h15 Were non-avian dinosaurs ectotherms (cold-) or endotherms (warm-blooded)? <predator/prey, length cubed, insulation>

Hammer and his colleagues say they can clearly make out the aorta and two ventricles in the X-rays [of "Willo"]. —Tina Hesman, reporting for *Science News*, April 22, 2000.[1]

Comments:

Really, it's a stunner. —Dale. A. Russell

In the old days, this would have just been a hard rock in the way, and I would have destroyed it. —Michael (Mike) Hammer.

We may have been throwing away the best parts. —Michael K. Stoskopf

The surprise would be that *all* non-avian dinosaurs were cold-blooded. Reptiles today are all cold-blooded but, as **Robert T. (Bob) Bakker** has vigorously argued, some dinosaurs have features that suggest warm-bloodedness or evident lifestyles that do. Some dinosaurs ranged into, or dwelt in, Pangea's polar latitudes.[2] Small (presumed) dinosaurs early evolved into flying reptiles (order Pterosaursia), some with "hair" (insulating protofeathers), and some dinosaurs (infraorder Ceolosaura) had insulating true-feathers as have warm-blooded birds (class Aves).[3]

At rest, a warm-blooded (endothermic, homeothermic) animal by its metabolism maintains a body temperature that is constant and slightly higher than the maximum environmental temperature. It cannot tolerate environmental temperatures, even marginally, above its body temperature for long and will seek relief (inactivity, shade or a burrow, pant or sweat). When environmental temperatures are much below its body temperature, a warm-blooded animal has thick fat or fur or both, or feathers, to insulate its body from rapid heat loss and hypothermia (core body temperature too cold for normal muscular and cerebral functions). Shivering can generate body heat.

At rest, a cold-blooded (ectothermic, poikilothermic) animal has a body temperature that is marginally higher than the environmental temperature. As this, on a hot day in the sun, can exceed that which warm-blooded animals tolerate, cold-blooded is a misnomer. At the another extreme, some cold-blooded animals (Jack Layne, mentions six North American frog species, one European lizard, and a handful of North American turtles)[4] can freeze and, when thawed, live on.

As long ago as 1866, Harry Seeley, a young paleontologist known to Huxley, proposed that Pterosaurs likely were "hot blooded." Huxley, having noticed bird-like ilia in William Buckland's rhinocerine reconstructions of dinosaurs, was permitted in 1867 by John Phillips, their Oxford curator, to reassemble hadrosaurs as bipedal (as Joseph Leidy had proposed in 1858 for his American finds). These dinosaurs with chests housing "bird-like heart and lungs," he suggested were warm-blooded. However, skin impressions of mummified hadrosaurs since found show no sign of feathers or fur, insulating features that if present would corroborate warm-bloodedness (***Figure h15.1***).

In the 1980s,[5] Armand de Ricqles made the case that the obligate bipedalism (for example, *T rex*'s puny arms ruled out it going four footed) of some dinosaurs required a high metabolism for them to sustain their stance while standing still. Also, the giant brontosaur quadrupeds, as is known from the trackways they left, kept their tails off the ground (although, in the main tracksite at Dinosaur Valley State Park, Texas, a lone possible tail drag-impression is seen overprinted at one point by the three toed track of a following predator), and there is no evidence that they slumped when not walking.

Bones develop from soft cartilage that is replaced by the mineral apatite (calcium phosphate). Bone, as in the human thighbone (femur) is either, as in the shaft, a solid shell (thickness from two to eight millimeters) about a cavity filled with fatty yellow-marrow, or is, as at the ends, a meshwork of thin (less than a millimeter thick) struts and cross connections, called *trabecular bone*, with pores filled with red marrow (about 70 of the volume) that produce the blood cells. The great structural strength yet lightness of trabecular bone comes from the orientation and interconnections of its bone fillagree, as was noted in 1866 by a Swiss engineer, Karl Cullman. In Adam Summers' telling of the tale, Cullman happened upon the bisected head of a femur in a colleague's laboratory and saw in it the pattern of girders in the heavy-duty crane he had just designed for a loading dock. "Why, that's my crane!" he exclaimed.[6] Some dinosaur bones are penetrated by numerous passageways that may be, as in mammal bones, haversian canals (ramifying blood vessels enclosed by fast growing bone). Fast growth rate implies warm-bloodedness as a general model formulated by Geoffrey B. West in 2001 indicates for ontogenic (history of how an organism changes in the course of its life) growth in a wide variety of animals including mammals (cow, pig, rabbit, guinea pig, shrew), fishes (salmon, cod, guppy), birds (heron, hen, robin), and a shrimp.[7] However, Tomasz Owerkowicz's study of monitor lizards has shown that activity of these cold-blooded reptiles can introduce haversian canals into their bones also as these are reformed and modified throughout life. Indicative of cold-bloodedness, some dinosaurs have solid bone with seasonal growth rings. But some hibernating-mammals have similar in a limited way (as so in bears' teeth and tail bones).

