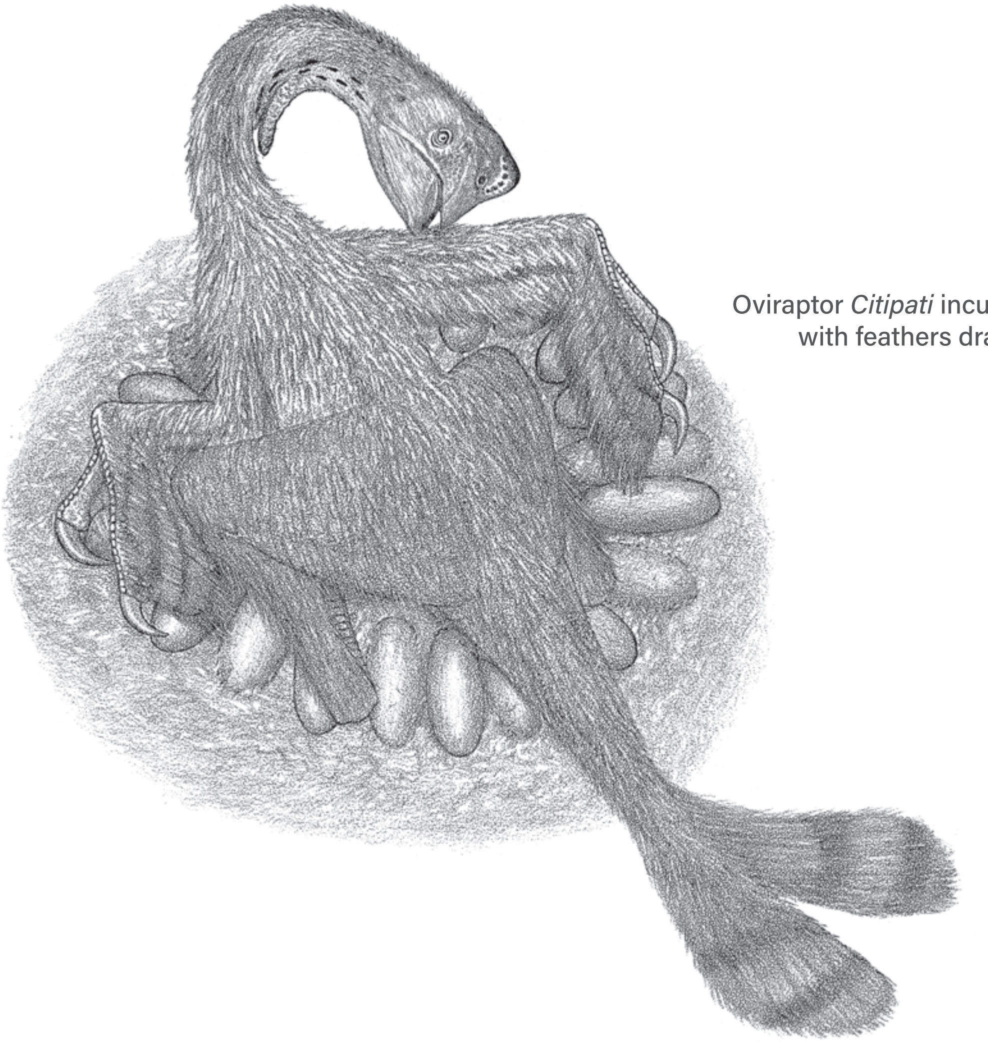
In reptiles and birds, the penis or paired penises (if either are present) and the testes are internal, and this was the condition in dinosaurs. Most birds lack a penis, but whether any dinosaur shared this characteristic is unknown. Presumably copulation was a quick process that occurred with the female 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. The need of sauropods to copulate supports the ability of these giants, including the biggest and those with long forelimbs, to stand on the hind legs alone. The vertical armor plates of stegosaurs probably required a modification, with the male resting his hands on one side of the female's pelvis.

At least some dinosaurs from theropods to sauropods to ornithopods produced hard-shelled eggs like those of birds, rather than the softer-shelled eggs of reptiles including crocodilians, 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. For example, not a single eggshell fragment attributable to the many sauropod species that inhabited the enormous Morrison Formation has yet been found. A fast-growing and diverse collection of eggs and nests is now known for a wide variety of Jurassic and Cretaceous dinosaurs, most from the latter half of the latter period. Firmly identifying the producer of a given type of egg requires the presence of intact eggs within the articulated trunk skeleton, 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. Dinosaur eggs ranged from near-perfect spheres to highly elongated and in some cases strongly tapered. 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 egg matches the size of the gigantic 12 kg (25 lb) eggs laid by the flightless elephant bird *Aepyornis*, which, as big as it was at nearly 400 kg (800 lb), was dwarfed by many dinosaurs. The eggs of the huge sauropods, for instance, weighed less than 1 kg (2 lb). The largest dinosaur eggs discovered so far weighed 5 kg (11 lb) and probably belonged to 1-tonne-plus oviraptors.

There are two basic reproductive stratagems, 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, Mesozoic dinosaurs were consistently r-strategists that typically laid large numbers of eggs in the breeding season, although dinosaurs isolated



Dinosaur eggs to same scale



Oviraptor *Citipati* incubating a nest, based on a fossil, with feathers drawn short enough to show eggs

on predator-free islands might have been slow breeders. This 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 in part by eating the giant eggs. Sauropods appear to have placed the largest number of eggs in a single nest, up to a few dozen. Giant dinosaurs were very different in this respect from giant mammals, which are K-strategists that produce few calves that then receive extensive care over a span of years. Nor did any dinosaur nurse its young via milk-producing mammary glands. It is possible 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. Crocodilians 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.

Some dinosaur eggs whose makers have yet to be identified were buried in a manner that implies they were immediately abandoned. This was probably true of the eggs of sauropods. The large, vegetation-covered nests that can be attributed to the giants were structured in a rather irregular manner that differs from the more organized nests tended by adults. There is evidence that at least some sauropods deposited their eggs near geothermal heat sources. Because large numbers of nests were created at the same time and place, the adult sauropods would have risked denuding the local vegetation as well as trampling their own eggs if they remained to guard their nests. Also in danger of being trampled were the hatchlings, which were thousands of times less massive than their parents. Laying so many eggs in so many nests helped overwhelm the ability of the local predators to find and eat all the eggs and emerging hatchlings, although a fossil shows a large snake feeding on a just-emerged hatchling. Some prehatchling reptiles in mass nests start vocalizing to better coordinate their synchronous emergence, even though doing so risks attracting egg and hatchling eaters. Trackways indicate that small juvenile sauropods formed their own pods, independent of multitonne adults. Other trackways further indicate that sauropod calves joined full-sized adults only after a few years, when they had reached about a tonne, large enough to keep up and not be stepped on in the process. The mature sauropods probably paid the young ones no particular notice and were unlikely to have even been closely related to them. In this scenario, the juveniles were seeking the statistical safety of being near aggressive grown-ups able to battle the biggest predators.

Also apparently forming juvenile pods were at least some ankylosaurs. The intact skeletons of over a dozen large *Pinacosaurus* juveniles have been found grouped together, apparently killed at the same moment by a dune slide. The absence of an adult suggests that the growing armored dinosaurs were moving together as an independent gang.

The compact nests of duck-billed hadrosaurs have a structural organization that suggests they were monitored by adults. Hadrosaurs may have regulated the temperatures of their mound nests like megapode fowl. The nests seem to form colonies in at least some cases, and breeding hadrosaurs were not so large that they would have stripped the local flora if they remained to care for their young. In many hadrosaur nests the eggs are so thoroughly broken up that they seem to have been trampled on over time, and skeletons of juveniles considerably larger than hatchlings have been found in the nests, so the young hadrosaurs did not immediately abandon their nests. The heads of baby hadrosaurs had the short snouts and large eyes that encourage parental behavior. These factors suggest that the parents opened the mounds as the eggs hatched and then brought food to the altricial juveniles while they remained in the nest. This arrangement would have avoided the problem of stepping on the tiny hatchlings, provided them protection from predators, and improved growth rates by supplying the nestlings with plenty of food while the youngsters saved energy by remaining immobile. What happened when hadrosaur juveniles left the nest after a few weeks or months is not certain—the still-extreme size disparity between the parents and their offspring favors the latter forming independent pods until they were large enough to join the adult herds.

