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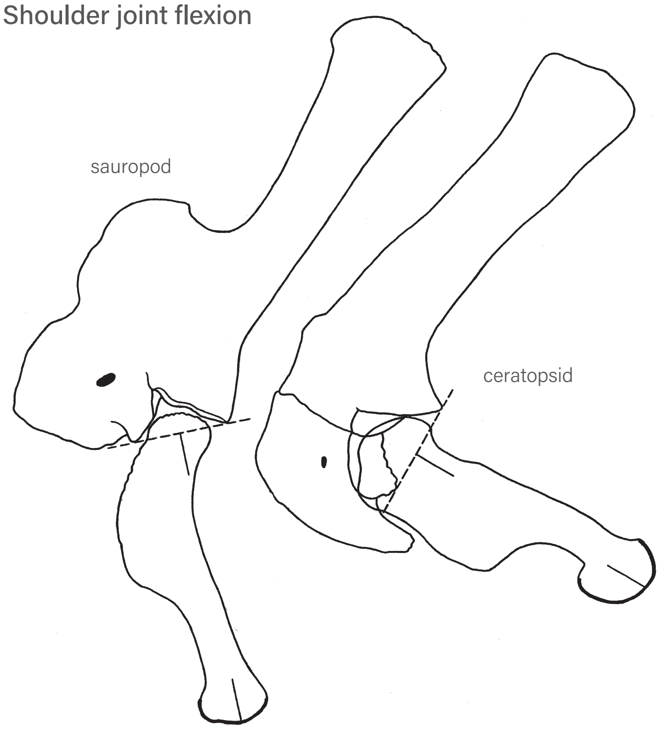
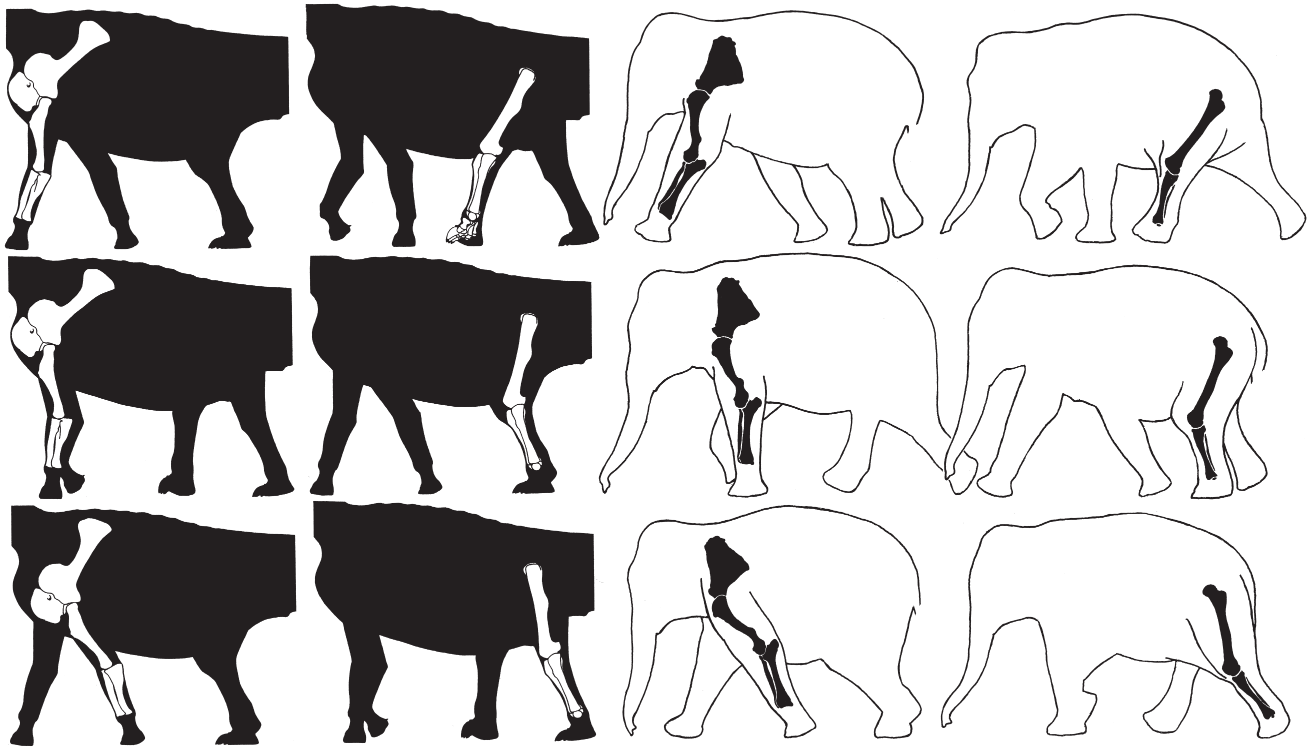
Shoulder joint flexion



including many giants, the normally flexed knee could not be fully straightened because doing so disarticulated the outer femoral condyle from its contact with the groove formed by the proximal end of the fibula and tibia—this remains true in birds, as can be observed with the carcass of an uncooked chicken or turkey. In sauropods and stegosaurs, the upper end of the fibula was elongated a little, so that it continued to articulate with the condyle of the femur when the knee was entirely straight. The sauropod and stegosaur ankle was straight and had minimal mobility, like those of elephants and tortoises.

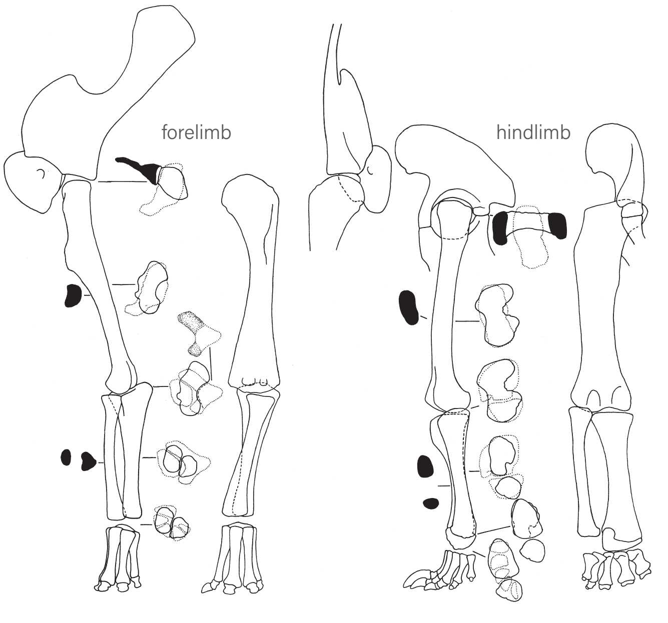
Because sauropods were so big-bodied, it might be tempting to imagine that their legs were laden with great, bulging body-builder muscles in order to bear their massive mass on land. But the similarly built elephants have modest limb muscles. The upper arm and the thigh are narrow. The shank muscles are especially unimpressive; hardly any fibers are on the front of the tibia, much as we can feel by hand on the front side of our own tibia. Elephant leg muscles are so modest because their vertically directed limb bones were posed to bear the weight load with little muscle work, and there was not a need to operate the nearly immobile foot. And elephants cannot run, so they do not need the power—conversely, their modest muscle are a reason they are slow. The same would have been true of sauropod limbs. The upper edge of the ilium was visible in these herbivores, in the same way that the pelvic bones of a cow can be seen under the skin. Because prosauropods were small-hipped, they did not have broad thigh muscles, either. At the knee, the tibia had a substantial forward-projecting cnemial crest, so there would have been a chicken-leg-like drumstick bundle of muscles on the upper shank that operated the feet via tendons. As usual with dinosaurs, the upper end of the sauropodomorph



Fast ambling sauropod and elephant leg action humerus bulged out a little, and the crest of the humerus formed a prominent contour along the upper front edge of the arm. The elbow joint and muscles around it formed a large bulge in front view; subtler bulges were at the wrists and ankles. The latissimus dorsi sheet on the flanks that helped pull back the arms likely formed a contour where it entered the back of the upper arm.

Being borne on elephantine-style arms and legs, sauropods would have had similar locomotary performance. Elephant races show they top out at an unimpressive 25 km/h (15 mph) or so; claims of faster speeds are spurious. Lacking the bouncy, flexed joints and long, mobile hindfeet, or the powerful limb muscles, needed to propel animals into a run with a suspended phase in which all feet are in air for a brief moment in the limb cycle, elephants are limited to an amble, a four-legged form of a walk-run in which at least one foot is always in contact with the ground. This is true regardless of size; juvenile elephants cannot move any faster than their parents. From when sauropods left their nests to when they died, they, too, were unable to achieve a true run with a suspended phase. Some calculations propose that gigantic sauropods were slower than elephants. But the longer stride length that comes from bigger dimensions should have allowed supersauropods to get to 25 km/h or so.

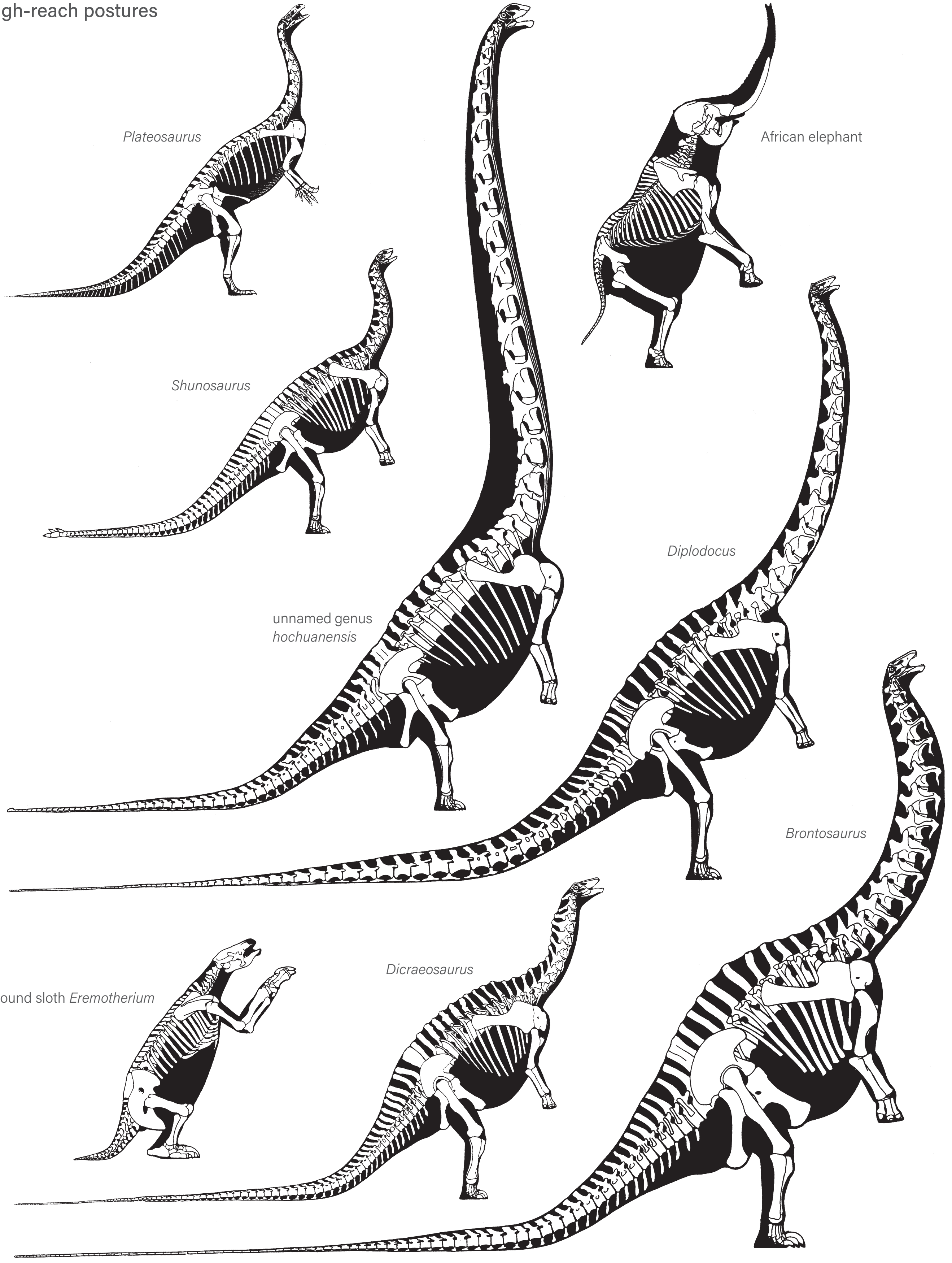
In principle, the top speed of extinct land creatures were recorded and can be determined by the measurements of the high-speed trackways they left behind. In practical terms, animals take the great majority of their steps while walking at a comfortable, sustainable walking pace. And the soft, mucky, slippery flats in which the trackways were usually preserved discouraged running. The speed at which a fossil trackway was laid down can be approximated—with emphasis on the approximated—by correlating the stride length of the trackway with the length of the articulated leg, from the hip joint to the base of the foot. The latter can be estimated from the length of the foot, which is four to one in a surprising array of animals, including prosauropods and sauropods, except that the ratio may have been five to one in some lithe diplodocines. Mammals and birds of all sizes tend to walk at speeds of about 3–7 km/h (average 3 mph). Note that squirrels will bound rapidly, halt for a moment, then bound some more, stop, and so on. Humans and their dogs typically move at a similar overall pace, as do elephants. This is because the cost of locomotion per given distance scales closely to available aerobic power as size increases, so being big does not provide a major advantage. Sauropod tracks show them walking 1–10 km/h (1–6 mph), broadly matching normal elephant paces. Fossil trackways recording speeds near maximum are rare because animals don't run very often, especially on wet, soft substrates, and none are known for sauropodomorphs.