Living and extinct carnivores and herbivores, for at least the past 65,000 years in each of five continents and 25 oceanic islands, have a *largest size* that covaries with land area. However, for their *size contrast* in each land area, Jared Diamond in 2001 reports a rule: largest warm-blooded herbivores weigh about 14 times as heavy as the biggest warm-blooded carnivores (for example, mammoths preyed on by lions in North America and saber-toothed cats in South America), whereas, at greater contrast, cold-blooded herbivores weigh about 33 times as heavy as carnivores. However, this rule applied to dinosaurs so underestimates the size contrast of dinosaur herbivores and carnivores that no certain inference follows that they had the metabolism of cold-blooded animals.

Bakker's case in 1986 for dinosaur warm-bloodedness listed: brain size of the small predators is large compared to their body size, which implies high metabolic rate; and, dinosaur predator/prey ratios are small (3 to 5 per 100).[8] For example, the giant Cretaceous carnivorous (scavenger?) *Tyrannosaurus rex* are some of the rarest dinosaurs. Only 11 specimens of *T. rex* were known until 1990, although a rash of finds since then have added 10 specimens (*see* Topic *h16*). However, the predator/prey ratios of the dinosaurs needs to be adjusted Alan Craig cautions, for the average life-spans of those being counted. Small bodied tyrannosauroids, as 1.6 meters long *Dilong paradoxus*, a putative *T. rex* ancestor, did have soft pelts of 2-cm-long protofeathers (fibers called "hair").[9]

Possibly, large dinosaur herbivores were cold-blooded because that would minimize food requirements (sauropod digestion of bolted food was aided by gastroliths) and because large size can, by large volume compared to surface area, maintain body heat generated by activity.

Phytoliths produced by living relatives of the ancient plants found in the fossil layers in Dinosaur Provincial Park in Alberta, Canada, are described by David A. Krauss in 2001 to be trapped in the chewing surfaces of 25 percent of herbivorous-dinosaur teeth found there. Evidently, ceratopsian dinosaurs ate a high proportion of tough-leafed cycads, while hadrosaurs (duckbill dinosaurs) favored ferns.[10] However, strikingly preserved even to a network of tendons and a frill like a rooster's comb that ran along its back, is "Leonardo," a mummified (more than 90 percent complete, 80 percent of skin is intact) young adult (2 ton, 7 meters long) of herding duckbill dinosaurs (*Brachylophosaurus canadensis*) now at the Phillips County Museum in Malta, Montana. When it died, 77 million years ago, it fell onto a sandbar along an ancient river. Preliminary stomach pollen analyses find a last meal of magnolia and conifer. Mixed into this, and indicating a subtropical environment, are spores of fern and liverwort which in life can't survive even a short period of dry conditions. "Something had to shut down the normal process of decomposition within just a few days," marvels Michael J. Everhart, "making it equivalent," curator Nate L. Murphy points out, "of stumbling across a long dead, but intact, elephant in a steamy tropical jungle." [11]

Study of coprolites (fossilized feces) can also shed light on what is eaten. Numerous examples of large plant-filled coprolites from herbivorous dinosaurs, are found. But not easy, recounts B. Bower, is “assigning coprolites to theropod dinosaurs because sites with their fossils often also contain skeletons of other carnivorous animals that could have produced bone-filled feces.” In 1998, scatologist sleuth Karen Chin identified with pinched-nosed accuracy a 44 centimeters long lump of whitish-green rock discovered on an eroding hillside in the badlands of Saskatchewan, Canada, as a coprolite.[12] By virtue of its massive size—bigger than a loaf of bread—a deduction is that it was left by a large theropod that inhabited the locale of the associated 65 million year old sediments, and is “rare tangible evidence of theropod diet and digestive processes” possibly *T. rex*. The coprolite contains bone fragments from a juvenile ornithischian dinosaur—perhaps part of the head frill of a *Triceratops*. The masticated, condition of the bone shards in the coprolite supports Gregory M. Erickson’s prior contention that *T. rex*’s teeth were strong enough to crunch through bone,[13] and deflates a contending opinion that theropods like modern crocodiles, which have extremely acidic stomachs, completely dissolved the bones of their prey.