Little is known about the nesting of large predatory theropods. 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. 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.

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 birdlike 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. 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. 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 aveairfoilans ideally represent the near-avian arrangement expected in the dinosaurs closest to birds. 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. The same has been found adorning the nose of titanosaur sauropod embryos, and this may have been true of other Mesozoic dinosaurs.

Whether small birdlike theropods and many other dinosaurs continued to care for their young after they hatched is not known but is plausible. The best evidence for dinosaur parenting of juveniles found so far is among small ornithischians. A compact clutch of nearly three dozen articulated juvenile (about a tenth of a kilogram, or a fifth of a pound) *Psittacosaurus* skeletons was found in intimate association with the remains of an adult over a dozen times heavier. There is dispute over whether this is a true association between a parent and its offspring; if it is, the situation seems to parallel that of some ratite birds, which gather the offspring of a number of females into a large crèche that is tended by a set of adults. It is possible that the tightly packed collection of psittacosaurs was entombed in a fossil burrow. Again, it is possible that males as well as females were at least sometimes involved to some degree in parenting, as per many living dinosaurs.

Parental care probably ranged from nonexistent to extensive in dinosaurs and in a number of cases probably exceeded that seen in reptiles or even crocodilians, rivaling that of birds. However, no dinosaur lavished its offspring with the parenting typical of mammals, and because dinosaurs did not nurse, it is likely that most of them could grow up on their own either normally, or if something happened to the grown-ups.

Ornitholestes hermanni

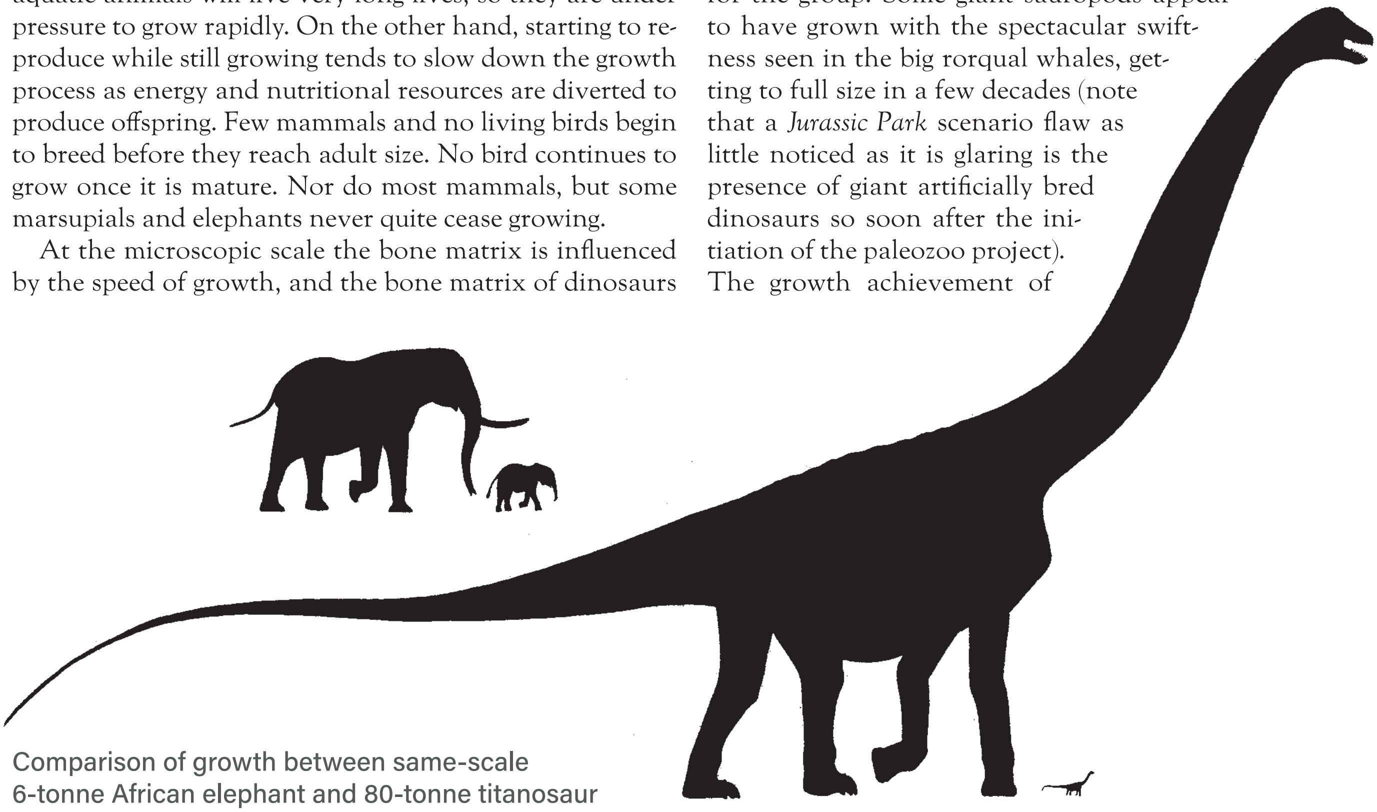
GROWTH

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 crocodilians, including the extinct giants, which 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 of 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 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, but 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 a growing 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, birdlike troodont theropod whose bone rings seem to have been laid down multiple times in a year, perhaps because it was reproducing while growing. The earliest, smallest armored dinosaurs look like they were in the reptilian growth zone, like some mammals. Most small dinosaurs fall along the lower end of the mammalian zone of growth, perhaps because they were reproducing while immature. Rates of growth were variable in prosauropods, as was final adult size to a remarkable degree. Most gigantic dinosaurs appear to have grown as fast as similar-sized land mammals, with the hadrosaurs and ceratopsids—which did not lay down growth rings when juveniles—apparently being particularly quick to mature for the group. Some giant sauropods appear to have grown with the spectacular swiftness seen in the big rorqual whales, getting to full size in a few decades (note that a *Jurassic Park* scenario flaw as little noticed as it is glaring is the presence of giant artificially bred dinosaurs so soon after the initiation of the paleozoo project). The growth achievement of



Comparison of growth between same-scale 6-tonne African elephant and 80-tonne titanosaur the greatest sauropods is astonishing. Giant mammals get a head start, being born as large calves only a few dozen times smaller than the adults, and then being nourished with enormous amounts of nutrient-dense milk. Hatchling sauropods had to expand their mass tens of thousands of times in just a few decades and with little or no nourishment provided by the adults. Armored dinosaurs appear to have grown less quickly than the others.

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 rights 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 rapid growth with rather short life spans of 20 to 30 years. Other giant theropods did not grow as extremely fast and lived longer, up to half a century. Sauropods seem to have enjoyed similarly long life spans—whether they made it to a full century or beyond is not documented, but this would not be surprising in the case of the biggest examples. If they did, they may have matched the life spans of much smaller giant tortoises.

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 crocodilian 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 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 that 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, reptilelike 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 a wide variety of dinosaurs show that they normally walked at speeds of over 3 km/h, 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 exceeded the reptilian maximum.

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 protodinosaurs, the first theropods, and the prosauropods 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 dinosaurs had the large hips able to support the large thigh muscles typical of more aerobically capable animals. Among the big-hipped dinosaurs, the relatively sluggish therizinosaurs, stegosaurs, and armored ankylosaurs were likely to have had lower energy budgets than their faster-moving relatives.