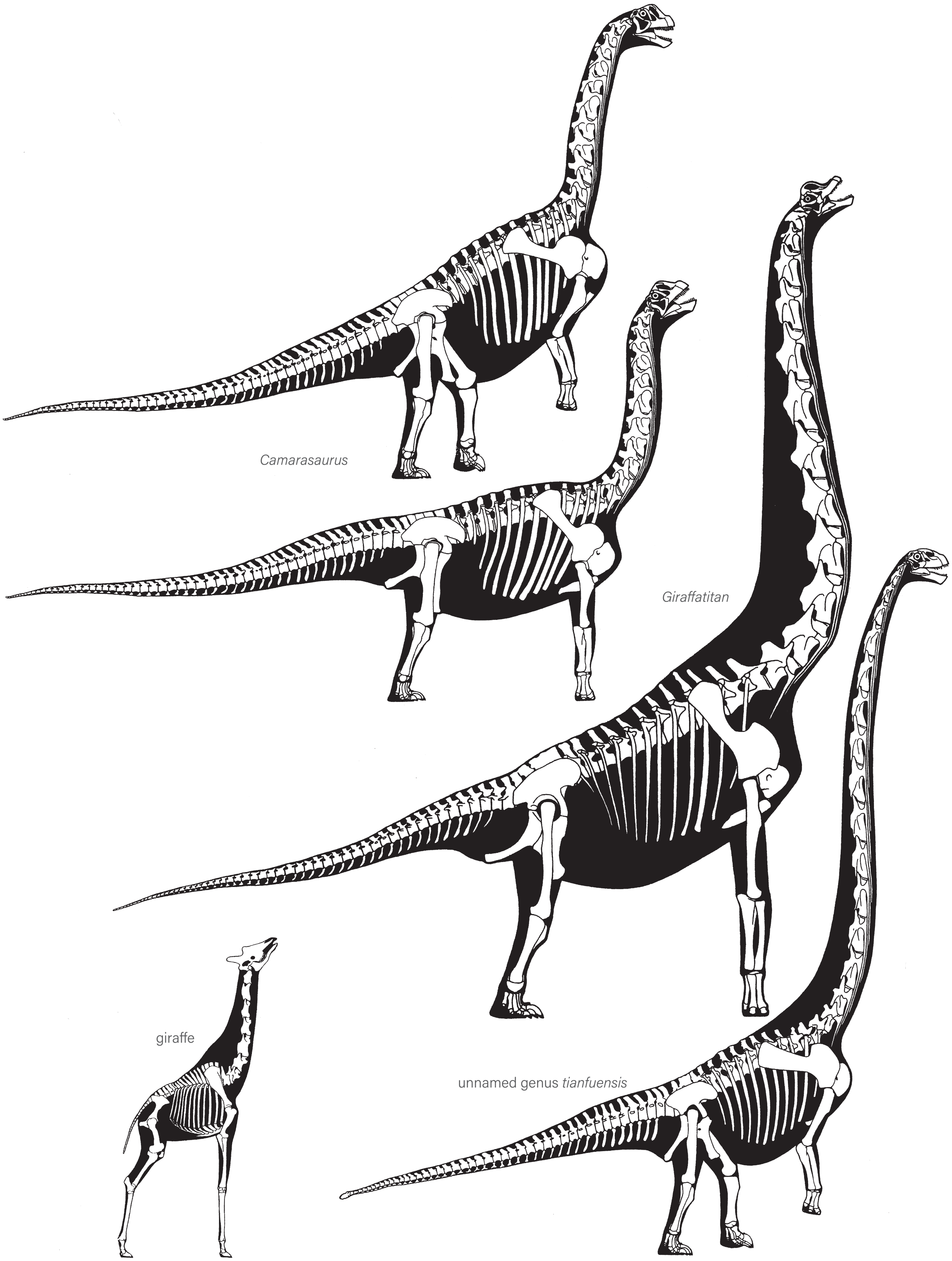


Sauropod limb articulation and posture

Being bipedal to varying degrees, prosauropods could easily stand and slow walk with the body subvertical, using their heavy tails as props when not moving, to maximize their upward reach to crop desirable vegetation. Although they were big-armed, the hindlimb-dominant sauropods could all readily rear up, too—they had to do so for males to mount females. Notably, African savanna elephants rear up fairly often to feed on choice items, even though they are heavy-headed, forelimb dominants without substantial tails; for reasons not known, Asian elephants go bipedal in the wild much less often, if ever, despite their ability to do so in circus performances. The rearing ability of sauropods varied as well. Most appear not specialized to go bipedal to feed, although it may not have been a rare habit among the big-tailed dinosaurs. Diplodocoids were especially hindlimb dominant, being big-hipped, heavy-tailed, and short-bodied. To that add they had special sled-shaped chevrons beneath their tails like those of kangaroos, which use their tails as props. The group had the attributes that indicate they were specialized to rear up on legs and tail and stand tripodally. This was taken to an extreme in apatosaurs, with their especially massive pelves, tall hip vertebrae, and extra short trunks. With the pelvis titled up so strongly, the legs would have had trouble functioning properly, so the knees were probably somewhat flexed, as per rearing elephants. This was an immobile posture. A number of other sauropods also had the sled chevrons that indicate habitual tail-prop rearing. In some sauropods, the hips were retroverted and, along with the base of the tail, were flexed upward relative to the trunk vertebrae. This allowed the trunk to be held strongly pitched up while the hips and tail remained horizontal. This was best developed in camarasaurs, most of all *C. lewisi*. The therizinosaur theropods also had this peculiar arrangement. Their pelvic retroversion allowed the herbivorous bipeds to maximize vertical reach via an erect body while high browsing.

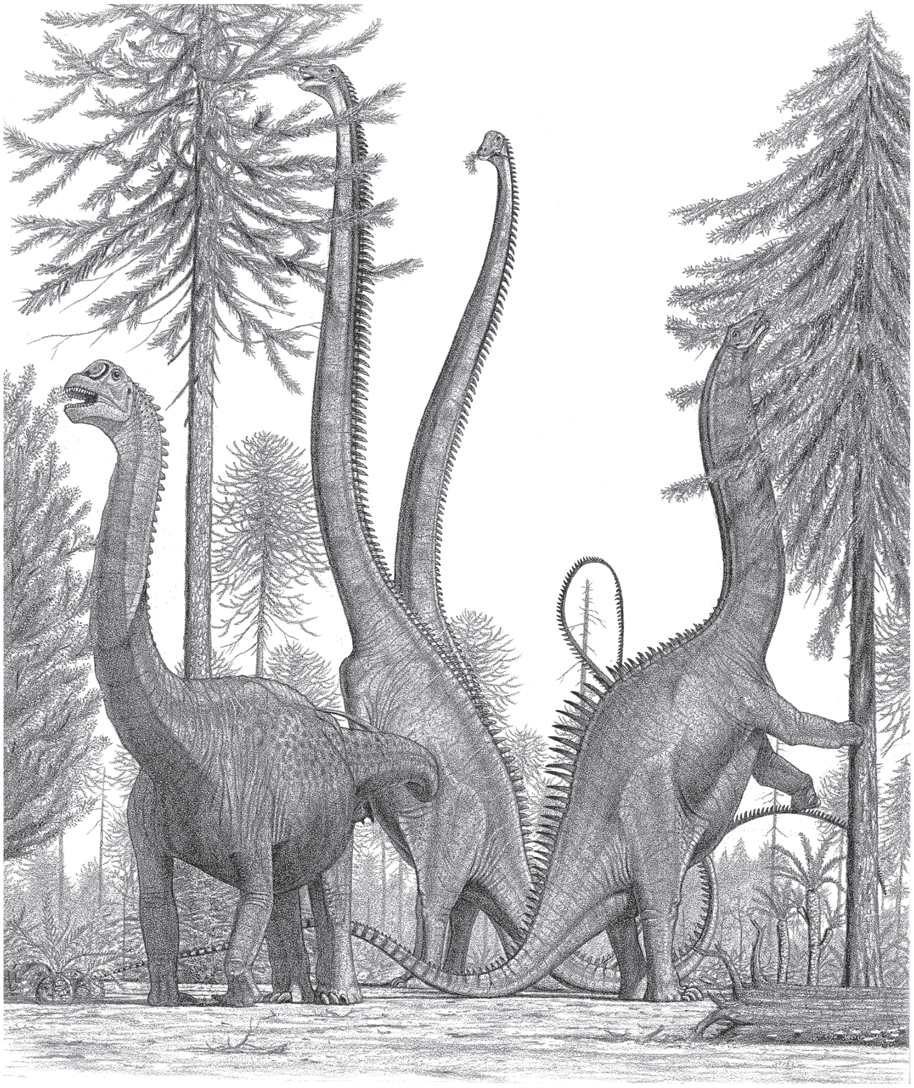
High-reach postures




*Camarasaurus*
*Giraffatitan*
giraffe
unnamed genus *tianfuensis*

A popular conceit is that a super-sauropod shook the ground with each ponderous step even when slow walking. This is nonsense: elephants walk with essentially no sound on clear, solid soil. A herd of stampeding sauropods, on the other hand, would have been a thundering ground shaker.

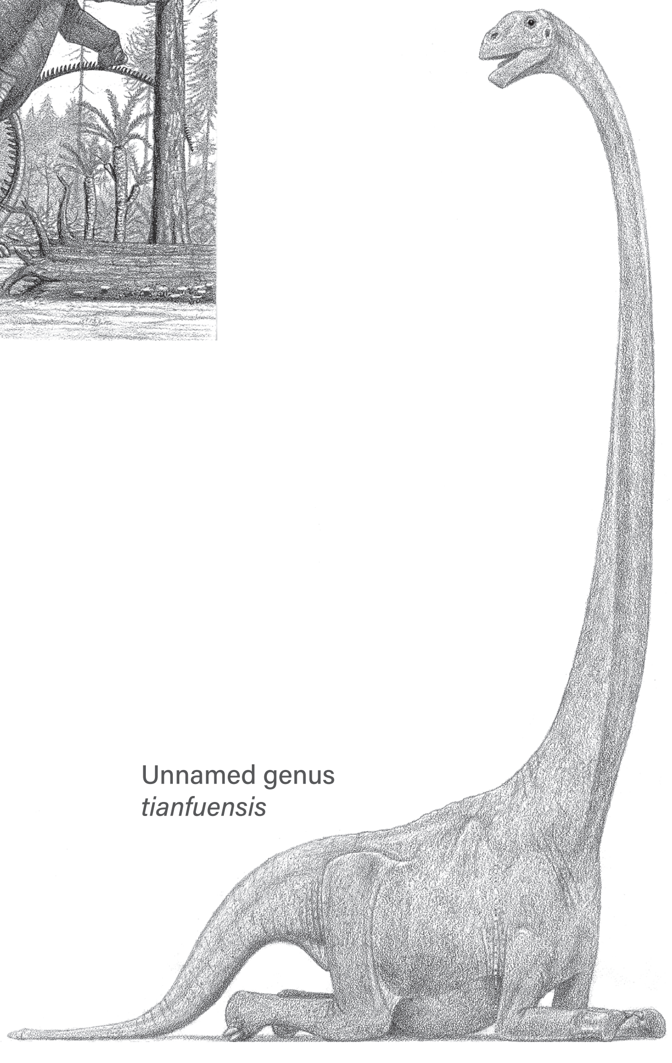
When not on the move, how did the dinosaurs rest? This would have been easy for the modestly sized prosauropods. They could lie on their bellies with limbs tucked up beneath them, or on their sides. Matters were not so simple for ponderous sauropods. Elephants can lie on their sides, but the endless necks of many sauropods would seem to preclude them from doing so. When resting on their abdomens, the legs could not be tightly folded up, the same as with elephants.



*Camarasaurus*, *Barosaurus*, and *Brontosaurus*

In camarasaurs, the slanted hips seem less than optimal because the backward pelvic tilt was sufficient to come close to hindering leg action when quadrupedal. The explanation is that, when rearing, the camarasaurs' hips were then horizontal to the ground, so the hindlegs could operate properly and the animals could slow walk on their two legs alone. Some other sauropods had somewhat retroverted hips that indicate they could also do a bipedal slow walk. Brachiosaurs, too, had the tilted-back pelvis; this was associated with their up-tilted trunk related to their very long arms. Brachiosaurs would seem least prone to rearing, but this does not mean they would not do it when it was the only means of reaching high-quality browse.

A few sauropod trackways consist of only hindprints. These could record occasional bipedalism. Or the big hindfeet were stepping onto the smaller foreprints—elephants normally overimprint this way. Another possibility is that hip-heavy sauropods were poling along the bottom with the hindlegs while swimming.



Unnamed genus *tianfuensis*

## SKIN AND COLOR

Most dinosaurs are known from their bones alone, but we know a substantial amount about dinosaur body coverings from a rapidly growing collection of fossils that record their integument. It has long been known that large, and some small, dinosaurs were covered with mosaic-patterned scales. These can be preserved as impressions in the sediments before the skin rotted away, but in numerous cases, traces of keratin are still preserved. Footprints sometimes preserved the shape of the foot pads. Lizard-like overlapping scales were not common among dinosaurs and have not been found among sauropodomorphs. No trace of a body covering is yet known for a prosauropod, except for some footprints that record the scales on the bottom of the feet. Among sauropods, there is a fair amount of material, much recently found and not yet detailed. None has been documented from the heads. Skin patterns are known for juveniles as well as adults.

As is common for dinosaur scales, those of mature sauropods are generally semihexagonal. Size is very variable, ranging from 5 to 30 mm (0.3–1.5 in). The dimensional difference can be seen in a small patch, although there is a possibility that scales higher up on the body tended to be larger than those on the underside. Sometimes a large scale is ringed by smaller ones, forming a rosette, another frequent dinosaur feature. Evidence of organization into larger patterns has not been seen in adults. The scales are fairly flat, but they are not smooth-surfaced. Unlike other dinosaurs, mature sauropod scales sport dense fields of small, beadlike, protruding papillae 1–3 mm in size (less than an eighth of an inch)—sauropod skin would have had a rather rough texture. Because sauropod scales were usually not large, they tend to disappear from visual resolution when viewed from a dozen feet or more.

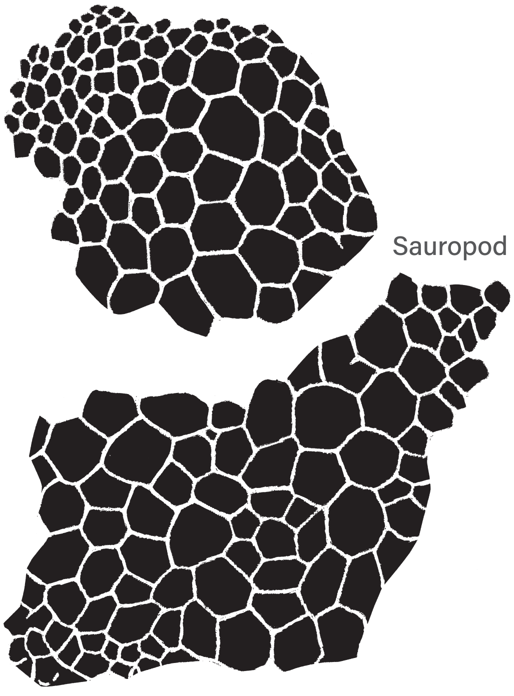
Embryo sauropod scales are generally similar to those of their parents, albeit far smaller and sometimes more beadlike, and lack the papillae. There were rows of larger scales that may have run atop the backbone. Scale scraps from what may be a larger growing diplodocid include squarish and rectangular scales sometimes set in irregular rows, which may have followed the line of skin folds where limbs blended into the body.

For decades, sauropods were, ironically, restored like giant mammals in that their dorsal midlines were left unadorned—this even though midline frills were known in hadrosaurs, albeit not ceratopsids. The plain back art ceased when it became known that spiky frills like those of iguanas ran atop diplodocids, all the way to the tips of their whip tails. The midline scale rows of the embryos may have been the ontogenetic predecessor of the frills. It is generally presumed that frills were universal among sauropods and perhaps prosauropods, although this is not certain; some examples may have had partial frills.