Food demands are an indicator of metabolism rate. Mammals and birds burn ten times more food calories per day than do lizards and turtles of the same size. Activity is something else. As John Harold Ostrom (1928-2005) in 1992 pointed out: “Over the short haul a good ectothermic biologic ‘machine,’ the southwestern whip lizard (*Cnmidophorus*), for example, can outrun a perfectly good endotherm, the well-known road runner (*Geococcyx*), but an ectotherm lacks the stamina necessary to stay in front of an endothermic predator for very long.” Even so, the cold-blooded agility of Jesus Lizard (*Basiliscus basiliscus*) by running on water is unsurpassed. There is evidence, however, that the giant carnivorous dinosaur bipeds ran slowly and trod carefully to avoid a trip-and-fall that surely would have resulted in a head-crushing impact with the ground. Not to worry: Biomechanical modeling, by John R. Hutchinson and M. Garcia in 2002, 1) makes clear why a bipedal chicken lords it over an alligator when running, 2) gives estimates of quick running speeds of small biped dinosaurs in agreement with their fossil track strides, and 3) when applied to a 6000 kg bipedal *T. rex*, shows that muscles in *each* of its legs would need to equal 99% of its body mass to generated the forces necessary for it to run.[14] Conclusion: *T. rex* didn’t. However, do not sing about this as confessions of John R. Hutchinson with animator Stephen M. Gatesy in 2006 make all such folderol.[15]

John R. (Jack) Horner finds significant that herding dinosaurs (the hadrosaurs and the ceratopsians) appear in Late Cretaceous when deciduous forests came into being. Seasonality of that food source could have required migrations of the herbivores. Colony nesting could have evolved for reasons (group protection) that it has for some bird species. From egg size, duckbill dinosaurs (hadrosaurs) were 18 to 20 inches long when they hatched. Bone histology shows rapid growth occurred while the young were of nest size and continued until they were about 20 feet long. Thereafter, rest lines in the bones suggests that the metabolism slowed way down as growth continued to a maximum length of 35 feet.[16] High metabolism requires a steady, high, food intake. If comparable to birds, the warm-blooded young would have doubled or tripled their size during a nesting period of three or four weeks. At least one of their (non-avian herbivore) parents would have had to forage on foot beyond the already cropped periphery of the rookery ... (any further speculation becomes a just-so story).

In 1993, P. I. (paleontological investigator) Mike Hammer chanced upon an ornithischian dinosaur fossil, genus *Thescelosaurus*, in outcrop on a South Dakota ranch. Dubbed “Willo,” it had a heart with a single aorta and two ventricles.[17] Such is indicative of a four chambered heart (as in birds and mammals) that enables the high metabolic rate and activity of a warm-blooded animal. However, in Willo a pulmonary vessel (which carries blood to the lungs) is conspicuous by its absence. So Willo could have had a second aorta. That would compromise an hypothesis that it was warm blooded. Also, crocodiles, alligators, caimans, and gavials, have four chambered hearts (other living reptiles have two aortas) and they are cold-blooded.[18]

Slow growth rate is associated with cold-bloodedness. Alligators and tortoises (cold-blooded) may attain a weight of 1 metric ton but they take many years to pass a weight of 100 pounds whereas an ostrich (warm-blooded) reaches this weight in less than a year.[19] All extant (living) birds are warm-blooded and their growth rates are rapid (birds evolved from theropod ancestors). Mammals are all warm-blooded, and elephants, rhinos, giraffes and whales grow rapidly to weigh many tons. How do dinosaurs, which were advanced reptiles compare? Dinosaur bone analyses by Gregory M. Erickson and others in 2001 indicate that relative to extant reptiles (which retain the primitive condition of reptiles), "small dinosaurs grew at moderately rapid rates, similar to those of marsupials, but large species attained rates [as determined from growth lines on low-weight bearing bones as the fibula, gastralia and pubis that did not loose interior to become hollow with age as did the leg bones] comparable to those of eutherian mammals and precocial [self-feeding as hatchlings (down covered)] birds." (*Precocial* species hit the ground running as it were, whereas *altricial* species as mammals, or perching birds that have naked hatchlings, have young that require prolonged parental care.) Dinosaur growth-rate plotted against time is a sigmoidal curve (conventional for vertebrates) that scales with size so that the small dinosaur (bird?) *Shuvuuia deserti*, near hatching size for the first 2 years, grows to near adult size (weighing ~2 kg) in year 3, and the giant dinosaur *Apatosaurus excelsus*, near hatching size for 5 years, grows to near adult size (weighing ~25,000 kg) in 7 years. *T. rex* (normal life span of 28 years) after age 14 packed on 2.1 kg per day to be skeletally mature at age 20. This fast short-life, reflects Erickson, made *T. rex* the "James Dean of dinosaurs." [20]