That many dinosaurs 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. This would have been especially true of the ultratall sauropod giants. Just how much so is, however, a matter of question because it is not certain whether extra-tall creatures are stuck with just using ever higher blood pressures to push blood many meters above heart level, or whether they can utilize a siphon effect to partly reduce the vertical loads in the blood column. Some work on giraffes suggests the latter is operative to some level, but further research awaits.

It has long been questioned, incorrectly, how high-metabolism sauropods could have fed themselves with the small heads that made their long necks possible. The small head of a sauropod was like the small head of a tachyenergetic emu or ostrich—it was basically all mouth. Most of the head of herbivorous mammals consists of the dental batteries they use to chew food after it has been cropped with the mouth, which is restricted to the front end of the jaw. Also, sauropod heads are not as small as they look—the mouths of the biggest sauropods could engulf the entire head of a giraffe. The breadth of the sauropod mouth is the same as that of herbivorous mammals of the same body mass. If a tachyenergetic sauropod of 50 tonnes ate as much as expected in a mammal of its size, then it needed to consume over half a tonne of fresh fodder a day. But that is only 1 percent of its own body mass, and if the sauropod fed for 14 hours each day and took one bite per minute, then it needed to bite off only about half a kilogram of plant material each time.

That would have been easy for the sauropod's head, which weighed as much as a human body and had a mouth about 0.5 m (1.5 ft) wide. As far as big-headed dinosaurs, the sophisticated dental batteries of ceratopsids and hadrosaurs, being very similar to those of herbivorous mammals with similar chewing complexes, presumably likewise evolved to facilitate feeding a high level of energy turnover.

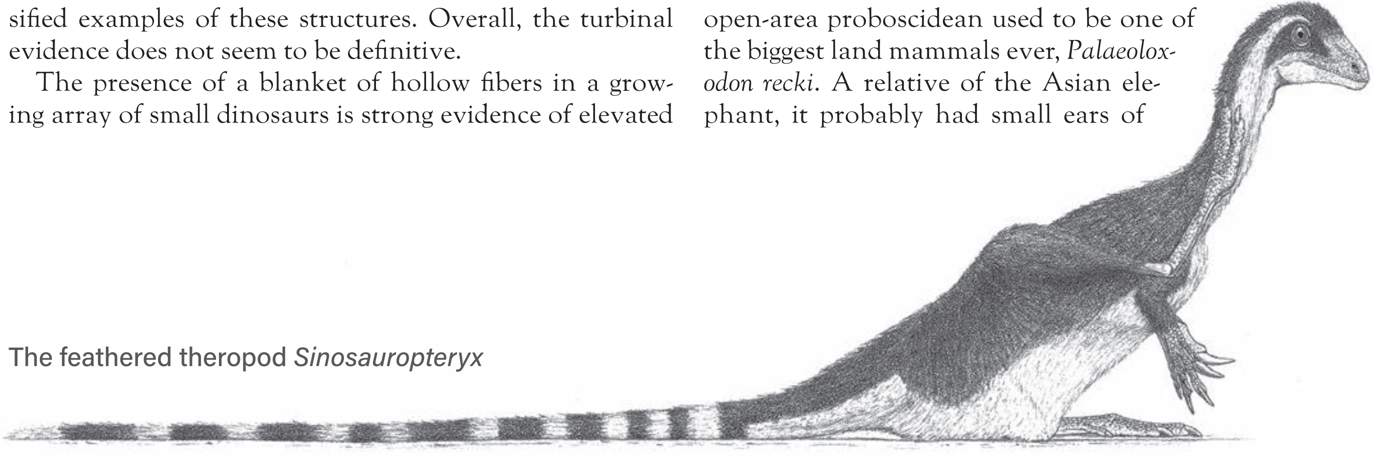
If we turn from eating to breathing, an intermediate metabolism is compatible with the unsophisticated lungs that protodinosaurs, early theropods, and prosauropods appear to have had. Too little is known about the respiration of ornithischians to relate it to metabolic level, except that the possible presence of a mammal-like diaphragm in ornithopods hints that they had a mammalian level of oxygen intake. The highly efficient, birdlike, air sac–ventilated respiratory complex of avepod theropods and sauropods is widely seen as evidence that elevated levels of oxygen consumption evolved in these dinosaurs. Sauropods probably needed a birdlike breathing complex in order to oxygenate a high metabolic rate through their long tracheae. Some reptiles with low energy levels had long necks, some marine plesiosaurs among them, but because they had low metabolic rates, they did not need air sacs to help pull large volumes of air into their lungs.

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, and other dinosaurs, ceratopsids most of all, had very large passages able to accommodate very large, unossified examples of these structures. 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 amounts of food needed to grow rapidly. Tachyenergetic juveniles either gather the food themselves or are fed by their parents. That 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 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



The feathered theropod *Sinosauropteryx* 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.

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. The presence of sauropods in some of the wintry habitats in northern Australia and central Asia directly refutes the hypothesis that big dinosaurs used their bulk to keep warm by retaining the small amount of internal heat produced by a reptilian metabolism; only a higher level of energy generation could have kept the body core balmy and the skin from freezing. 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. At the other end of the size spectrum, sauropods are missing from the most extreme polar regions, probably because the cold, dark winters left them without enough food to power their titanic bodies.

Bone isotopes have been used to help assess the metabolism of dinosaurs. These can be used to examine the 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 crocodilians from the same formations. An ankylosaur shows evidence of being heterothermic. Because the armored dinosaur lived at a high latitude, it is possible that it hibernated in the dark winter, perhaps bedding down in dense brush where it was protected by its armor against the chill as well as predators.

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. And the sample of dinosaurs is also too limited to allow high confidence in the results to date. This 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 that have 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 theropods and sauropods great and small remaining so, while some ornithischians irregularly reverted to bradyenergetic ectothermy, 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 dinosaurs 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 are the tall sauropods with their high circulatory pressures, and polar dinosaurs that remained active in the winter and needed to produce lots of warmth. At the opposite extreme, early dinosaurs, slower-growing and slower-moving armored forms, and the 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 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, perhaps 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 crocodilians, pterosaurs, all dinosaurs including birds, some pelycosaurs, 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.