Most sauropods were not armored. Titanosaurs bore substantial osteoderms up to 400 mm (1.3 ft), half that size or less being typical. Shapes were usually oval, also subcircular, teardrop, sometimes occasionally elongated. In profile, they were shallowly subtriangular. Sometimes there was a midline ridge that probably ran forward and aft. These have not been found in place, were not highly numerous on a given individual, and did not form a dense pavement, as they do on ankylosaurs. They may have been set in a couple of rows or more on the flanks, but that is speculative.

It cannot be overemphasized that illustrating sauropods with elephant-like wrinkled skin is entirely incorrect. Such a peculiar integument is limited to proboscideans—rhino skin, for instance, is not similarly wrinkled. Throat and neck wattles and similar soft-tissue display structures are plausible on prosauropods and sauropods. Some lizards have vertical skin folds around the shoulders, and such is possible in these dinosaurs. There is evidence that simple protofeathers evolved at or before the base of the dinosaurs. If so, they were lost at some point in sauropodomorphs, perhaps among the basal prosauropods. That issue awaits more fossil evidence.

Pigment capsules are allowing the colors of feathered dinosaurs to be determined to a fair extent, and such is now being done for some of the dinosaur skin fossils that incorporate original tissues. Those include a diplodocid that had a yellowish or ginger color. This indicates that sauropods were not a uniform gray in the manner of giant continental mammals, although it is quite possible that some of them were such. The hypothesis offered by some 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 than



Sauropod scales

the dull gray, nonscaly skin of big mammals to carry bold and colorful patterns like those of reptiles, birds, tigers, and giraffes, and the color vision of dinosaurs may have encouraged the evolution of colors for display and camouflage. Sauropodomorphs adapted to living in forested areas may have been prone to using greens as stealth coloring; drier areas probably favored more browns and tans. Being dark-skinned could pose overheating problems for species living in hot climes; for those living at higher latitudes, dark may have been better. Small dinosaurs are the best candidates for bright and/or bold color patterns like those of many but not all small lizards and birds. Dinosaurs would be likelier to bear disruptive color patterns when very vulnerable juveniles than when adult. On yet another hand, because humans lack vision in the UV 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 females that look bland and much the same—feature dramatic UV 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, 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 reptilelike, 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 glide back and forth easily, 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.

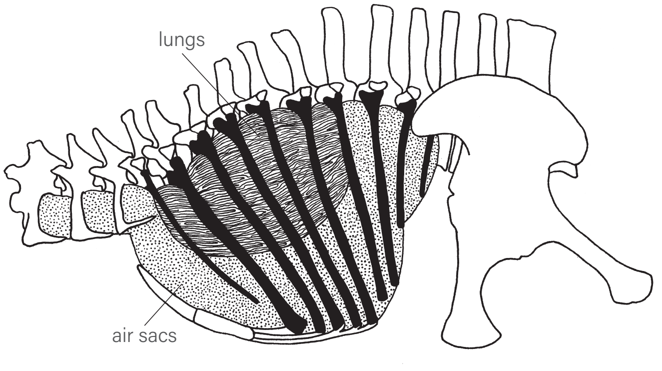
It is widely agreed that all dinosaurs probably had fully four-chambered, high-capacity, high-pressure hearts. Hearts make up to 0.5–1 percent of overall mass, so those of giant sauropods would have weighed hundreds of kilograms (twice as many pounds), comparable to whales of similar size. The super tall sauropods would have needed, like giraffes, special vascular adaptations—among them extra powerful muscles of the left ventricle that power arterial blood—to cope with the problems associated with fluctuating pressures from very high to neutral as the animal stood with the oxygen-demanding brain many meters above the heart and feet, or lay down, or raised and lowered its head from drinking level to the maximum vertical reach. During the latter, extra strength, tension-resistant tissues were needed to contain the high pressures below heart level, especially in the feet. Blood makes up about a twelfth of total body mass, so a 50 tonne sauropod would have contained about 4 tonnes, or 4,000 L (1,000 gal), of blood, again similar to great whales. 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 these dinosaurs should have as well, leaving them a little inferior in $O_2$ capacity.

The respiratory complexes that oxygenated and decarbonized sauropodomorphs evolved considerably over time. Restoring the respiratory complexes of saurischians is aided by birds being members of the group. Birds have the most complex and efficient respiratory system of any vertebrate. Because the lungs are rather small, the chest ribs that encase them are fairly short, but the lungs are internally intricate, so they have a very large gas-exchange area. The lungs are also rather stiff and set deeply up into the strongly corrugated ceiling of the rib cage. The lungs do not dead-end; instead, they are connected to a large complex of air sacs whose flexibility and especially volume greatly exceed those of the lungs. Some of the air sacs invade the pneumatic vertebrae and other bones, but the largest sacs line the sides of the trunk; in most birds, the latter air sacs extend all the way back to the pelvis, but in some, especially flightless examples as observed in kiwis and ostriches, 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.

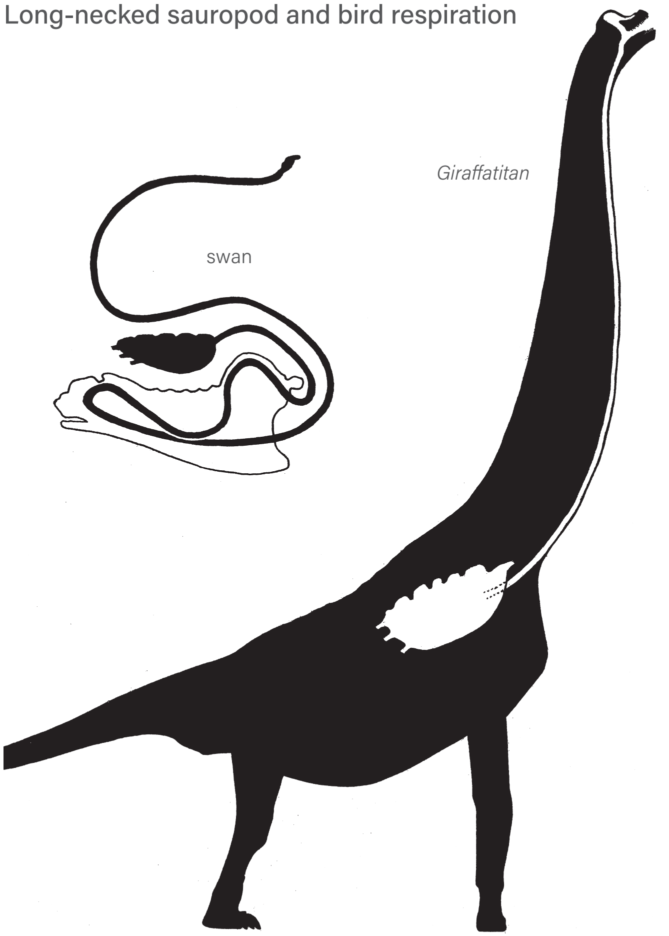
The system is set up in such a manner that most of the fresh inhaled air does not pass through the gas-exchange portion of the lungs but instead goes first to the air sacs, from where it is injected through the entire lungs in one direction on its way out. Because this unidirectional airflow eliminates the stale air that remains in dead-end lungs at the end of each breath and allows the blood flow 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 earliest 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. Theropods would go on to evolve increasingly extensive and capable systems until they reached the near-avian and then fully avian condition. Early euprosauropods, too, started to show signs of incipient air sacs. Sauropods show strong evidence that they independently developed an air-sac system approaching that of birds in complexity. The vertebrae were usually highly pneumatic, sometimes including the base of the tail. 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 that possessed by birds. Lacking an elongated sternum and long aft ribs, the air sacs should have been limited to the rib cage, leaving the abdomen free to be entirely filled with digestive organs. 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.

Sauropod respiratory complex



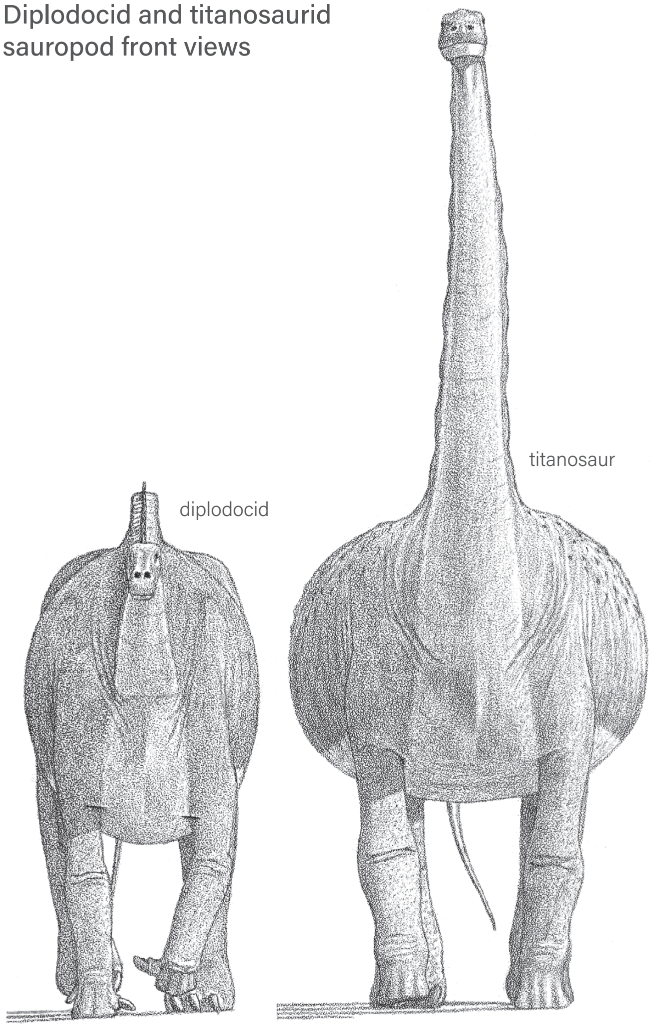
Long-necked sauropod and bird respiration



## DIGESTIVE TRACTS

Herbivorous reptiles and birds lack the ability to thoroughly chew the plant materials they crop and ingest. Vegetation is swallowed with minimal oral processing and then broken down in the gut. Many plant-eating birds use gastroliths, aka gizzard stones, to help physically pulp the foliage by abrasion, crushing, and churning before further abdominal operations. In smaller birds, this is grit; in larger examples, such as ratites, gravel-sized hard stones, polished by constant tumbling and muscular contractions, are used in stone-rolling gizzard mills. Ornithischian dinosaurs paralleled herbivorous mammals in being oral processors that feature dental batteries covered by cheeks to extensively

Diplodocid and titanosaurid sauropod front views

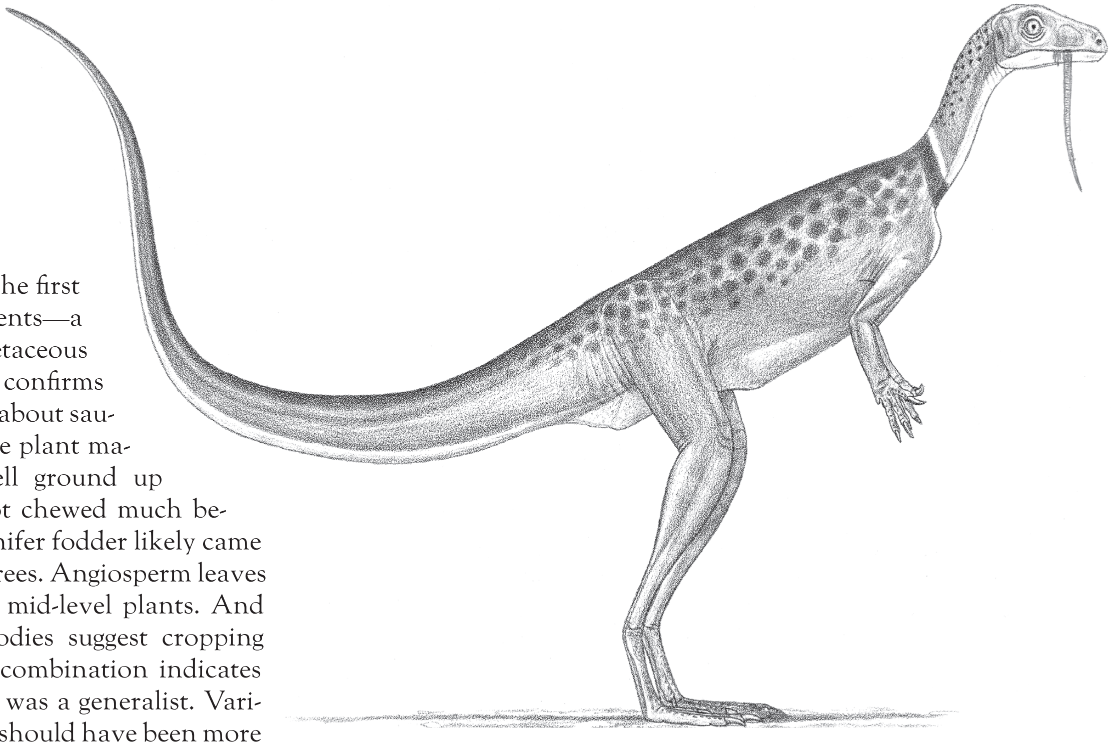


masticate plant stuffs before it is swallowed—or in the case of ruminants, after the material has undergone biochemical treatment in the gut and is regurgitated for physical breakdown by the teeth and reswallowed. The digestive organs make up in the area of a sixth of total mass in plant consumers. All herbivores use a bacterial gut flora to help deal with plant fibers and cellulous. The degree to which this is done depends on the nature of the digestive tract and the digestibility of the food—this is done at some cost, because the microbes use about a quarter of the nutrients and calories for themselves. The digestive complex of a gigantic sauropod would contain a tonne or so of symbiotic microbes. At a given size, tachyenergetic endotherms with high metabolic rates and aerobic budgets need to consume and digest more food than bradyenergetic endotherms, up to 10 times as much or more.

Lacking food-grinding dental batteries, sauropodomorphs were not sophisticated oral processors. The majority of prosauropods had narrow, pointed mouths as part of lightly constructed, moderately muscled skulls suitable for browsing leaves and twigs that were on the delicate side. A few prosauropods had stouter skulls able to take on somewhat tougher foliage. The cheeks that appear to have been present on at least some prosauropods and early sauropods should have allowed them to mash food before swallowing. Modest food chewing may explain why prosauropods did not have particularly big, fermenting tummies.