Dinosaurs fail in one test that would be definitive proof according to John A. Ruben of endothermy. Computerized tomography (CT) scans of several hadrosaurs and theropods failed to show the presence of respiratory conchae (turbinites).[21] Turbinites are thin, scroll-shaped, bones or cartilage in the nasal passages of almost all modern endotherms.[22] Covering these, a moist mucus membrane helps humidify air drawn in. When the animal exhales the vital function is found to be the dried-out mucus in the nose that then absorbs water vapor, keeping it in the body (which explains, in part, how a camel can go for long periods breathing dry desert air between drinks of water). ❑

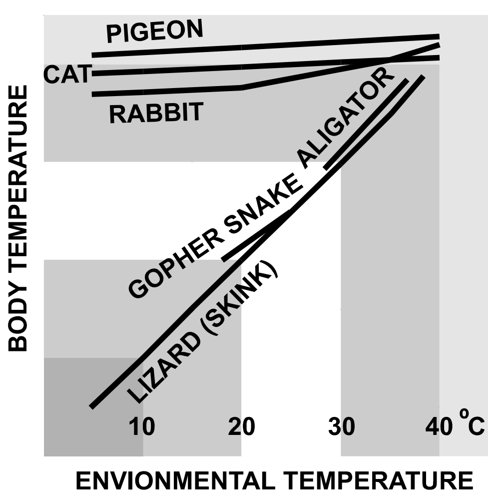

Figure h15.1 [23] Graphical comparison of typical extant endotherms with fur (rabbit, cat) and feathers (pigeon) with some reptilian ectotherms (lizard, snake, alligator). "Warm-blooded" applies fairly meaningfully to endotherms, but to call ectotherms "cold-blooded" is misleading as their behaviorally regulated blood temperature can range from frozen, as in the case of some wintering-dormant frog species, to as hot as that of endotherms when warmed by the sun. Endotherms have circadian body temperatures. Human normal body temperature is not a steady 98.6 °F but cycles 95.9 (early morning) to 101.3 °F (late afternoon). (*Note*: A quick and ready way to convert Celsius degrees to Fahrenheit degrees in the shown (human tolerated) range is to double the number and add thirty.)

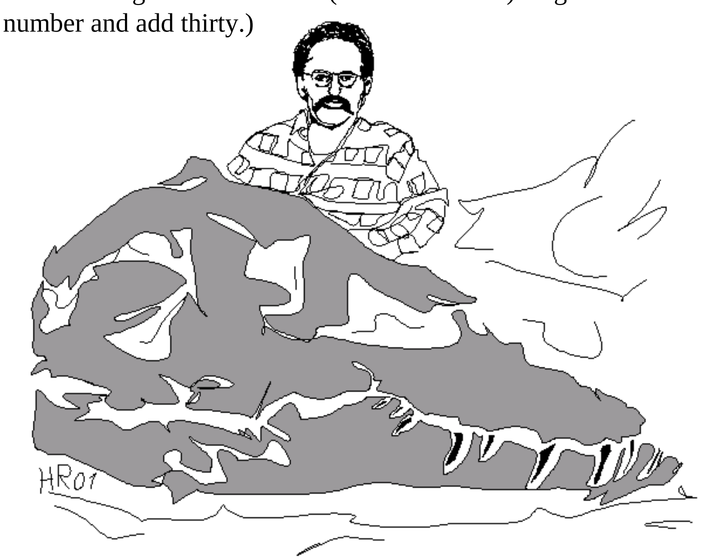

Figure h16.1[1] **Larson and "Sue" in happier times.** Gene Meieran in 1998 considering the dealings surrounding Sue and the imprisonment of Peter Larson, expressed the reality that professionals almost all get "their start as private collectors." Fossils that weather out of the ground, unless collected, risk being destroyed by erosion and the tramplings of animals. Were these not collected by serious amateurs, fine displays in museums would be the poorer.