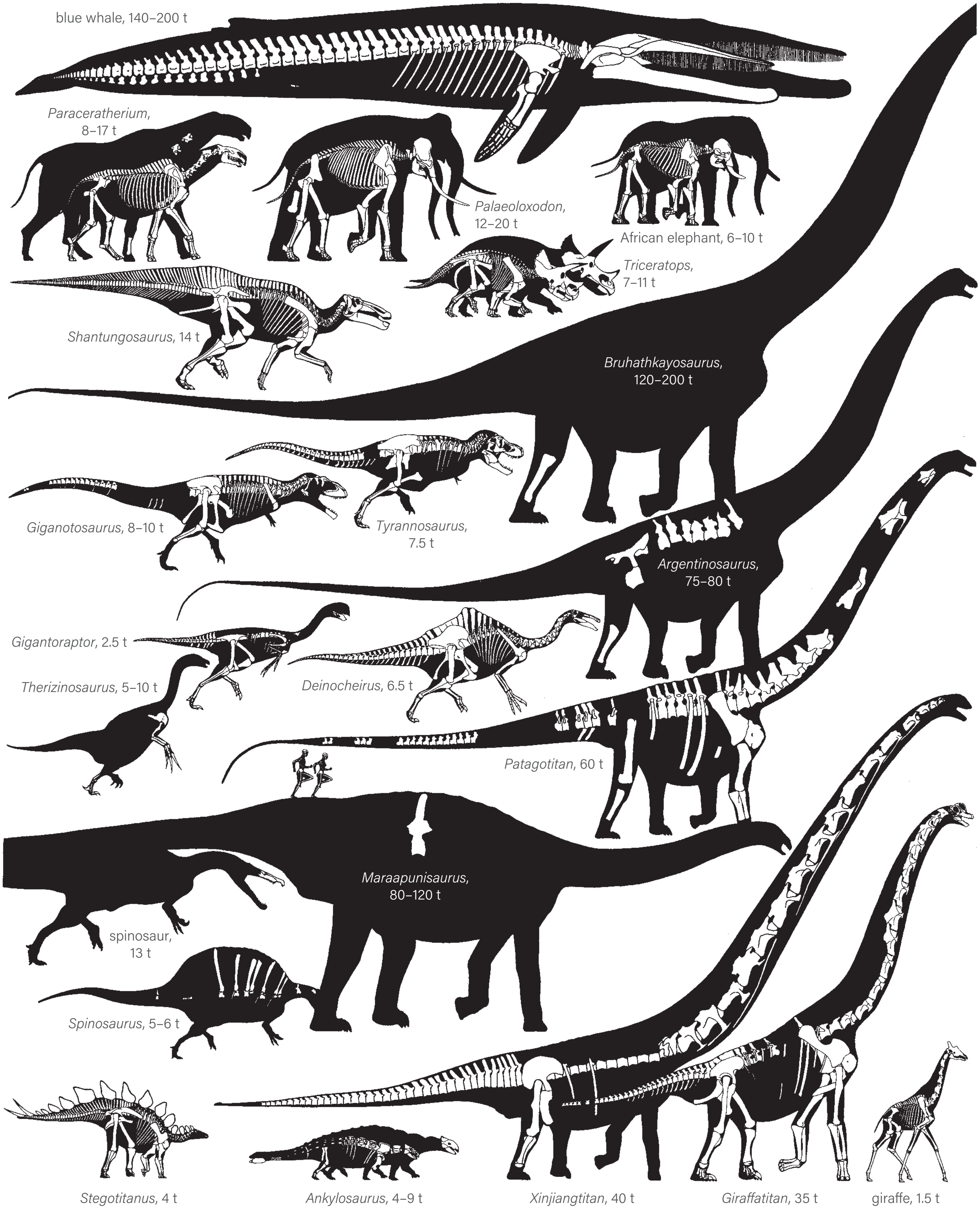
A long-term debate asks what specifically it is that leads animals to be tachyenergetic and endothermic. One hypothesis proposes that it is habitat expansion, that animals able to keep their bodies warm when it is cold outside are better or exclusively able to survive in chilly places—near the poles, 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 protodinosaurs, 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. Sauropods exceeded the size of the largest land mammals, mammoths, and the long-legged paracerathere rhinos of 15 to 20 tonnes by a factor of at least four to five and apparently matched the most massive whales.

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 that were predaceous, exceeded a tonne, as have mammals since then, is compelling evidence that they too had high aerobic power capacity and correspondingly elevated energy budgets. The ultimate example of great height driven by elevated metabolics is seen in ultratall sauropods. Their extreme height indicates that their hearts could push blood many meters up against the gravity well at pressures up to two or three times higher than the 200 mm Hg giraffes need to oxygenate their brains. And it is unlikely that such tall and massive animals in danger of fatal injury from falling could risk a moment of hypoxic wooziness from an oxygen-deprived brain. If so, then sauropods had hardworking hearts whose high energy demands would have required a very high level of oxygen consumption. Supertall animals would have needed, like giraffes, special vascular adaptations to cope with the problems associated with fluctuating pressures as the animal stood or lay down, and raised and lowered its head from drinking level to the maximum vertical reach.

Only sauropods have exceeded 20 tonnes on land. The question is, why that unique biological achievement? Very tall necks like those of sauropods and giraffes evolve in an evolutionary feedback loop that involves two distinct but reinforcing factors. Increasing height serves as a dominance display that enhances reproductive success by intimidating rivals and impressing mates. This is similar to other reproductive displays such as the tails of peacocks and the giant antlers of big cervids. And as the head gets higher, the herbivore also has a competitive feeding advantage over shorter herbivores in accessing the enormous food resources, in the crowns of tall trees, that provide the power source needed to pump blood to the brain, held far above the heart, that



Dinosaur giants compared with mammals

allows the animal to reach all that food. Sauropods could take this to an exceptional extreme because, lacking dental batteries and big brains, sauropod heads were relatively small, so sauropods were able to evolve extremely tall necks that in turn required enormous bodies to anchor them upon and to contain the hardworking hearts they needed. With their more toothy big heads, mammals are apparently limited to the 6 m (20 ft) height of giraffes. The tallest sauropods were able to reach up to maybe 20 m (60 ft)—without better understanding of how animals get blood really high up, it is not known whether that was the maximum animal height attainable. Also possibly helping sauropods become supersized were the pneumatic vertebrate and other air sacs that had evolved to improve respiratory capacity in tune with the high metabolic rates needed to be so tall and heavy. Those lightened the load on their bones and muscles somewhat, which could have been especially pertinent regarding the elongated necks. This option has not been available to mammals, or to ornithischian dinosaurs for that matter. But this effect should not be exaggerated, in part because recent work is showing that sauropods' internal air spaces were not as dramatically density reducing as has been widely thought.

The hypothesis that only tachyenergetic animals can grow to enormous dimensions on land is called terramegathermy. 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 crocodilians 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 to both retain internal warmth when it is chilly and keep external heat out and store heat on hot days.

Another, subtle reason that dinosaurs, particularly supersauropods and theropods, 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 habitat'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 half a tonne 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 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. It is notable that supersauropod fossils are particularly rare, indicating small populations. Because the bulk of the biomass of adult herbivorous dinosaurs 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 predators could reach 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.

It is as common as it is seemingly logical to think that being titanic in water—it being buoyant—is easier than dwelling under the full force of planetary gravity on land. But paleohistory indicates otherwise. Really big whales did not exist until very recently. For over 30 million years most or all whales were not all that big, rarely if ever exceeding around 20 tonnes. It was under the unusual conditions of ice age oceans in which cold water currents spurred higher levels of food productivity, plankton particularly, that the super baleen whales of 50–200 tonnes suddenly appeared. Back in the warm seas of the Mesozoic, reptiles and fish reached only 20 to perhaps 30 tonnes. Before the Pleistocene ocean chill, the biggest fish were 50-tonne supersharks like megalodon. In comparison, 50–200-tonne supersauropods were wandering about Mesozoic continents from the Late Jurassic to the very end of the era with little or no interruption for around 90 million years. The extra-tall land giants had the size-sustaining advantage that there were always forests full of calorie-packed big trees, a few trillion of them, to grow titanic on—until K/Pg events suddenly wrecked those forests and the equitable climate across the globe. With no small-headed dinosaurian herbivores to regain whalelike bulk and multistory height on land, land mammals have proven unable to reach a couple dozen tonnes.

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 and whales. In the dinosaur era it occurred between orca-sized theropods and whale-sized sauropods, hadrosaurs, and ceratopsids.

MESOZOIC OXYGEN

Oxygen was absent from the atmosphere for much of the history of the planet, until the photosynthesis of single-celled plants built up enough oxygen to overwhelm the processes that tend to bind it to various elements such as iron. Until recently it was assumed that oxygen levels then became stable, making up about a fifth of the air for the last few hundred million years. Of late it has been calculated that oxygen has fluctuated strongly since the late Paleozoic. The problem is that the results are themselves variable. They do agree that the oxygen portion of the atmosphere soared to about a never-seen-again third or more during the late Paleozoic, when the great coal forests were forming and, because of the high oxygen levels, often burning. It is notable that this is when many insects achieved enormous dimensions by the standards of the group, including dragonfly relatives with wings over 0.5 m (2 ft) across. Because insects bring oxygen into their bodies by a dispersed set of tracheae, the size of their bodies may be tied to the level of oxygen.