Sauropodomorph abdominal evolution was a story of increasingly plump bellies over evolutionary time. The first sauropods switched to more massive digestive complexes than prosauropods, with larger gut floras that could more extensively and efficiently digest tougher vegetation that was gathered in most cases by bigger, stronger teeth. The cheeks were lost. Tooth wear was often extensive, reflecting the cropping of rougher foliage, including thicker branches, as well as grit picked up with ground cover. Diplodocoids and titanosaurs converted to radically altered heads, with the teeth converted to slender pencils set tightly together at the front of a more squared-off mouth that allowed rapid cropping of foliage from both branches and the ground. The most straight-across jaws were largely for grazing, like broad-lipped white rhinos. The result was very fast tooth wear that was made up for with very rapid replacement of the teeth. Titanosaurs went the furthest with their enormous plant-processing bellies; approaching the end of the Mesozoic, all sauropods were broad-beamed. Well-rounded, hard stone, gastroliths found in association with sauropodomorphs and littering the sediments indicate they helped the food processing by churning the food in the gizzard. In healthy herbivores, the ingested fodder, bacterial gut flora, feces, and gizzard stones if present, make up 10–20 percent of the animal's total mass. There is no evidence that sauropods evolved an ultra-efficient ruminant-like cud chewing system like those of artiodactyl ungulates; such work only in animals of medium size in any case. As a side effect of being nonruminants, sauropodomorphs would not have released large quantities of methane into the atmosphere.

Late Jurassic sauropod gastrolith, actual size

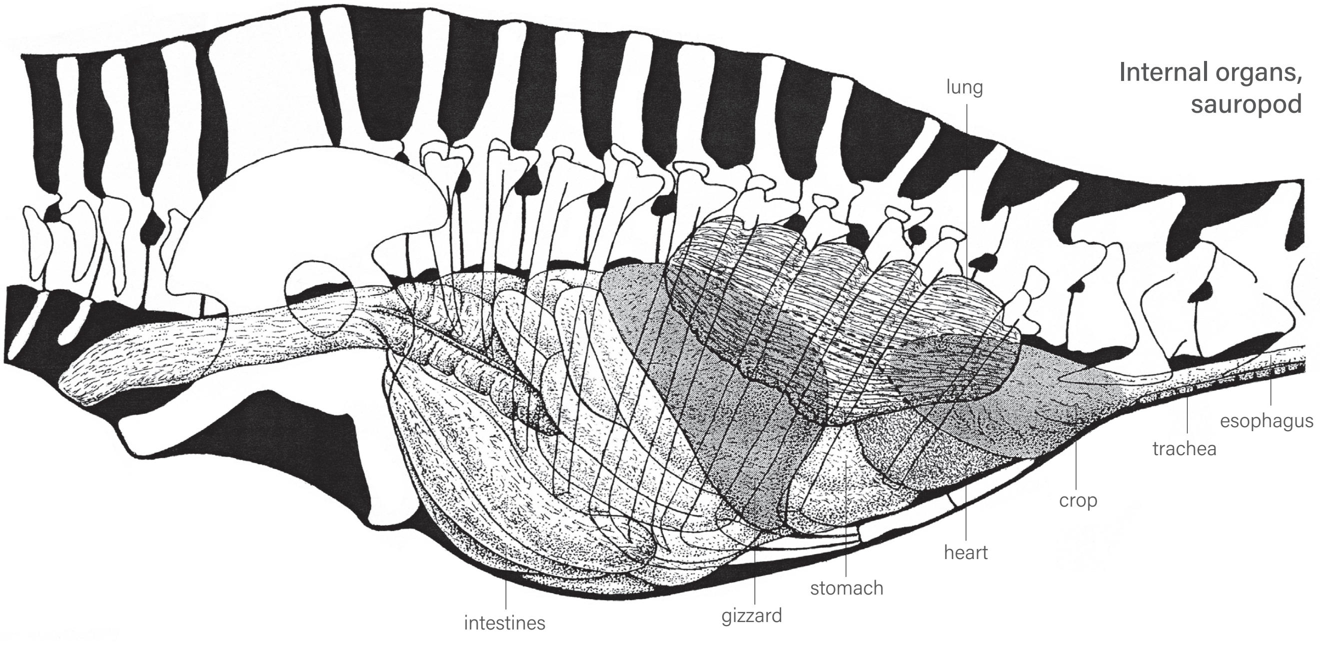


Predaceous
*Eoraptor*

A new finding of the first fossilized gut contents—a cololite—with a Cretaceous Australian specimen confirms the general thinking about sauropod diets. That the plant materials were not well ground up means they were not chewed much before swallowing. Conifer fodder likely came from the crowns of trees. Angiosperm leaves were probably from mid-level plants. And seed-fern fruiting bodies suggest cropping ground cover. This combination indicates this early titanosaur was a generalist. Various other sauropods should have been more specialized in their dietary habits.

Having some sharp teeth, the first prosauropods were omnivores. But the all blunt-toothed euprosauropods and sauropods could have readily reached out with their long necks and snapped up unwary protein- and calcium-rich creatures small enough to swallow whole from the ground and in vegetation, as do ratite birds. The victims could have included lesser dinosaurs and juveniles, including the odd baby sauropod.

Sauropodomorphs needed to drink copious quantities of water to supplement what they obtained via fresh vegetation. For a gigantic sauropod, this could be a few hundred liters of water a day (a fourth as much in gallons), most of all when it was hot, and much of the $H_20$ was used for cooling. Mammals can suck up water in quick order. Among diapsids, only pigeons are known to do so; the rest have to lift their heads and let the water drain down their gullets. Repeating this motion could have been awkward for sauropodomorphs with necks meters long, and spending time at the edge of water can be dangerous due to crocs and such. To solve these problems, it is plausible that the dinosaur group evolved a water-pump system.



Internal organs, sauropod

## 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. Any binocular vision tied to the overlapping fields of vision in prosauropods and sauropods would have been modestly developed at best. Reptiles and birds have full color vision extending into the UV 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, including large sauropods, 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. Sauropodomorph eyes faced to the sides, maximizing the area of visual coverage for detecting potential threats at the expense of the binocular view directly ahead, which the herbivores did not need.

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. In the dinosaur mold, prosauropods and sauropodomorphs often had extremely well-developed, voluminous nasal passages, with abundant room at the back for large areas of olfactory tissues. In prosauropods and some sauropods, such as camarasaurs, the olfactory lobes of the brain were large, verifying their highly effective sense of smell. Those of diplodocoids indicate more average olfactory abilities. Herbivorous dinosaurs probably had to be approached from downwind to keep them from sensing their attackers and going on alert.

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 the detection of high-frequency sound. 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 help them 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 sauropodomorphs could not detect very high frequencies. Nor were the auditory lobes of these dinosaurs' 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. The big ears of sauropods had the potential to capture very low frequencies, allowing them to communicate over long distances, as can their elephant analogs. 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 prosauropods and especially the long-necked sauropods 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. 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 most Mesozoic forests, prairies, and deserts were filled with the sounds of sauropodomorphs.

## GENETICS

As more fossils are found in different levels of geological formations, the evidence is growing that dinosaurs, sauropodomorphs included, 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. Prosauropods and sauropods had the same genetic diversity as their direct avian descendants, which may have been a driving force behind their multiplicity.

## DISEASE AND PATHOLOGIES

Planet Earth 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 relations.

Some skeletal pathologies appear to record internal diseases and disorders. Fused vertebrae are fairly common. Among them are a cofused pair of camarasaur neck-base bones that apparently froze together late in life, perhaps ossification of arthritis; being fixed upturned may have made it difficult for the animal to bend its neck down far enough to drink. The pneumatic space in a sauropod neck shows sign of a common avian respiratory fungal infection. 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. Healed bite marks in the tails of sauropods indicate that they survived attacks by allosaurs and tyrannosaurs. A prosauropod apparently lost the last third of its tail to an attack that it survived at least initially. Some sauropods' ribs were fractured. Some sauropod foot bones show signs of stress fractures. Over all, despite or perhaps because of sauropods' size and slow speeds, they show relatively little evidence of impact injury. That said, some of the dinosaurs presumably died either slowly or quickly from the pathologies we find in their fossil remains.

# 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 over all 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 prosauropods and sauropods were reptilian both in size relative to the body and in structure. 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 enlarged spinal cavity in the pelvic region of many small-brained dinosaurs was an adaptation to coordinate the function of the hindlimbs 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 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 sauropodomorphs often formed social groups is supported by some single-species bone beds that do not appear to have been death traps and 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.

Trackways are the closest thing we have to motion pictures of the behavior of fossil animals. A significant portion of the trackways of prosauropods and sauropods show the prints of solitary animals, indicating that the makers were not part of a larger group. A number of trackways 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 sometimes the parallel trackways are crisscrossed by the trackways of other dinosaurs that appear to have been free to travel in other directions. Some sauropod prints were laid in tight groups that are the harbingers of animals deliberately moving as a joint collective containing up to dozens of individuals.

The degree of organizational sophistication of the groups was not as high as those of birds and mammals, which normally contain the offspring of the parents. Sauropod herds were probably more similar to fish schools. A key clue is that the great herd formations lack small juveniles—unable to keep up with the enormous grown-ups and subject to being trampled upon, juveniles under a tonne moved in their own pods. 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 of
a herd of sauropods

## REPRODUCTION

It has been suggested that some dinosaur species exhibit robust and gracile morphs that represent the two sexes. It is difficult either to confirm or to deny many of these claims because it is possible that the two forms represent different species. There is as yet little if any evidence that dimorphism was present into sauropodomorphs, although this can by no means be ruled out.

Reptiles and some birds and mammals, including humans, achieve sexual maturity before reaching adult size, but most mammals and extant birds do not. Sauropodomorphs followed the reptilian scheme—for giant sauropods to wait decades until they reached full size before replacing themselves would have been maladaptive.

The sauropodomorphs lacked many of the specialized display devices in terms of bone-based horns, head crests and frills, and the like found on many dinosaurs. What they did have were their usually long necks and tails, which could be used for display, midline frills, perhaps wattles in some examples, and sheer size in the case of big examples. Some or all prosauropods and sauropods could have engaged in intricate ritual display movements and vocalizations during competition and courtship that have been lost to time. Because height as reflected by the neck was probably a prime form of display—including via rearing—displays may have been prone to be frontal. The ability of titanosaurs to use the ball-and-socket tail-base vertebrae to curl their whip-tipped tails over their backs may have been a display device for mating purposes. While the brachiosaurs, with their high shoulders, towering necks, and small tails, certainly would have put emphasis on frontal, the diplodocoids are harder to parse out. Their large whip tails look like fine display organs, but diplodocoids may have emphasized rearing to make an impression, in which case the tail would be on the ground—possibly, they had complicated display routines in which necks were emphasized tripodally and then tails in lateral presentations. If diplodocoid and titanosaur tail whips could go supersonic to generate sonic cracks, as some propose and others oppose, the sounds could have been an auditory supplement to intraspecific presentations. Very likely, sauropods used their booming voices to make an impression on opponents and potential mates. While intraspecific competition is often peaceful in order to minimize damage to the participants, it can be forceful and even violent, as per battling male hippos that may kill one another. Rearing sauropodomorphs could have assaulted one another with their thumb claws if they had them; tail-bouncing prosauropods could also lash out with their hindclaws. Those sauropods with small tail clubs probably wacked each other's flanks.

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 himself. The need of sauropods to copulate supports the ability of these giants, including the biggest and those with long forelimbs, to stand on the hindlegs alone.

At least some dinosaurs, including sauropods, produced hard-shelled eggs like those of birds, rather than the softer-shelled eggs of reptiles, including crocodilians, and monotremes. 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 appear to have been soft-shelled, indicating that there was considerable variation in the feature in dinosaurs, perhaps even within and between 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. 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. Prosauropod and sauropod eggs were subcircular. Those of the former were about 60–70 mm in diameter (2–3 in) and 100 g (3.5 oz), about twice the size of chicken eggs and broadly similar to crocodilians and big monitor lizards. The only sauropod eggs are those of titanosaurs—what other sauropods were doing remains oddly unknown. They ranged from 120 to 300 mm (up to a foot) and from 0.6 to 10 kg (up to 22 lb). The largest known eggs are those of the elephant bird *Aepyornis maximus*, which were a little larger than the observed sauropod maximum—the biggest eggs of a living bird are those of ostriches, at 150 mm (half a foot) and 0.7 kg (1.5 lb). Incubation periods for large reptile eggs range from a couple to many months, and such would have been true for prosauropods and sauropods, a half or year or substantially more being plausible for their bigger eggs. Some ratites create communal nests in which more than one female lays their eggs, and this may have been true of some dinosaurs.

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 expand its population quickly 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. Sauropodomorphs were r-strategists that typically laid large numbers of eggs in the breeding season. This helps explain why breeding sauropodomorphs laid much smaller eggs than birds at a given adult size. With supersauropods putting out eggs not as large as those of superbirds a hundred times lighter, the sauropodomorphs were emphasizing egg numbers over size in the reptilian mode. By contrast, birds produce a modest number of relatively large eggs and provide the chicks with considerable parental attention. One r-strategist bird group is the big modern ratites, which produce numerous eggs to overcome the high predation rate of their offspring while inside and later outside the eggs. This is in contrast to the great island ratites, which 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 their delicious supereggs. Sauropods appear to have placed the largest number of eggs in a single nest, up to a few dozen. The physiological demands of laying down so much calcium so quickly in the forming shells may be a reason titanosaurs had armor osteoderms to tap into for extra calcium during egg formation. The fast-breeding dinosaurs were very different from giant mammals, which are K-strategists that produce few calves that then receive extensive care over a span of years, including nursing the young via milk-producing mammary glands.

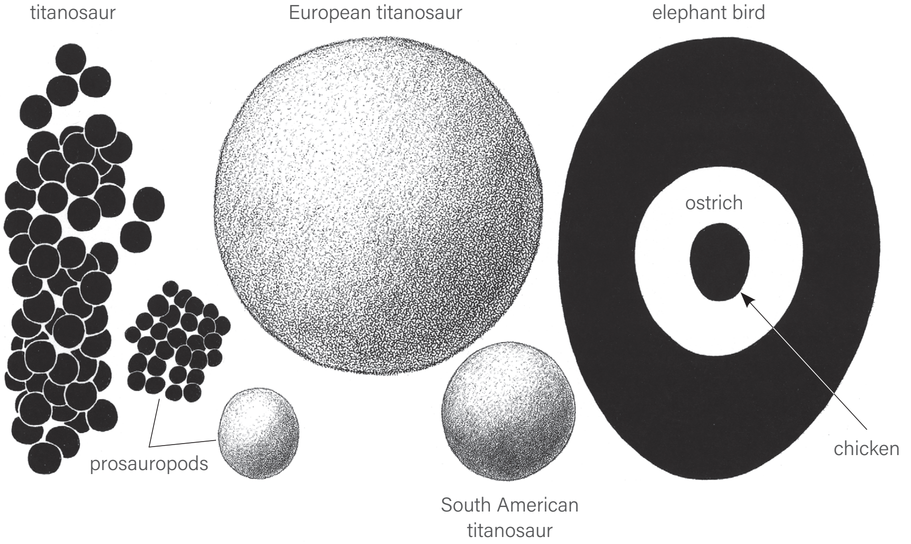
The hatchlings of all reptiles are precocial, having bones and joints ossified well enough, and muscles strong enough, to be able to leave the nest immediately after getting out of their eggs. Baby sea turtles demonstrate this when they immediately skitter across the beach into the waves. Birds are much more variable. Some are very precocial from the get-go; megapode fowl chicks can fly shortly after hatching. Others are highly altricial, unable to leave the nest for extended periods and dependent upon their parents to bring them food until they fledge.