But in the Mesozoic the situation is less clear. Oxygen levels may have plunged precipitously, sinking to a little over half the current level by the Triassic and Jurassic. In this case oxygen availability at sea level would have been as poor as it is at high altitudes today. Making matters worse were the high levels of carbon dioxide. Although not high enough to be directly lethal, the combination of low oxygen and high carbon dioxide would have posed a serious respiratory challenge that could have propelled evolution of the efficient air sac respiration of pterosaurs and some dinosaurs. But other work indicates that oxygen did not plunge so sharply, and in one analysis it never even fell below modern levels, being somewhat higher in most of the era. Reliably assaying the actual oxygen content of the atmosphere in the dinosaur days remains an important challenge.

THE EVOLUTION—AND LOSS—OF AVIAN FLIGHT

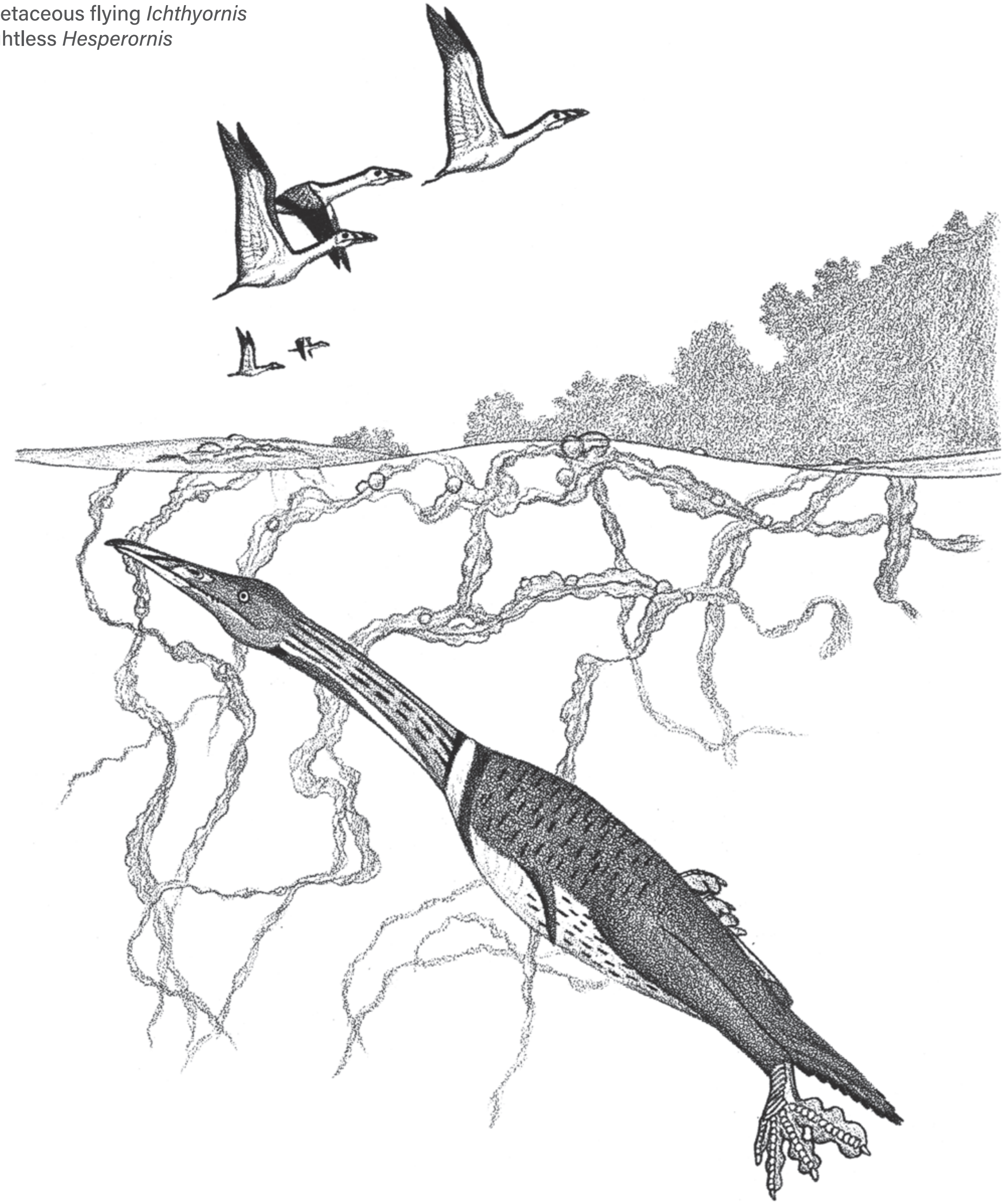
Powered flight has evolved repeatedly among animals, including numerous times in insects in the late Paleozoic and three times in tetrapods—pterosaurs in the Triassic, birds in the Jurassic, and bats in the early Cenozoic. In all cases among vertebrates, flight evolved rapidly by geological terms, so much so that the earliest stages have not yet been found in the fossil record for pterosaurs and bats. The means by which flight evolved in pterosaurs remains correspondingly obscure, although their having wing membranes attached to their legs favors it starting out as arboreal gliding. The fact that bats evolved from tiny insectivorous mammals, and the recent discovery of an early fossil bat with wings smaller than those of more modern forms, show that mammalian flight evolved in high places.

The origin of birds and their flight is much better understood than it is for pterosaurs and bats. This knowledge extends back to the discovery of Late Jurassic *Archaeopteryx* in the mid-1800s and is rapidly accelerating with the abundant new fossils that have come to light in recent years, especially from the Early Cretaceous, and from the middle of the Jurassic before *Archaeopteryx*. We can conclude that dinosaurian flight was not yet developing in the Triassic because while sediments from that time preserve an array of flying insects and early pterosaurs, nothing dinoavian has shown up. However, a major fossil gap exists because little is known about what was happening in the Early Jurassic and most of the middle of that era. Also hindering greater understanding is that the fine-grained deposits that best preserve small flying creatures are largely limited to a few geographic locations, mainly northeast China in the Middle Jurassic and Early Cretaceous and Europe in the Late Jurassic, and it is unknown what was happening in the rest of the world.

When it was assumed that birds did not evolve from dinosaurs, it was correspondingly presumed that their flight evolved among climbers that first glided and then developed powered flight. This has the advantage of our knowing that arboreal animals can evolve powered flight with the aid of gravity, as bats almost certainly did, and probably pterosaurs too. When it was realized that birds descended from deinonychosaurs, many researchers switched to the hypothesis that running dinosaurs learned to fly from the ground up. This has the disadvantage of uncertainty over whether it is practical for tetrapod flight to evolve among ground runners working against gravity.

The characteristics of birds indicate that they evolved from dinosaurs that had first evolved as bipedal runners and then evolved into long-armed climbers. If the ancestors of birds had been entirely arboreal, then they should have been semiquadrupedal forms whose sprawling legs were integrated into the main airfoil, as in bats. That birds

Late Cretaceous flying *Ichthyornis* and flightless *Hesperornis*



are bipeds whose erect legs are separate from the wings indicates that their ancestors evolved to run. Conversely, how and why ground animals would directly develop the long, strongly muscled arms and wings necessary for powered flight has not been adequately explained. The hypothesis that running theropods developed the ability to fly as a way to enhance their ability to escape up tree trunks itself involves a degree of arboreality. Small theropods, with their grasping hands and feet, were inherently suited for climbing. Some avepod theropods show specializations for climbing, especially scansoriopterygids, *Xiaotingia*, *Archaeopteryx*, and microraptorine dromaeosaurs.