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, which 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.

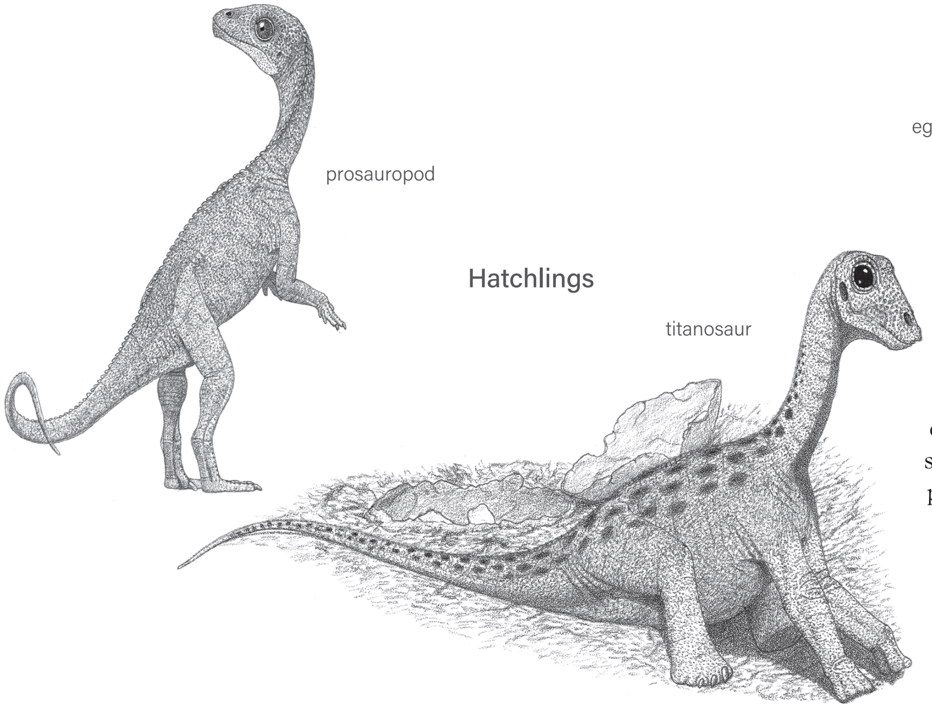
Reptiles lay their large numbers of eggs in pairs, and sauropodomorphs did so as well, not singly as per birds. Prosauropod and sauropod eggs were buried in rather irregular nests in the reptilian norm. Hand and foot claws helped in digging the shallow, broad pits. In some prosauropod nests, many eggs are tightly packed in rows. It is difficult to see what purpose this would have served, so it is not certain if the mother deliberately arranged them that way. With the big-bellied parents too large to brood their eggs, incubation was via ground heat, possibly facilitated by fermenting vegetation included in mulch spread atop the nest. Nests were in colonies, presumably because the soil conditions in the location were optimal, and putting so many nests in the same place would have overwhelmed the local egg eaters. There is evidence that at least some sauropods deposited their eggs near geothermal heat sources.

The known skeletons of prosauropod hatchlings have poorly ossified bones and joints, indicating they were altricial babies unable to leave their nests immediately. This in turn indicates that their parents stayed near the nests, providing protection against egg stealers and possibly monitoring the nest's temperature and adjusting the amount of material above the eggs to keep them at the optimal heat level, like megapode fowl. Once hatched, the nestlings should have been dependent upon their parents for food for weeks up to a few months. Not being especially large, the nesting parents would not have stripped the local flora bare, and the amount of forage needed by nestlings of a few kilograms or less would have been trivial—unlike small birds, which have to work frantically all the daylight hours to keep their perpetually ravenous altricial nestlings satisfied. Because foraging required leaving the nest, it is probable that more than one parent was involved in caring for their charges, one of them staying at the nest to protect the contents while the other was away. The later duck-billed hadrosaurs appear to have practiced a similar form of parental nestling care. It is plausible that at least some of the smaller sauropods did so, too.

Giant adult sauropods would have risked denuding the local vegetation as well as squashing their own eggs if they remained to guard their nests. Also in danger of being trampled were the hatchlings, which at only a few kilograms 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 sauropod hatchling. Some prehatchling reptiles in mass nests start vocalizing to coordinate their synchronous emergence, even though doing so risks attracting egg and hatchling eaters. Sauropod parents leaving their nests to their fates explains why trackways show the small, precocial juveniles formed their own pods. The inevitable high losses of these slowly ambling, weakly armed youngsters were made up for with sheer numbers. Wandering sauropod babies may have been at risk of being picked off at random by grown members of their own species. The young of giant sauropods joined full-sized adults only after a few years, when they had reached hundreds of kilograms. 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 big predators. In the best-known herd trackway, there are only a few really big grown-ups—one of 50 tonnes, another of 30 tonnes, five 20 tonners, the rest on down to over a tonne. This is entirely different from the much more sophisticated herds of elephants, which are made up mainly of adult females collectively raising their


Eggs and nests

Titanosaur hatchling skull


Hatchlings

few calves, including newborns. Prosauropod parents may have been able to allow their offspring to tag along in familial groups once they were large enough to leave the nest, similar to ratites and some other birds. As the juveniles fed themselves, they would have enjoyed the intentional protection of their parents. If any prosauropods nested communally, then the adults would be looking after not only their own young but also youngsters that were not their own.

Because no sauropodomorphs, even the prosauropods, lavished offspring with anything close to the parenting typical of lactating mammals, their progeny could grow up on their own even if the adult population crashed. A juvenile mammal is likely dead if it loses its mother, as is true of many bird chicks.

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, as was the likely norm for the entire group.

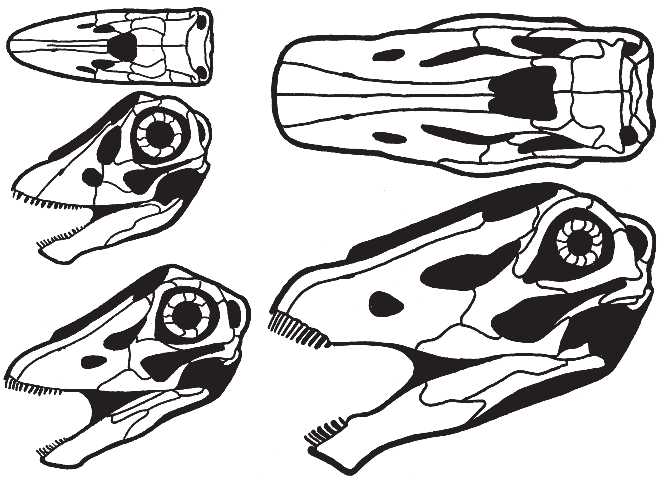
# GROWTH

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.

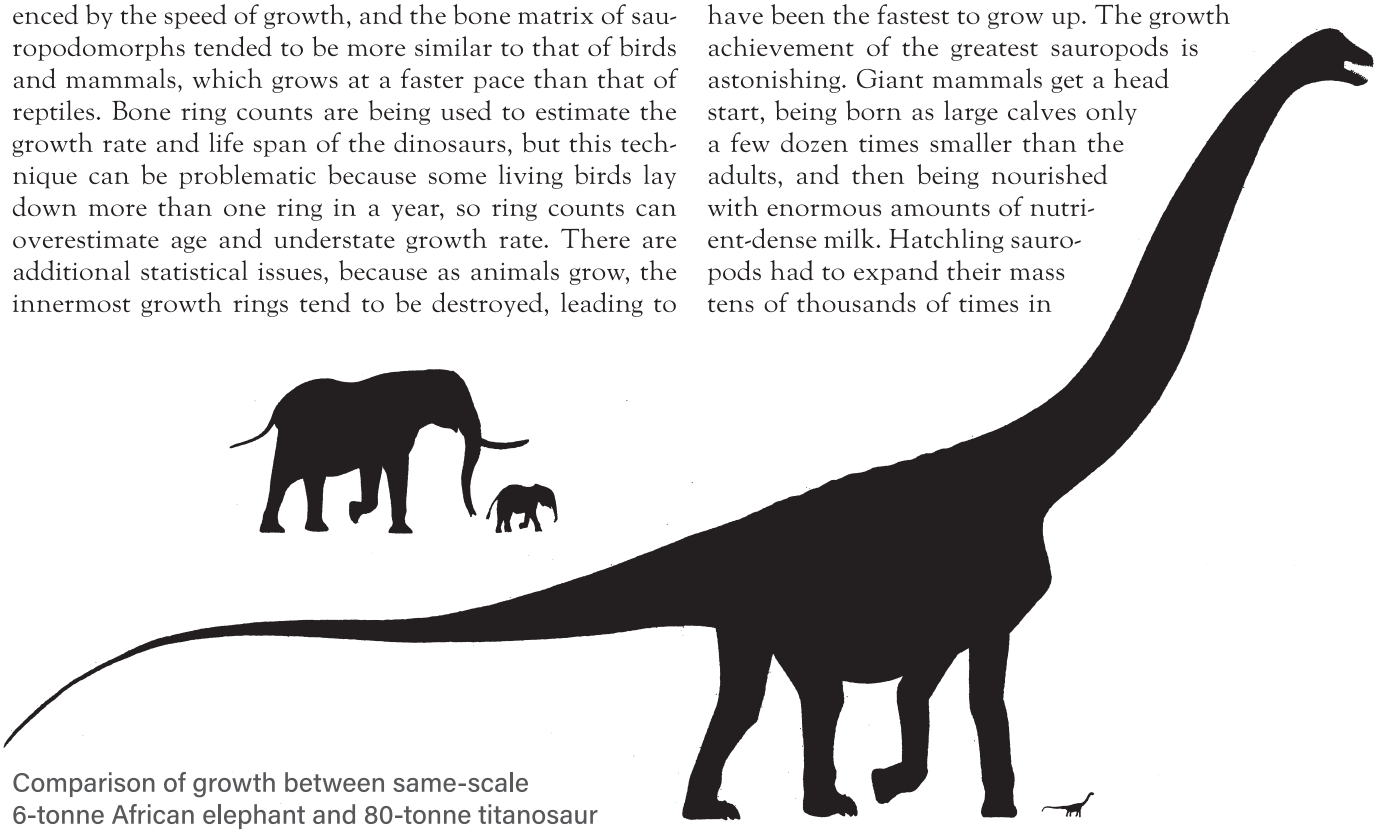
Some marsupials and large primates, including humans, grow no faster or only a little faster than the fastest-growing land reptiles. Other mammals, including other marsupials and a number of placentals, grow at a modest pace. Still others grow very rapidly; horses are fully grown in less than two years, and aquatic whales can reach 50–100 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.

Diplodocus growth series



At the microscopic scale, the bone matrix is influenced by the speed of growth, and the bone matrix of sauropodomorphs 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 the 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 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. The sauropodomorphs sampled so far appear to have grown at least somewhat faster than land reptiles. Rates of growth were variable in prosauropods, as was final adult size to a remarkable degree. Modestly sized sauropods appear to have grown as fast as similarly sized land mammals. 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. Titanosaurs may have been the fastest to grow up. The growth achievement of 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



Comparison of growth between same-scale 6-tonne African elephant and 80-tonne titanosaur just a few decades and with little or no nourishment provided by the adults.

Although they do not undergo metamorphosis like many invertebrates, fish, and amphibians, many amniote tetrapods experience considerable allometric modification in body form and proportions as they grow up, humans being an example. Relative head size is typically larger at the beginning, and it is common for large land animals to start out as lightly constructed and gracilely legged and become more robust in body and especially limbs with maturity—gangly foals compared to adult horses are a paragon of that pattern. Sauropods are notable in that they did not change all that much with growth, being fairly isometric in body, limb, and tail proportions. The load-bearing femur was not particularly slender in even small juveniles and was quite attenuated in some gigantic examples. This exceptionally low degree of change—even in view of the extreme change in total size in many, albeit not all, sauropods—reflects their slow gait at all sizes, like elephants whose proportions remain fairly similar as they age. Sauropod heads did become somewhat smaller with greater size, and necks longer, but even the teenagers had small heads and their necks were never short. Teen to adult camarasaur heads were isometric, because even as adults their snouts were short, the retention of a juvenile feature into adulthood being neoteny. Growing diplodocoids and titanosaurs underwent substantial snout elongation and broadening as their heads became increasingly horse-shaped; the juveniles' relatively narrow snouts reflected a shift from being selective feeders of digestible plant items to courser materials. While growing prosauropods did not multiply their size as much as sauropods, they underwent more extensive alterations more typical of amniotes. Their heads started out relatively large, with a very short rostrum and short neck, and their arms became relatively shorter as adults became more bipedal.

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 sauropodomorphs lived longer than similarly tachyenergetic mammals or birds of the same size. Sauropods seem to have enjoyed similarly long life spans, although whether they made it to a full century or beyond is not documented—but would not be surprising in the case of the biggest examples. If they did, they may have matched the life spans of much smaller and less energetic 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 form of power production 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 (54°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, the more active an animal can be, but even warm reptiles have limited sustained 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 exploit oxygen for power over time is probably the chief advantage of being tachyenergetic. Tachyenergetic animals also use anaerobic power briefly to 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–111°F), with birds always at least at 38°C (100°F). 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 similarly 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. On the big side of the spectrum, elephants and whales have metabolic rates that are a continuation of the tachymetabolic norm and are well above those expected in reptiles of the similar bulk. It is possible for very large bradymetabolic animals to retain most of the heat they generate with their bulk, so they can be low-metabolic-rate endotherms. The common practice to refer to high-energy animals simply as endotherms is correspondingly simplistic, so creatures with high resting and active metabolisms are correctly referred to as tachyenergetic.

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

As diverse as the energy systems of vertebrates are, there appear to be things that they cannot do. All insects have low, 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, 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.

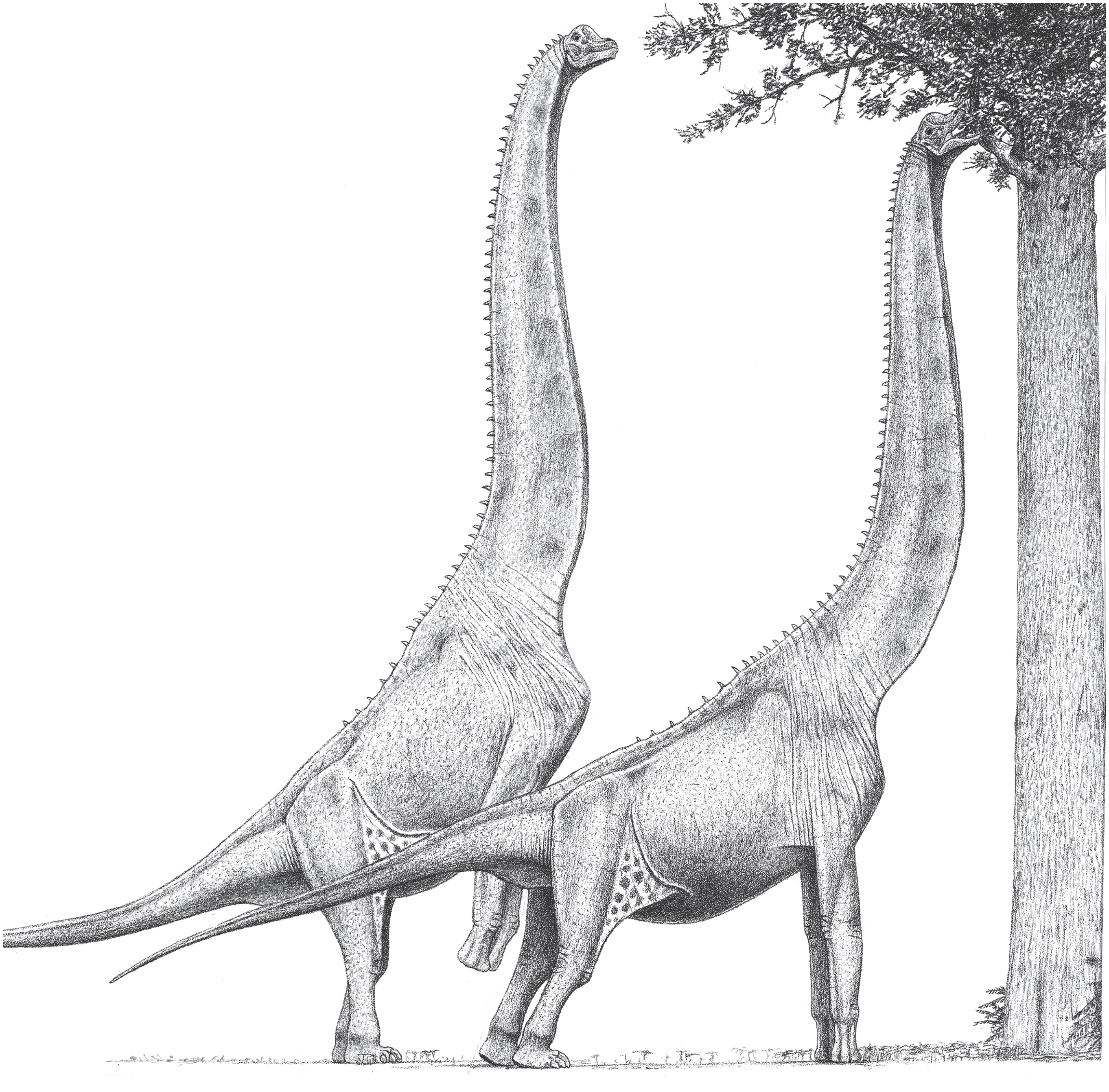
The general assumption until the 1960s was that dinosaur energetics was largely reptilian, but most researchers now agree that dinosaurs' power production and thermoregulation were closer to those of birds and mammals. It is also widely agreed that because dinosaurs were such a large group of diverse 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 (2 mph). The long, erect legs of sauropodomorphs 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 trackways of prosauropods and sauropods show that, like most dinosaurs, they normally walked at speeds over 3 km/h, much faster than the slow speeds recorded in the trackways of prehistoric reptiles. The dinosaurs' legs and the trackways they made both indicate that the animals' 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, sauropods among them, had the large hips able to support the large thigh muscles typical of more aerobically capable animals.

That many dinosaurs, including all long-necked prosauropods and sauropods, 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 how high-metabolism sauropods could have fed themselves with the small heads that made their long necks possible. But there is no relationship between head size and metabolism. Herbivorous lizards, mammals, and some birds have large heads relative to their bodies; the largest birds have small heads. The small head of a sauropod was like that of a tachyenergetic emu or ostrich—it was basically all mouth. Most of the large heads of herbivorous mammals consists of the dental batteries they



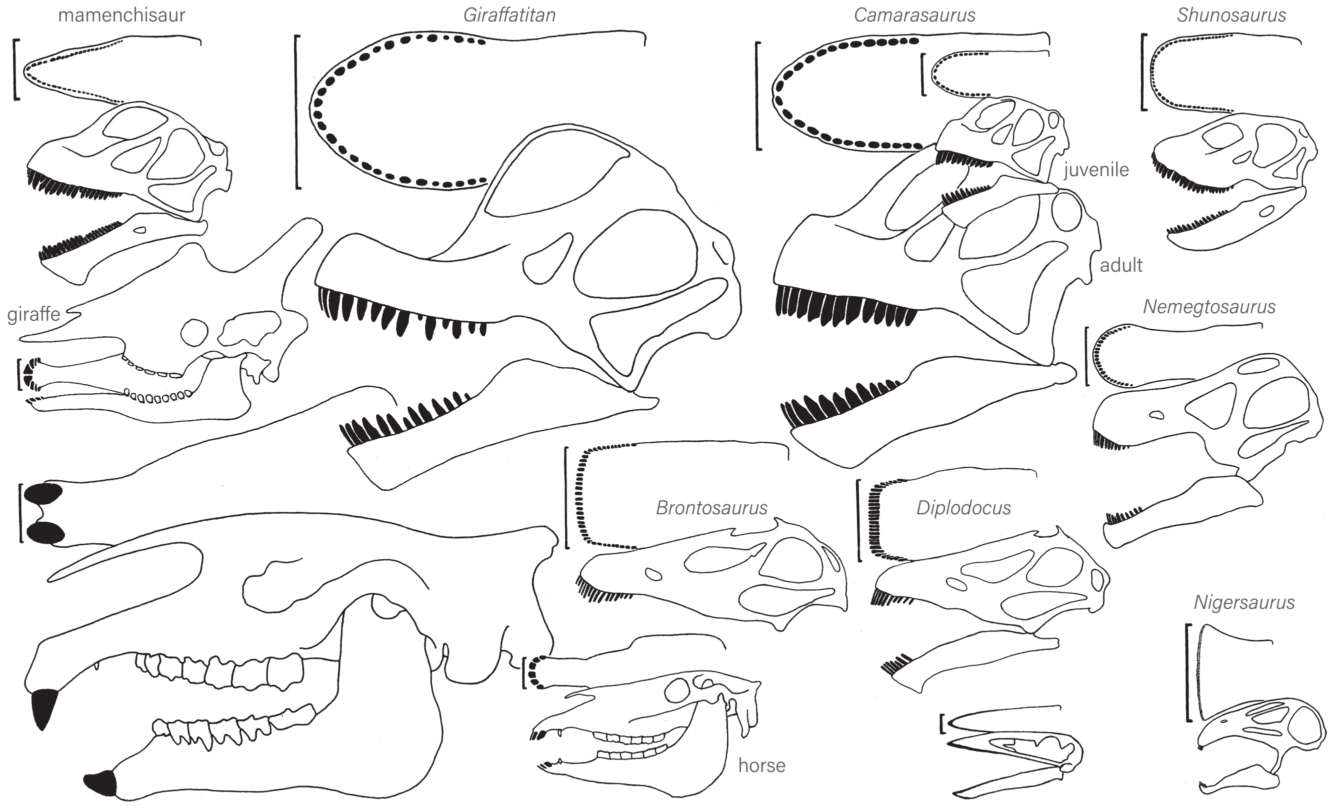
*Giraffatitan brancai*

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—that is an illusion created by the size differential with their titanic bodies—with the mouths of the biggest sauropods able to engulf the entire head of a giraffe. Prosauropod mouths were as broad as those of herbivorous mammals or birds at a given body mass, and the breadth of the sauropod mouth is an isometric extension of that line. If a tachyenergetic sauropod of 50 tonnes ate as much as a mammal of its size is expected to eat, then it would have 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 would have needed to bite off just half a kilogram (1 lb) or so 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 wide (1.5 ft). Making it all the easier was that the sauropod did not need to take time to give each bit a good chew before swallowing, which it could do almost as fast as it cropped the foliage.

Turning from eating to breathing, an intermediate metabolism is compatible with the unsophisticated lungs that prosauropods appear to have had. The highly efficient, birdlike, air sac–ventilated respiratory complex of sauropods is widely seen as evidence that elevated levels of oxygen consumption evolved in these dinosaurs; no animals with reptilian energetics have such sophisticated respiratory complexes. Sauropods probably needed a birdlike breathing complex in order to oxygenate a high metabolic rate through their long tracheae.

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 reptiles breathe more slowly, they 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 the turbinals 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 biggest birds have the relatively smallest heads and correspondingly small respiratory passages, in parallel with sauropodomorphs. The turbinal evidence is not definitive.

The low exercise capacity of land reptiles appears to prevent them from being active enough to gather enough food to grow rapidly. In a biological 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,



Mouth widths

such as those of sauropods, either gather the food themselves or are fed by their parents in other cases. That sauropodomorphs grew at rates faster than those seen in land reptiles indicates that the former had higher aerobic capacity and energy budgets. It has been suggested that sauropods experienced a radical drop from mammalian to more reptilian energetics as they matured. This would have required an extreme transformation of their cellular biology and organ operations that never occurs in living animals, such probably not being possible. If anything, the increasingly high power output demanded by the increasingly high-pressure respirocirculatory complex needed to get the blood up to the brains ever more stories higher than the heart may have required rising metabolisms as the animal skyscrapers completed growth.

A hot topic has been the long-standing concern by many that the big sauropods would have overheated in the Mesozoic greenhouse if they had had avian or mammalian 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—they have been observed striding across the sunny, shadeless landscape when the temperature was 38°C (100°F). It is widely thought that elephants use their big 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, so the ear activity tamps down. Nor was the big-eared African elephant the main savanna elephant until fairly recently; the dominant open-area proboscidean used to be one of the biggest land mammals ever, *Palaeoloxodon recki*. A relative of the Asian elephant, it probably had small ears of little use for shedding body heat at any temperature. It is actually small animals that are most in danger of suffering heat exhaustion and heat stroke because their small bodies pick up heat from the environment very quickly. The danger is especially acute in a drought, when water is too scarce to be used for evaporative cooling. Because large animals have a low surface area/mass ratio, they 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. Put a small dog without water in an open field from which it cannot escape on a hot, sunny day and it will die. An elephant in the same circumstances will not be happy, but it will live. 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. Sauropods may have taken an activity break in the shade on hot middays when possible, but it was not critical. To be avoided was engaging in combat at such times, but the giant theropods would also have stressed themselves out heatwise and were not likely to attack at noon.

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. That sauropods are missing from the most extreme polar regions is probably because the cold, dark winters left them without enough food to power and warm up their titanic bodies. The sauropods' long necks would have been a particular source of heat loss to the environment not present in other large dinosaurs.

The small, altricial juveniles of prosauropods, stuck in their open nests and exposed to the elements, including cooling rains, would have benefited from, if not needed to have, elevated metabolisms.

The isotopes of chemical elements in bones 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 dinosaurs large and small were more homeothermic, and therefore more tachyenergetic and endothermic, than crocodilians from the same formations. One study found evidence for increasing metabolic rates with growth in sauropods, which if correct is in accord with the power requirements of their increasing height.

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. 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. It is likely that sauropodomorphs, like birds and some mammals, 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. Big sauropods' daily body temperatures should have fluctuated strongly as they stored heat during hot days and off-loaded it into the night sky. Because dinosaurs lived on a largely hot planet, it is probable that most had high body temperatures of 38°C (100°F) or more to be able to resist overheating. The possible exception was again high-latitude dinosaurs, which may have adopted slightly lower operating temperatures and saved some energy, especially if they were active during the winter. Some researchers have characterized dinosaurs as mesotherms intermediate between reptiles, on the one hand, and mammals and birds on the other. But because some mammals and birds themselves are metabolic intermediates, and dinosaurs were probably diverse in their energetics, with some in the avian-mammalian zone, it is not appropriate to tag dinosaurs with a uniform, intermediary label.

A horsepower is the work that can be aerobically sustained without undue fatigue by a large workhorse over a work period of some hours, such as turning a wheel pump or pulling a plow. When going all out anaerobically for a brief period—while pulling a heavy sled in a competition at a country fair, for example, or when a thoroughbred wins the Triple Crown—a horse can do about 15 hp. Male human athletes can put out a third of a horsepower indefinitely, and about 2.5 hp briefly, over twice that of a nonathlete. With energy output scaling to the three-quarters power of mass, a 70 tonne sauropod was capable of producing a maximum of about 500 hp anaerobically and could sustain 30 hp aerobically, similar to that of giant whales.

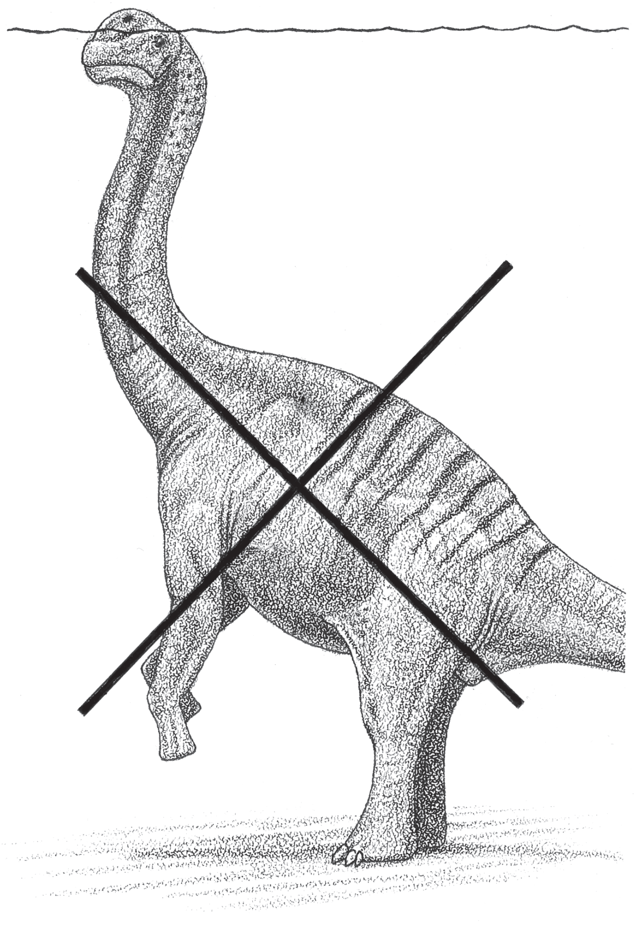
Until the 1960s, it was widely assumed that high metabolic rates and/or endothermy were an atypical specialization among animals, being limited to mammals and birds, and perhaps some therapsid ancestors of mammals, and the flying pterosaurs. The hypothesis was that being tachyenergetic and endothermic 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, especially the big ones, 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 natural selection via DNA survival 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. Another hypothesis 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 aerobic-wise. 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 sustained activity levels. So both hypotheses are operative, and which is more so depends on the biocircumstances—including being really big on land.