Avian flight may have evolved among predatory dinosaurs that spent time both on the ground and in the trees, with long arms that facilitated the latter. Leaps between branches could have been lengthened by developing aerodynamically asymmetrical pennaceous feathers that turned the leaps into short glides. As the feathers lengthened, they increased the length of the glides. When the protowings became large enough, flapping would have added power, turning the glides into a form of flight. The same flapping motion would have aided the rapid climbing of trees via the air rather than scrambling up trunks and branches. Selective pressures then promoted further increases in arm muscle power and wing size until the level seen in *Archaeopteryx* was present. The flying deinonychosaur had an oversized furcula and large pectoral crest on the humerus, which supported an expanded set of muscles for flapping flight. The absence of a large sternum shows that its flight was weak by modern standards. As bird flight further developed, the sternum became a large plate like those seen in dromaeosaurs. Fixed on the rib cage with ossified sternal ribs, the plate anchored large wing-depressing muscles and later sported a keel that further expanded the flight muscles. Adaptations at and near the shoulder joint improved the ability of the wing to elevate, increasing the rate of climb in flight. At the same time, the hand was stiffened and flattened to better support the outer wing primaries, and the claws were reduced and lost. The tail rapidly shortened in most early birds until it was a stub. This means that birds quickly evolved a dynamic form of flight, much more rapidly than pterosaurs, which retained a long tail stabilizer through most of the Jurassic. The above adaptations were appearing in Early Cretaceous birds, and the essentially modern flight system had evolved by the Early Cretaceous.

For all its advantages, flight has its downsides, including all the energy that is absorbed by the oversized wing tissues, especially the enormous flight muscles. Nor can flying birds be especially large. A number of derived birds with clawless hands have lost flight even on the continents, and dinobirds with only modest flight abilities and clawed hands that could be used for multiple purposes would have been more prone to losing the ability to take to the air. Yet the conventional view of dinoavian evolution does not include a single case of the loss of flight outside birds proper. This scenario is critically flawed because the possibility that weak early fliers rarely if ever lost flight over the nearly 100 million years of the Late Jurassic and Cretaceous is not viable; it would have been happening all the time. After all, continental tetrapods have undergone the massive reversals needed to again become flippered marine swimmers numerous times, and losing flight is much easier and simpler to do. Reversals both modest and radical are frequent features of Darwinian evolution.

Functional anatomical evidence for the loss of flight includes the presence in nonfliers of flight features that are normally retained in neoflightless birds. These include large squarish sternal plates supported by bony sternal ribs; bony uncinate processes on the ribs; strong flexion between horizontal, strap-shaped scapula blades strongly flexed relative to the vertical; elongated coracoids; folding arms; a number of details of the hand including stiffening and fusing of elements; bird/pterosaur/bat-style propatagium airfoil surfaces stretching from shoulder to wrist forward of the elbow; and stiffened, slender, pterosaur-like or very short birdlike tails. All these adaptations are needed for dinosaur fight, and attempts to explain them as exaptations before the evolution of flight are at best speculative. Many of these attributes apply to nonflying dromaeosaurs, whose early examples appear to have been better adapted for flight than *Archaeopteryx*. The small-armed dromaeosaurs were almost certainly neoflightless, like big ground birds. *Anchiornis* suggests that deinonychosaurs began to lose flight in the Late Jurassic, with troodonts their possible neoflightless evolutionary offspring. Therizinosaurs and oviraptorosaurs show many of the anatomical signs that some level of flight was present early in their evolution. It is particularly telling that the early flying jeholornithiform birds and flightless therizinosaurs shared strikingly similar skulls, as did in turn the deeply parrot-beaked omnivoropterygid birds and oviraptorosaurs. Such deep convergence happening once, as the conventional scenario proposes, is not likely, and it happening twice is a real evolutionary stretch. Very close relationships, in both cases involving the loss of flight expected to spawn off from such crude fliers, are the superior bioevolutionary scenario. That it turns out that basal oviraptorosaurs had retroverted pubes like flying protobirds is further evidence their ancestors once flew Mesozoic skies. The alvarezsaurs are another potential neoflightless clade. In the Cretaceous, birds themselves lost flight on occasion, most famously the widely distributed marine hesperornithiform divers, as well as some chicken- to ratite-sized European birds of uncertain relationships known from near the end of the period.

DINOSAUR SAFARI

Assume that a practical means of time travel has been invented, and, *The Princeton Field Guide to Dinosaurs* in hand, you are ready to take a trip to the Mesozoic to see the dinosaurs' world. What would such an expedition be like? Here we ignore the classic time paradox issue that plagues the very concept of time travel. What would happen if a time traveler to the dinosaur era did something that changed the course of events to such a degree that humans never evolved to travel back in time and disrupt the timeline in the first place?

One difficulty that might arise could be the lack of modern levels of oxygen and/or extreme greenhouse levels of carbon dioxide (which can be toxic for unprepared animals), especially if the expedition traveled to the Triassic or Jurassic. Acclimation could be necessary, and even then, supplemental oxygen might be needed at least on an occasional basis. Work at high altitudes would be especially difficult. But, as noted earlier, oxygen deprivation may not have been the case. Another problem would be the high levels of heat chronically present in most dinosaur habitats. Relief would be found at high latitudes, as well as on mountains.

If the safari went to one of the classic Mesozoic habitats that included gigantic dinosaurs, the biggest problem would be the sheer safety of the expedition members. The bureaucratic protocols developed for a Mesozoic expedition would emphasize safety, with the intent of keeping the chances of losing any participants to a bare minimum. Modern safaris in Africa require the presence of a guard armed with a rifle when visitors are not in vehicles in case of an attack by big cats, hippos, buffalo, rhinos, or elephants. Similar weaponry is often needed in tiger country, in areas with large populations of grizzlies, or in Arctic areas inhabited by polar bears. The potential danger level would be even higher in the presence of flesh-eating dinosaurs as big as rhinos and elephants and able to run down a human who could potentially be out of breath because of the low oxygen. It is possible that theropods would not recognize humans as prey, but it is at least as likely that they would, and the latter would have to be assumed. Aside from the desire to not kill members of the indigenous fauna, rifles, even automatic rapid-fire weapons, might not be able to reliably bring down a 5-tonne allosauroid or tyrannosaur, and heavier weapons would be impractical to carry about. Nor would the danger come from just the predators. A herd of whale-sized sauropods would pose a serious danger of trampling or impact from tails, especially if they were spooked by humans and either attacked them as a possible threat or stampeded in their direction. Sauropods would certainly be more dangerous than elephants, whose high level of intelligence allows them to better handle situations involving humans. The horned ceratopsids, even less intelligent than rhinos, and probably with the attitudes of oversized pigs, would pose another major danger. Even medium-sized dinosaurs could pose significant risks. An attack by sickle-clawed dromaeosaurs, for instance, could result in serious casualties. So could assault by a squadron of parrot-beaked peccary-like protoceratopsids. As for the pterosaurs, the giant azhdarchids are not creatures one would want to get particularly close to.

But there would be another danger that would be as small as it is big: microbes. Expedition members would be at risk of picking up exotic Mesozoic disease organisms they would not be immune to, and at least as bad would be the danger of contaminating the ancient environment with a host of late Cenozoic viruses, bacteria, and parasites that could seriously disrupt Jurassic and Cretaceous life.

The combined menaces, small and big, would mean that time-traveling dinosaur watchers would probably be banned from directly interacting with the ancient habitats. Instead of walking about under the Mesozoic sun and stars, breathing ancient fresh air, binoculars in hand, they would always have to wear microbe-proof biohazard suits when not in vehicles, and habitats would likewise need to be sealed against microbes getting in or out. Dwelling in dinosaur habitats would be a lot like living on the moon or Mars—a very artificial experience in which paleonauts would be significantly detached from the fascinating world around them, always respiring pretreated air. An advantage of being in biosuits would be temperature control, which would eliminate dealing with the extreme heat prevalent in much of the Mesozoic. Also dealt with would be issues with the composition of the atmosphere. Travel by foot would probably be largely precluded in habitats that included big theropods, sauropods, and ceratopsids. Expedition members would have to move about on the ground in vehicles sufficiently large and strong to be immune from attacks by colossal dinosaurs. Movement away from the vehicles would be possible only when drones showed that the area was safe. Even in places lacking giant dinosaurs, there would be the peril of a biosuit being breached by an assault by a smaller dinosaur—any such penetration from any cause would require some level of medical care, quarantine at least. Defensive weapons might be necessary, although pepper spray guns might suffice. Yet another danger in some Cretaceous habitats would be elephant-sized crocodilians that might snap up and gulp down whole a still-living human unwary enough to go near or in the waters where dinosaurs hung out.