## THE LARGELY TERRESTRIAL LIFE

Illustrations showing giant, long-necked sauropods snorkeling in deep waters were not viable because water pressure at depth would have prevented inhalation. Whales can exhale as their chests are still deep, but to inhale, the body has to be awash and the lungs near the surface. In any case, sauropods could not stand in deep water for the obvious reason that they were low-density animals due to their pneumatic bones and associated air-sac complex. This is the opposite of hippos, which are so bone-dense that they cannot surface swim; instead, they bottom walk. While most land mammals are nearly awash when swimming and have to power swim to avoid drowning, pneumatic ratites have their upper backs above water, as would have sauropods. Buoyant diving birds have to use powerful propulsive organs and/or do aerial dives to get well underwater; sauropods lacked such. Deep fresh waters are rather rare in any case, and large rivers would be dangerous for deep-water walkers due to their powerful currents. Elephants are good swimmers that enjoy a safety factor by breathing through their trunks, which can be held well out of the water. The more buoyant long-necked sauropods, too, would have been safe swimmers. Those sporting very elongated cervical series may have had to stretch them out nearly horizontal to avoid tipping over or pitching forward. Prosauropods would have been fine swimmers; although not highly buoyant, the long necks of euprosauropods would have protected them from drowning. Adding to the absence of swimming specializations, including for snorkeling, was that sauropod nostrils were apparently not placed atop their heads.

Further deterring the life aquatic for sauropods was the scarcity of underwater sustenance. Flowering angiosperms, such as water lilies, did not inhabit fresh waters until the Early Cretaceous, and previous water plants were of low caloric and nutritive value. No modern land mammal feeds exclusively on aquatic vegetation; even hippos are land grazers. Deep rivers and lakes lack much in the way of bottom vegetation because light levels are too low. More nutritious plants, such as horsetails and later water grasses, lined Mesozoic waterways, but these could be accessed from firmer ground ashore.



That would have been a good feeding tactic because sauropod feet were poorly suited for aquatic habits. The hindfeet were largely large, rounded, toeless pads like those of elephants, and the latter are predominantly terrestrial. The dinosaurs' hands were worse, being unpadded pillar structures with little or nothing in the way of splayed fingers. In sauropod trackways, the handprints are normally deeper than those of the hindfeet despite the hindlimbs bearing more weight than the fore. That was because the pliable hindpad spread out the load over a large area, while the much smaller hands plunged deeper into the muds and sands. Had sauropods been water lovers, they would have had very different appendages. Some hand-only sauropod trackways may be those of long-armed examples poling along with the arms on the bottom while floating in sufficiently shallow waters. But with the lung-air-sac complex largely in the neck and chest area, sauropods would have been hip- and tail-heavy. At least some of the hand-only tracks are sauropods walking on sediments too firm to capture the large-area hindfeet prints but soft enough for the narrower hands to penetrate—or they are underprints in which only the deeper foreprints remain.

Because sauropods were seen as riverine and lacustrine animals, it was largely presumed that their ancient habitats were well-watered lands featuring major twisting rivers and clear-water lakes, rather like the Amazon basin. The geology of sauropod- bearing formations indicates otherwise. The rivers were often shallow, braided, and seasonally fluctuating, and lakes, if present, were likewise shallow and sometimes alkaline and saline. Sauropods appear to have been especially fond of formations that feature extensive carbonite caliche deposits. These need a combination of substantial wet-season rainfall, followed by soil-drying dry seasons, to form. In sauropod times, these would have been open, forested areas with riverine vegetation well suited for the high-browsing activities of tall sauropods. These lands would have had extensive fern cover between the trees that sauropods able to low browse could have exploited, at least in the wet seasons. During the dry period, these sauropods could have gone tripodal to dine on tree fodder that would have been sustained by the deep roots tapping into groundwater. Other sauropod habitats were more arid, with trees and underbrush concentrated along watercourses; this is similar to the habitats of the desert elephants, such as those of the Skeleton Coast. Other sauropod habitats look like they were rainier than the above.

*Coelophysis rhodensis* and *Massospondylus carianatus*

Substantial populations of large herbivores have a significant impact on the floras they feed on. Consider the browse lines that a modestly sized prosauropod would have left at heights up to 6 m (20 ft) or so. A 50 tonne sauropod would consume in the area of 200 tonnes of forage a year. Over 60 years, that would be about 12,000 tonnes, the weight of a World War II cruiser. The dinosaur would return about a third of that as fertilizing feces. Savanna elephants can extra dramatically alter landscapes by pushing down trees too tall to allow access to their upper foliage yet small enough to topple. Bigger, and with clawed forelimbs on hand, sauropods would have been able to fell larger trees as desired. During droughts seasonal or otherwise, sauropodomorphs could have used their hindclaws to dig for water—which other animals might have tapped into. This may help explain why the sauropods retained toe claws until their end-Mesozoic demise.

## DEFENSE

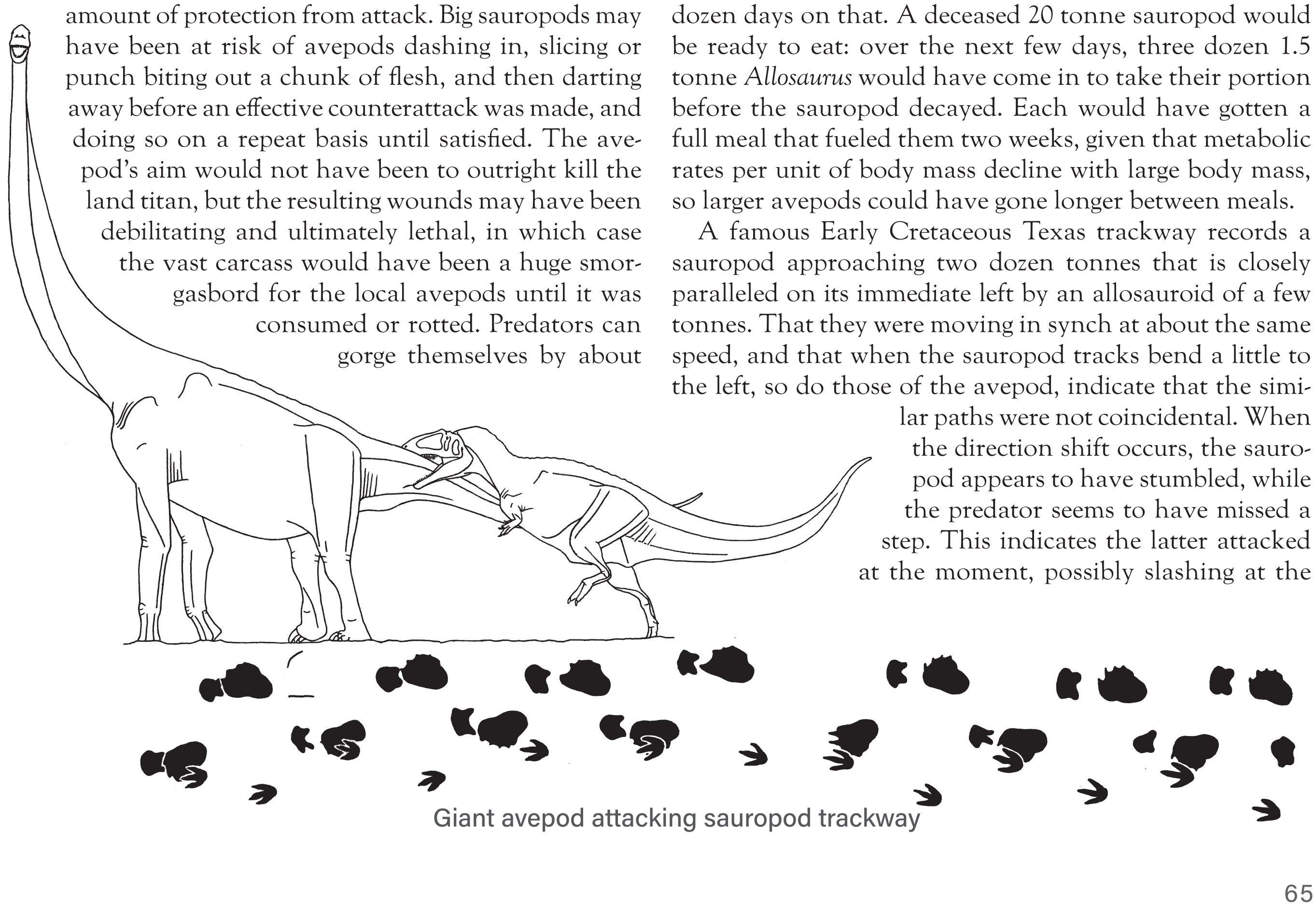
Adult prosauropods and sauropods were, like many herbivores, well armed and able to attempt to defend themselves when attacked. This would have been necessary because they had no hope of outrunning the bird-limbed theropods. Nor was hiding a viable option for giant sauropods that were prone to making considerable noise and presumably stank, like large herbivorous mammals—their predators would likely have been less odorous, allowing them to sneak up on them. On the other hand, the great dimensions of sauropods were a defense positive in that having a set of high-performance eyes with in the area of 360 degrees of vision held stories above ground level would have often aided in spotting danger at long distances, an ability boosted by rearing up when it seemed necessary. No other animals would have had this long-range predator detection advantage. Trying to stay out of sight was more viable for prosauropods, the lesser sauropods, and juvenile sauropods, although they, too, in some cases benefited from being able to stand tall to see approaching danger.

Having some sharp teeth, early prosauropods could have bitten at attackers when unable to dodge attack. Prosauropods could have lashed out with their large thumb and toe claws, using both sets while sometimes bouncing on their tails kangaroo-style. Sauropod battle qualifications usually but not always included sheer size, enormous tails up to 10–15 m long (35–50 ft), and weighing between 3 and 20 tonnes—often the total mass or more of the theropods attacking them—and, except for titanosauriforms, big, stout thumb claws. Why the latter were reduced and then lost in the last of the sauropods is a mystery. Swinging tails that among diplodocoids and titanosaurids were tipped with long, lashing whips that some believe could achieve sonic-crack-producing supersonic speeds, or with small tail clubs in some examples, and rearing to deploy hand claws would have posed stout defenses against even the biggest theropods. Hand-claw defense is used by anteaters, sloths, and probably the extinct giant ground sloths and the chalicothere horse relatives. Being bipedal up on two legs as per retroverted hipped camarasaurs would have had a mobility advantage over the more static tripodal stance of other sauropods. Primary sauropodomorph vulnerabilities would have been the leg retractors of the tail base and thighs and the slender, delicate neck, at least among those small enough for their neck base to be reached. The placement of

Early Jurassic *Coelophysis* and *Massospondylus*

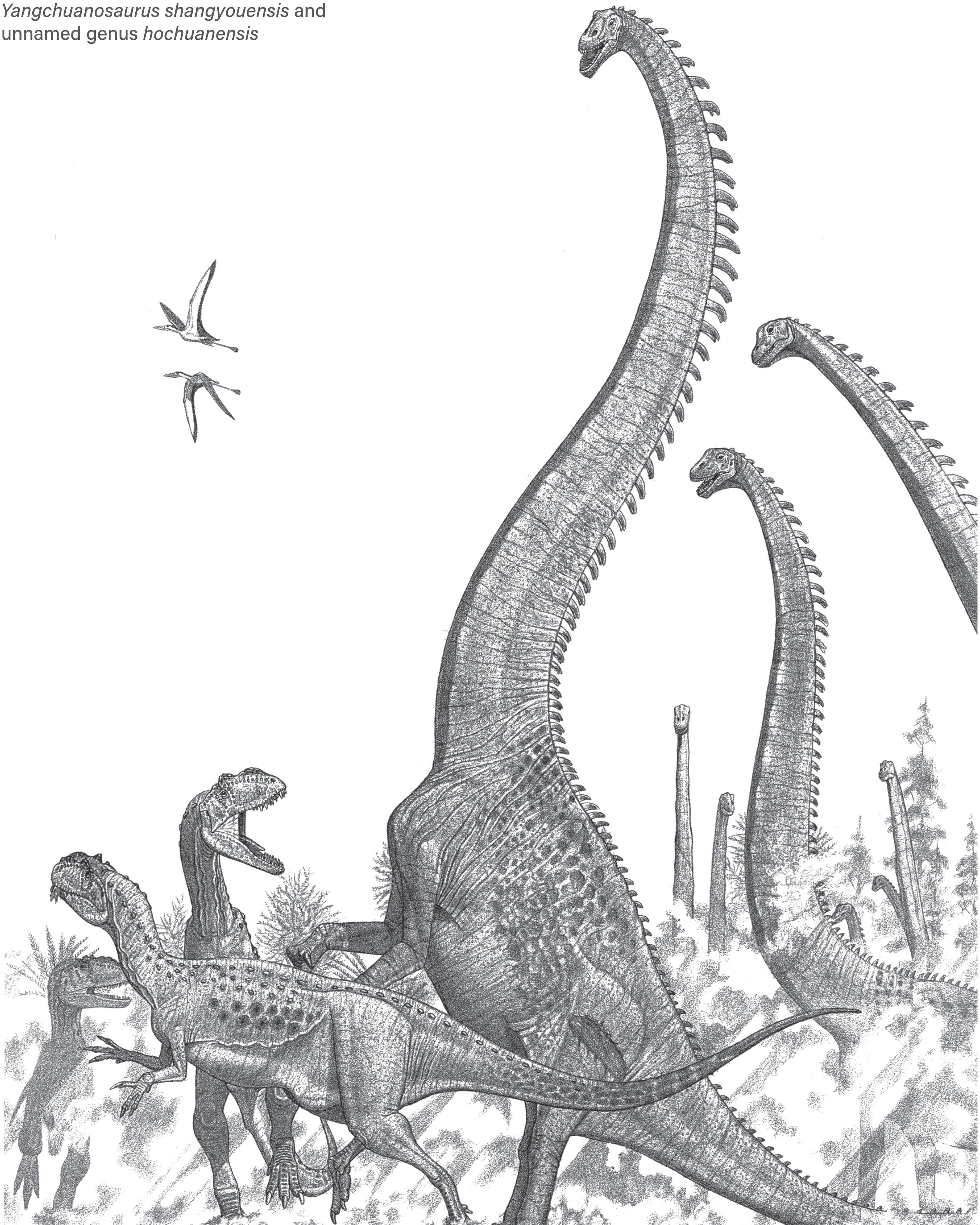
sauropods' cervical arteries and veins up between the neck ribs would have offered the critical blood-flow vessels a fair amount of protection from attack. Big sauropods may have been at risk of avepods dashing in, slicing or punch biting out a chunk of flesh, and then darting away before an effective counterattack was made, and doing so on a repeat basis until satisfied. The avepod's aim would not have been to outright kill the land titan, but the resulting wounds may have been debilitating and ultimately lethal, in which case the vast carcass would have been a huge smorgasbord for the local avepods until it was consumed or rotted. Predators can gorge themselves by about a quarter of their body mass, so they could have chowed down on the carcass for two or three days and gone for a dozen days on that. A deceased 20 tonne sauropod would be ready to eat: over the next few days, three dozen 1.5 tonne *Allosaurus* would have come in to take their portion before the sauropod decayed. Each would have gotten a full meal that fueled them two weeks, given that metabolic rates per unit of body mass decline with large body mass, so larger avepods could have gone longer between meals.

A famous Early Cretaceous Texas trackway records a sauropod approaching two dozen tonnes that is closely paralleled on its immediate left by an allosauroid of a few tonnes. That they were moving in synch at about the same speed, and that when the sauropod tracks bend a little to the left, so do those of the avepod, indicate that the similar paths were not coincidental. When the direction shift occurs, the sauropod appears to have stumbled, while the predator seems to have missed a step. This indicates the latter attacked at the moment, possibly slashing at the



Giant avepod attacking sauropod trackway

*Yangchuanosaurus shangyouensis* and unnamed genus *hochuanensis*



tail-based leg retractor muscles in order to try to cripple its target as part of a killing process. While latched onto its prey, the avepod was pulled along and misstepped, while the pained victim was pushed off balance. That the herbivore slowed down after the critical points suggests the attack was successful. Skeptics question the statistical likelihood that such an event would happen to be preserved, but the particular attack was probably one among many as the carnivore worked away at damaging its victim enough to kill it, perhaps over a period of hours and a few kilometers' distance.

Another tactic of desperation is to run into a body of water. This brings us to the conceit that was once the conventional wisdom—that dinopredators were hydrophobic to the degree that all an herbivore under pursuit had to do was go for a swim and leave the vexed theropod standing frustrated on the shoreline. The thin premise was that the narrow toes of theropods left them more prone to get mired or rendered them poorer swimmers. When it was thought that sauropods were predominantly aquatic, this was seen as their go-to predator defense. This water-escape notion has largely fallen by the wayside with the realization, based partly on the bottom-poling avepod trackways, that dinopredators were of course adept swimmers capable of pursuing their victims into water. And mammalian carnivores are known to chase down panicked mammalian herbivores that try the river or lake to escape.

But the water trick should not be dismissed out of hand. If a dinosaurian carnivore lived in Late Triassic environs in which watercourses were infested by very large crocodilian-like phytosaurs, or Cretaceous supercrocodilians up to 10 tonnes, then dashing into waters graced by such terrestrial-beast-drowning monsters would have been dangerous—and for the prey target, too, the water option may have been leaping from the frying pan into the fire. The exception being titanic sauropods. Fear of crocs may be why carnivorous mammals do not always chase game into tropical waters. And there may be no point for land predators to kill prey in crocodilian-dominated waters because the crocs will happily take over the carcass conveniently floating in the habitat in which they have the advantage. Only if a big dinosaur can quickly carry or drag its victim ashore and out of reach of crocodilian jaws is it advisable to dispatch it in the latter's territory in the first place. If the prey dinosaur was a nonpneumatic prosauropod that either lived before the age of big crocs or was willing to take the risk posed by Triassic and Cretaceous aquatic archosaur predators, resorting to water could be a good option for outfoxing a theropod. The latter would be too buoyant to dive after a nonpneumatic dinosaur if it dove beneath the surface in sufficiently deep water, where the theropod would not even be able to track it. The pneumatic sauropods could not do the deep-dive trick even when juveniles.

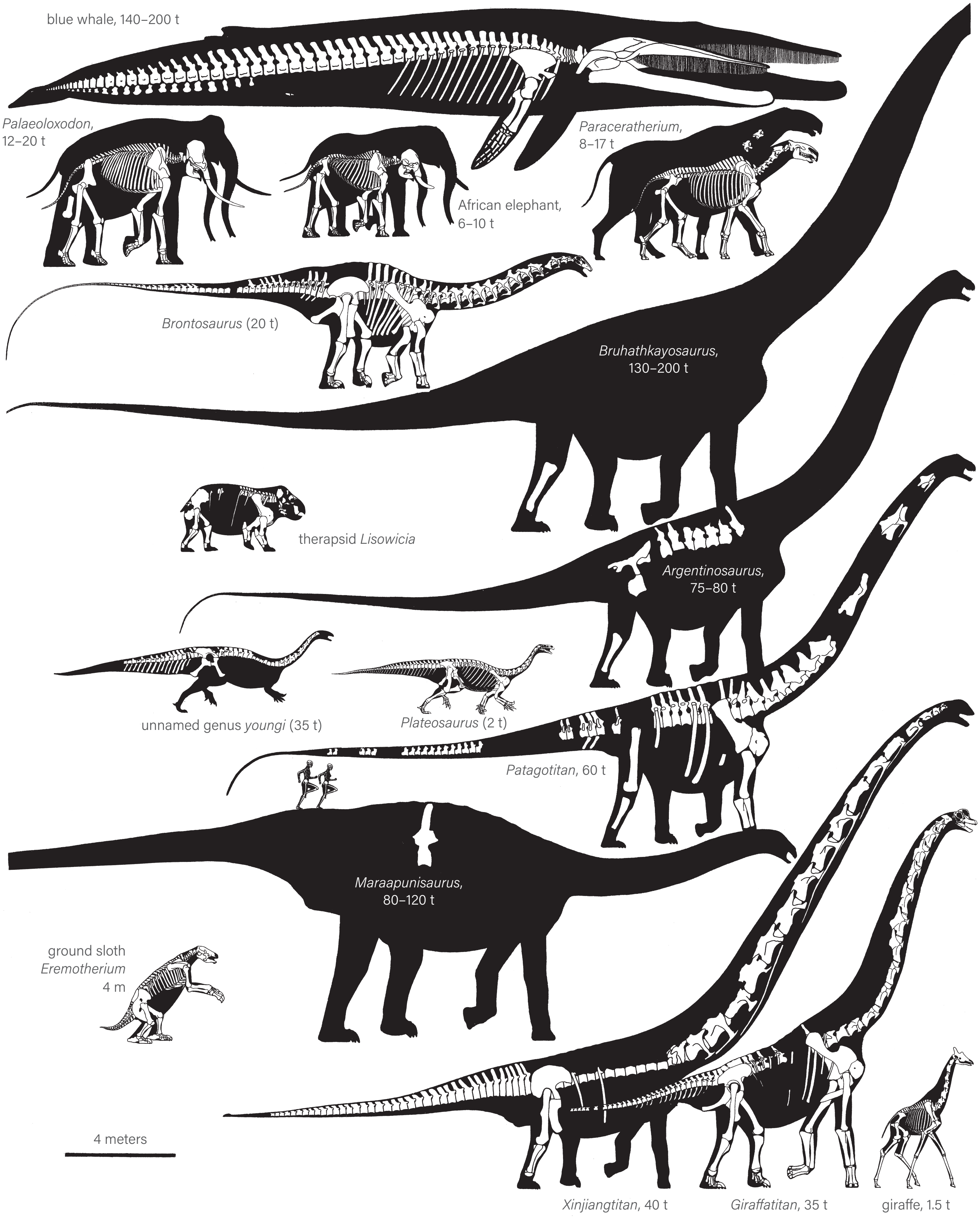
Titanosaurs were the only armored sauropodomorphs. What the osteoderms were really for is not clear. Although the specific arrangements are not preserved, it is clear that the armor did not form a dense protective cover like that of ankylosaurs, armadillos, or the latter's extinct glyptodont relations. Whether titanosaur armor would have been effective is not clear, but it may have improved the superficial protection somewhat. Titanosaurs faced the greatest supertheropod threat of the Sauropoda, initially in the form of giant allosauroids, so some extra fortification would have been helpful. The alternative hypothesis sees the skin bones as calcium reserves to aid rapid production of large numbers of big eggs that only titanosaurs among sauropods are so far proven to have produced, but this does not preclude other functions.

An advantage of nest care by the smaller sauropodomorphs would have been protection of the nestlings that otherwise would have been roaming on their own. Not being watched over, the hatchlings of sauropods would have been easy meals for small predators. In that case, rapid reproduction would make up for the heavy losses.

# 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 tonnes or more, as big as elephants and dwarfing the largest carnivorous mammals by a factor or 10 or more. A number of sauropods exceeded the size of the largest land mammals, mammoths, and the long-legged paracerathere rhinos of 15–20 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 unable 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 lift blood far above the level of the heart probably helps limit the size of bradyenergetic land animals. That a number of Mesozoic dinosaurs exceeded a tonne, as have mammals since then, is compelling evidence that they, too, had high aerobic power capacity and the correspondingly elevated energy budgets. The ultimate example of great height driven by elevated metabolics is seen in ultratall



Dinosaur giants compared with mammals

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 extra hardworking hearts whose high energy demands would have required a very high level of oxygen consumption.

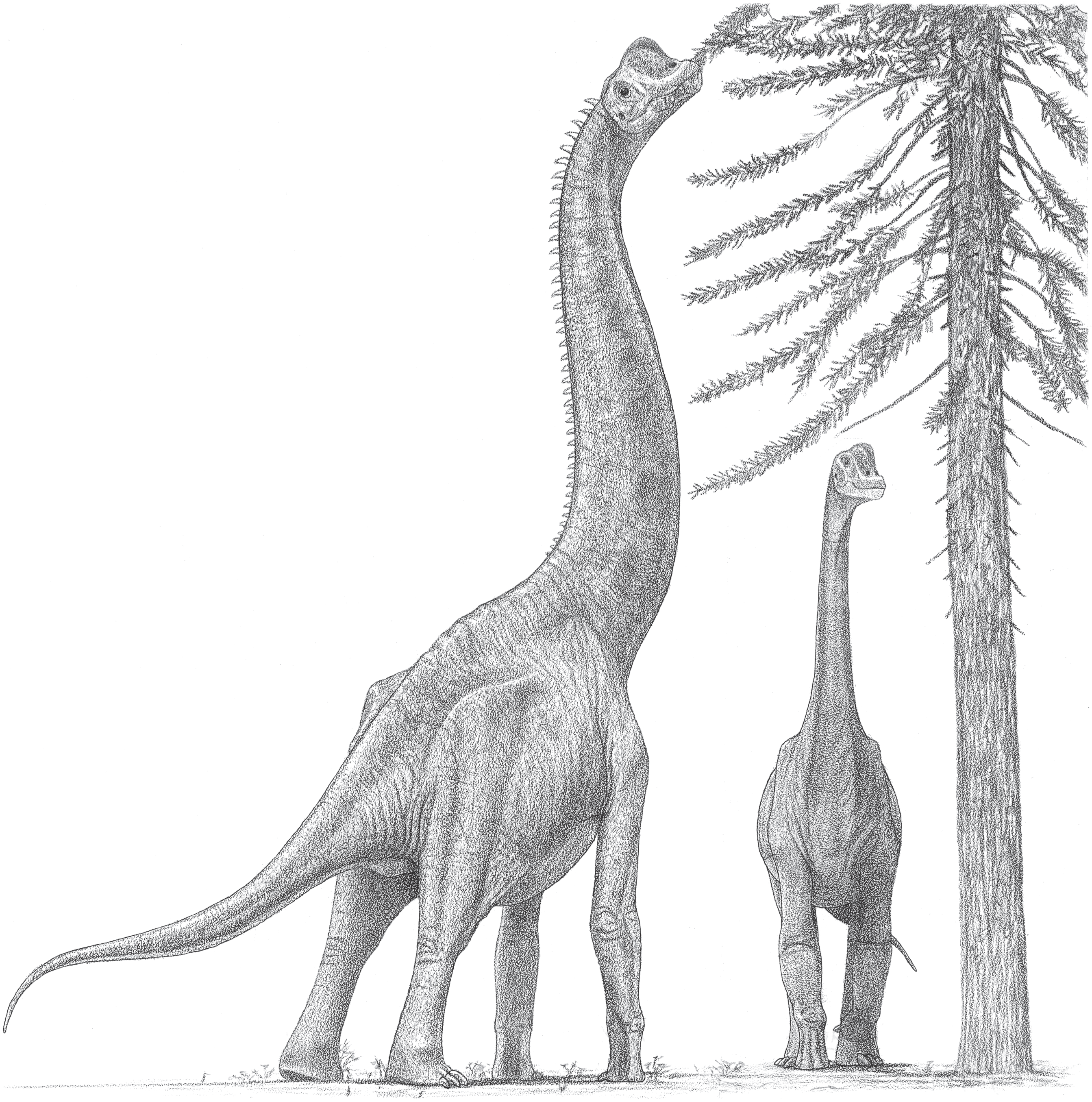
Only sauropods have exceeded 20 tonnes on land. The question is, why that unique biological achievement? Very tall necks like those of sauropods and giraffes evolve in an evolutionary feedback loop that involves two distinct but reinforcing factors. Increasing height serves as a dominance display that 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 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—and because of their extensive sinuses, low density—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 toothier 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. Not having such pressure problems, and able to use capillary action to draw water upward, trees can exceed 100 m (350 ft). Toward the other end of the size spectrum, those sauropods specialized with broad, squared-off mouths for grazing ground cover did not need supernecks or massive bodies to support them, and were relatively lightweight rhino-sized creatures. This disproves the belief that sauropod necks were long to improve low browsing—necks many meters long are so expensive to grow and maintain that they evolve only under strong, practical selective pressures that provide advantages short necks could not. It was otherwise-unreachable floral heights that made most sauropods tall and titanic. Very long necks can actually hinder grazing. They have to sweep back and forth over a wide area. That may sound like a good idea, but tall bushes and trunks scattered about the landscape, whether it be hills, flats, or shorelines, may frequently get in the way of the appendage; similarly, short-gunned tanks can have an advantage in wooded areas, where those with long weapons get caught up in the foliage. Herbivores specialized for feeding on low-lying flora don't need or benefit from long, awkward, and costly necks; they simply walk up to the plant, reach down, and eat it.

Also possibly helping those sauropods that did 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.

As is typical of terrestrial vertebrates, sauropod skeletons made up 15 percent of their total mass or a little more. The femurs of the larger examples would have weighed hundreds of kilograms; those of humans are in the area of a third of a kilogram. Like proboscideans and whales, sauropods of 10–100 tonnes or more would have consisted of over a quadrillion to tens of quadrillions of cells, compared to 50 trillion or so in a human.

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. If gigantothermy were true, then reptiles would be as big as mammals on land, but this is not so. This idea of gigantothermy 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 significantly athletic for extended periods. And 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—the gigantothermy hypothesis was originally founded on some errantly high measurements of resting metabolic rates of big leatherback sea turtles—which, in fact, have the low levels of energy production typical of reptiles. Also pushing animals to be big is improved thermoregulation. The ratio of high bulk to relatively low surface area makes it easier both to retain internal warmth when it is chilly and to keep external heat out and store internal heat on hot days.

Another, subtle reason that dinosaurs, particularly supersauropods as well as supertheropods, could become so enormous has to do with their mode of reproduction. Because big mammals are slow-breeding K-strategists that



Island dwarfed *Europasaurus*

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. Because sauropods 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 tonnes, perhaps on occasion 200

(continued...)

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# INDEX TO FORMATIONS

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