A safe way to observe the prehistoric creatures would be remotely via drones that could observe the winged archosaurs when on the ground and, even better, follow them in the air. Manned ultralights would work too, although they would have their own dangers. Also relatively safe would be visiting islands too small to sustain big predators.

A consequence of time travel for paleoartists would be the obsolescence of every single dinosaur life restoration. One possible exception might be the first dinosaur proven to be feathered, little *Sinosauropteryx*, its plumage and coloration still being the best understood. Much the same for *Microraptor*.

IF DINOSAURS HAD SURVIVED

Assume that the K/Pg impact is what killed off the dinosaurs, but also assume that the impact did not occur and that nonavian dinosaurs continued into the Cenozoic. What would the evolution of land animals have been like in that case?

Although much will always be speculative, it is likely that the Age of Dinosaurs would have persisted—indeed the Mesozoic era would have endured—aborting the Cenozoic Age of Mammals. Thirty million years ago western North America probably would have been populated by great dinosaurs rather than the rhino-like titanotheres. Having plateaued out in size for the last half of the Mesozoic, sauropods would probably not have gotten bigger, but the continuation of the ultimate browsers should have inhibited the growth of dense forests. Even so, the flowering angiosperms would have continued to evolve and to produce a new array of food sources including well-developed fruits that herbivorous dinosaurs would have needed to adapt to in order to exploit.

What is not certain is whether mammals would have remained diminutive or would have begun to compete with dinosaurs for the large-body ecological niches. By the end of the Cretaceous, sophisticated marsupial and placental mammals were appearing, and they may have been able to begin to mount a serious contest with dinosaurs as time progressed. Eventually, southward-migrating Antarctica would have arrived at the South Pole and formed the enormous ice sheets that act as a giant air-conditioning unit for the planet. At the same time, the collision of India and Asia, which closed off the once-great Tethys Ocean and built up the miles-high Tibetan Plateau, also contributed to the great planetary cool-off of the last 20 million years that eventually led to the current ice age despite the rising heat production of the sun. This should have forced the evolution of grazing dinosaurs able to crop the spreading savanna, steppe, and prairie grasslands that thrive in cooler climates. In terms of thermoregulation, dinosaurs should have been able to adapt, although growing winter food shortages may have been a problem for supersauropods. And the also energetic mammals may have been able to exploit the decreasing temperatures. Perhaps big mammals of strange varieties would have formed a mixed dinosaur-mammal fauna, with the former perhaps including some big birds. Mammals may also have proven better able to inhabit the oceans than nonavian dinosaurs, generating manatees, seals, and whales or beasts like them.

The birdlike dinosaurs evolved brains larger and more complex than those of reptiles toward the end of the Jurassic and beginning of the Cretaceous, but they never exceeded the lower avian range, and they did not exhibit a strong trend toward larger size and intricacy in the Cretaceous similar to the startling increase in neural capacity in Cenozoic mammals. We can only wonder whether dinosaurs would have eventually undergone their own expansion in brain power had they not gone extinct. Perhaps the evolution of large-bodied, big-brained mammals would have compelled dinosaurs to upgrade thinking performance as well. In such a competition, the better brain efficiency of the bird relatives might have proven an evolutionary advantage, all the more so when combined with full color vision.

The species *Homo sapiens* would not have evolved if not for the extinction of dinosaurs, but whether some form of highly intelligent, language- and tool-using animal would have developed is another matter. Modest-sized, bipedal, birdlike predatory theropods with grasping hands might have been able to do so, but the limitation to three fingers may have resulted in inferior manipulation. Or perhaps arboreal theropods with stereo color vision would have become fruit eaters whose evolution paralleled that of the increasingly brainy primates that spawned humans. Actual primates might also have appeared and evolved above the heads of the great dinosaurs, producing at some point bipedal ground mammals able to create and use tools. On the other hand, the evolution of superintelligent humans may have been a fluke and would not have been repeated in another Earthly timeline.

DINOSAUR CONSERVATION

If we take the above scenario to its extreme, assume that some group of smart dinosaurs or mammals managed to survive and thrive in a world of great predatory theropods and became intelligent enough to develop agriculture and civilization as well as an arsenal of lethal weapons. What would have happened to the global fauna?

The fate of large dinosaurs would probably have been grim. We actual humans may have been the leading factor in the extinction of a large portion of the megafauna that roamed much of the Earth toward the end of the last glacial period, and matters continue to be bad for most wildlife on land and even in the oceans. The desires and practical needs of our imaginary sapients would have compelled them to wipe out the giant theropods, whose low adult populations could have rendered them more susceptible to total loss than the not-so-big mammal carnivores. If whale-sized herbivorous dinosaurs were still extant, their low populations likely would have made them more vulnerable than elephants and rhinos. By the time the sapients developed industry, the gigantic flesh and plant eaters would probably already have been part of historical lore. If superdinosaurs had instead managed to survive in an industrial world, they would have posed insurmountable problems for zoos. Feeding lions, tigers, and bears is not beyond the means of zoos, but a single tyrannosaur-sized theropod would break the budget by consuming the equivalent of a thousand cattle-sized animals over a few decades. How could a zoo staff handle a 50-foot-tall sauropod weighing 30 or 50 tonnes or more and eating 10 times as much as an elephant?

WHERE DINOSAURS ARE FOUND

Because dinosaurs are long gone and time travel probably violates the nature of the universe, we have to be satisfied with finding the remains they left behind. With the possible exception of very high altitudes, dinosaurs lived in all places on all continents, so where they are found is determined by the existence of conditions suitable for preserving their bones and other traces, eggs and footprints especially, as well as by conditions suitable for finding and excavating the fossils. For example, if a dinosaur habitat lacked the conditions that preserved fossils, then that fauna has been totally lost. Or, if the fossils of a given fauna of dinosaurs are currently buried so deep that they are beyond reach, then they are not available for scrutiny.

All but a very small percentage of carcasses are destroyed at or soon after death. Many are consumed outright—particularly the juveniles and small adults—or in part by predators and scavengers, and almost all the rest rot or are weathered away before or after burial at some point. Even so, the number of animals that have lived over time is immense. Because at any given time a few billion dinosaurs were probably alive, mostly juveniles and small adults, and the groups existed for most of the Mesozoic, the number of dinosaur fossils that still exist on the planet is enormous, probably in the many hundreds of millions or billions of individuals.

Of these only a tiny fraction of 1 percent have been found at or near the small portion of the dinosaur-bearing formations that are exposed on the surface where the fossils can be accessed, or in the mines that allow some additional remains to be reached. Even so, the number of dinosaur fossils that have been scientifically documented to at least some degree is considerable. Some dinosaur bone beds contain the remains of thousands of individuals, and the total number of dinosaur individuals known in that sense is probably in the tens or hundreds of thousands. The question is where to find them.

Much of the surface of the planet at any given time is undergoing erosion. This is especially true of highlands. In erosional areas, sediments that could preserve the bones and other traces are not laid down, so highland faunas are rarely found in the geological record, the Yixian-Jiufotang lake-forest district being a notable exception, deposited in volcanic uplands. Fossilization has the potential to occur in areas in which sediments are being deposited quickly enough, and in large enough quantities, to bury animal remains and traces before they are destroyed by consumption or exposure. Animals can be preserved in deep fissures or caves in highland areas; this is fairly rare but not unknown when dealing with the Mesozoic. Areas undergoing deposition tend to be lowlands downstream of uplifting or volcanic highlands that provide abundant sediment loads carried in streams, rivers, lakes, or lagoons that settle out to form beds of silt, sand, or gravel. Therefore, large-scale formation of fossils occurs only in regions experiencing major tectonic and/or volcanic activity. Depositional lowlands can be broad valleys or basins of varying size in the midst of highlands, or coastal regions. As a result, most known dinosaur habitats were flatlands, usually riverine floodplains, with little in the way of local topography. In some cases the eroding neighboring highlands were visible in the distance from the locations where fossilization was occurring; this was especially true in ancient rift valleys and along the margins of large basins. The Yixian-Jiufotang did feature local volcanoes, which generally were not as common as paleoillustrators used to show them. Ashfalls can preserve skeletons en masse, but lava flows tend to incinerate and destroy animal remains. In deserts, windblown dunes preserve bones, and also when they slump when wetted by rains. Also suitable for preserving the occasional dinosaur carcass as floating drift are sea and ocean bottoms.

Most sediment deposition occurs during floods, which may also drown animals that are then buried and preserved. The great majority of preserved dinosaurs, however, died before a given flood. The bottoms and edges of bodies of water, whether streams, rivers, or lakes, are prime preservation locations. In some cases these watery locations lead to exquisite preservation, including soft tissues. Also good are floodplains, although nonburial before the next seasonal flood results in their degradation by feeding vertebrates and invertebrates and exposure. An extreme means of fossilization with near-perfect preservation is tree sap, but this can capture only small remains, or animal parts. Once burial occurs, the processes that preserve remains are complex and in many regards poorly understood. It is being realized, for instance, that bacterial activity is often important in preserving organic bodies. Depending on the circumstances, fossilization can be rapid or very slow, to the point that it never really occurs even after millions of years. The degree of fossilization therefore varies and tends to be more extensive the further back in time the animal was buried. The most extreme fossilization occurs when the original bone is completely replaced by groundwater-borne minerals. Some Australian dinosaur bones have, for instance, been opalized. Most dinosaur bones, however, retain the original calcium structure. The pores have been filled with minerals, converting the bones into rocks much heavier than the living bones. In some locations such as the Morrison Formation, bacterial activity encouraged the concentration of uranium in many bones—skeletons still below the surface can be detected by their radiation—leading to a radiation risk from stored bones. In other cases the environment surrounding dinosaur bones has been so stable that little alteration has occurred, leading to the partial retention of some soft tissues near the core of the bones.

While dinosaur bones are on the scarce side, their trackways are much more abundant, with a single individual being able to leave behind lots of prints. Prints are left in sediments sufficiently moist to record them, usually along the edges of water bodies such as streams, rivers, ponds, lakes, and ocean beaches. Sometimes they are stabilized by algal and bacterial mats that that keep them from eroding until the next influx of sediment preserves them. Or windblown sediments are the initial agent of preservation. Or the prints may be degraded, especially if made in soft mud that quickly slumped. Wet places are not necessary to retain prints, as some have been found on the flanks of fossil dunes. Most evocative are tracks associated with raindrop impressions from showers too brief to ruin the prints. Tracks are usually revealed by horizontal splitting of slabs, and in that case it is not always true that the print on view is the one directly impressed by the foot; if the print lacks foot pad scales, then the split layer may or may not be one above or below the surface stepped upon back in the Mesozoic. Sometimes prints are exposed in a vertical section as profiles. Generally, where trackways are common, bones are not, although this separation may be between levels in the same formation. Some places are dinosaur track freeways dense with trails, from little species and juveniles to giant adults; these are usually shoreline deposits patrolled by predatory dinosaurs and used as open traffic corridors. Trackways are often found as part of quarrying operations, where they may be studied before destruction, or removal for scientific or commercial purposes. Prints are the most common privately collected dinosaur fossils. As for other trace fossils, don't forget the poop that can be fairly abundant in some places—coprolites—and the polished gastroliths that may be present scattered in sediments that are otherwise barren of rocks. Eggs, often at least their broken shells, and nests are not extremely rare—having often been buried by the parents, their preservation is not all that surprising.

Although the number of dinosaur bones and trackways that lie in the ground is tremendous, all but a tiny fraction are for practical reasons out of reach. Nearly all are simply buried too deeply. The great majority of fossils that are found are on or within a few feet of the surface. Occasional exceptions include deep excavations such as construction sites and quarries, or mining operations. The famed *Iguanodon*s of Belgium were found in deep coal mines of the 1800s long since flooded. Even if deposits loaded with dinosaur fossils occur near the surface, their discovery is difficult if a heavy cover of well-watered vegetation and soil hides the sediments. For example, large tracts of dinosaur-bearing Mesozoic sediments lie on the Eastern Seaboard, running under major cities such as Washington, DC, and Baltimore. But the limited access to the sediments hinders discoveries, which are limited largely to construction sites made available by willing landowners. A dinosaur enthusiast, to the surprise of local professionals, recently found abundant prints as well as a squashed baby ankylosaur in suburban Maryland, most in creek beds. Coastal cliffs made up of Mesozoic deposits are another location for dinosaur hunting in forested areas, but they can be dangerous as they erode and collapse.

Prime dinosaur real estate consists of suitable Mesozoic sediments that have been exposed and eroded over large areas that are too arid to support heavy vegetation. This includes shortgrass prairies, badlands, and deserts. There are occasional locations in which dinosaur bone material is so abundant that their remains are easily found with little effort, especially before they have been picked over. Dinosaur Provincial Park in southern Alberta is a well-known example. In some locations countless trackways have been exposed. In most cases dinosaur bones are much less common. Finding dinosaurs has changed little since the 1800s. It normally consists of walking slowly, stooped over, usually under a baking sun, often afflicted by flying insects, looking for telltale traces. If really small remains are being looked for, such as fragmented eggshells, crawling on (padded) knees is necessary. Novices often miss the traces against the background of sediments, but even amateurs soon learn to mentally key in on the characteristics that distinguish fossil remains from rocks. Typically, broken pieces of bones on the surface indicate that a bone or skeleton is eroding out. One hopes that tracing the broken pieces upslope will soon lead to bones that are still in place. In recent years GPS has greatly aided in determining and mapping the position of fossils. Ground-penetrating radar has sometimes been used to better map out the extent of a newly found set of remains, but usually researchers just dig and see what turns up.

Now it becomes a matter of properly excavating and removing the fossil without damaging it while scientifically investigating and recording the nature of the surrounding sediments in order to recover the information they may contain. These basic methods have also not changed much over the years. On occasion thick overburden may be removed by heavy equipment or even explosives. But usually it is a job for jackhammers, sledgehammers, picks, or shovels, depending on the depth and hardness of the sediments and the equipment that can be brought in. When the remains to be recovered are reached, more-careful excavation tools, including trowels, hammers and chisels, picks, and even dental tools and brushes, are used. It is rare to be able to simply brush sand off a well-preserved fossil as in the movies, although this happy circumstance does occur in some ancient dune deposits in Mongolia. Usually sediments are cemented to some degree and require forceful action. At the same time, the bones and other remains are fragile, and care must be taken to avoid damaging them. And their position has to be documented by quarry maps, photography, or laser scanning before removal. Individual bones can be removed, or blocks of sediment including multiple bones or articulated skeletons may have to be taken out intact. Again, these operations are usually conducted under conditions that include flying insects, dust, heat, and sun, although tarps can provide shade. In Arctic locations heat is not a problem, but insect swarms are intense during the summer field season. The summer season has been abandoned in some locations because the melted sediments of river cliffs are a serious avalanche danger, so digs are conducted in the extreme Arctic cold.

(continued...)

INDEX TO DINOSAUR TAXA

INDEX TO FORMATIONS

When a formation is cited more than once on a page, the number of times is indicated in parentheses.