Part I: Growth Rates

The curves above represent the body mass (in tons) of the giant crocodylian *Deinosuchus* (line A) and the ceratopsian *Triceratops* (dashed line B), both of which are found in the Montana Group deposits of the American West.

1) At what age was *Triceratops* full-sized? 
2) At what age was *Deinosuchus* full-sized? 
3) Which of these reptiles grew at a rate more like a modern mammal (i.e., fast)? [ *Triceratops* | *Deinosuchus* ]

Part II: Predator-Prey Ratios

Robert Bakker has suggested that we can use “predator-prey” ratios to test if an extinct community were primarily endothermic, primarily ectothermic, or somewhere in between. The ratio (represented as the percentage of the total biomass made up of carnivores) would have higher values for ectotherms (with their lower food requirements) and lower for endotherms (which need to eat constantly in order to fuel their bodies). Based on theoretical and observational data, ectothermic communities should have predatory-prey ratios over 20%, while true endotherms should be below 7%.

Below are values Bakker discovered for various assemblages (from particular formations or localities) of fossils (and one modern: the Serengeti). These are arranged by the Amniote Radiation in which they occurred.
Mammals (5\textsuperscript{th} Radiation) are known to be endothermic. Essentially all researchers agree that basal synapsids (1\textsuperscript{st} Radiation) were ectothermic.

4) The values for the dinosaurian radiation are [ like basal synapsids | like mammals | intermediate ].

5) The values for the pseudosuchian radiation are [ like basal synapsids | like mammals | intermediate ].

6) The values for the therapsid radiation are [ like basal synapsids | like mammals | intermediate ].

**Part III: Dinosaur Respiration (Lungs)**

Food is only part of metabolism. Another important aspect is respiration: without oxygen, there isn’t much metabolism!! Recent work by Colleen Farmer, David Carrier, and Elizabeth Brainerd on modern animals have revealed a lot more diversity in vertebrate respiration than previously known. For example, mammalian breath (which uses the ribs plus a muscular diaphragm, but doesn’t use a throat pump) is just plain weird!

Here is a look at some of the techniques used to get air down into the lungs:

- **Buccal pumping** (swallowing air): used by air-breathing fish and amphibians
- **Gular pumping** (using an actively pumping throat): used by lizards and crocodilians
- **Costal breathing** (moving ribs in and out): all amniotes but ribless frogs
- **Diaphragm breathing**: mammals
- **Hepatic piston** (liver pumping): crocodilians
- **Air Sac pumping**: birds
Interestingly, both crocodilians and birds use their pelvic (hip) muscles in breathing. In the figure on the previous page, A is a modern alligator. When the rectus abdominis muscle contracts it pulls the pubis forward, pushing the liver forward and forcing air out of the lungs (expiration). When the ischiopubic and diaphragmatic muscles contract, it pulls the liver backwards, causing the lungs to expand and draw in air (inspiration). B shows respiration in a pigeon. During inspiration the sternum rotates downward and the longissimus dorsi muscles contracts to pull the tail up: together, these inflate some of the air sacs in the body. During expiration the infrapubic and suprapubic abdominal muscles contract to pull the sternum up and the tail down, pushing air out of the sacs. Below is a drawing showing the air sac system of a bird, in left lateral view. C, I, AT, PT, and AB are different individual air sacs—you don’t need to worry about that level of detail. The bold arrows show how the air sacs invade the vertebrae:

Farmer and Carrier have extrapolated back to suggest the following as the ancestral breathing condition for archosaurs (that is, the condition in the common ancestor of birds and crocodilians). To the left below is the primitive archosaur Euparkeria. As the ischiotruncus muscle contracts, it pulls the gastralia (belly ribs) down, which would expand the lungs. It seems that such a mode of breathing might be possible for primitive theropods. To the right is the hypothesized breath cycle for Allosaurus.
7) Dinosaurs tend to have long pubes and ischia for archosaurs. How might these skeletal changes be related to an increased lung capacity?

8) Ornithischian dinosaurs lack gastralia. Would it be possible for them to use the ancestral archosaur mode of breath?

To the left are the pelves of some advanced ornithischians, so that the pubis (or the pubis plus ischium) can move relative to the ilium.

9) A is the pelvis of Triceratops in left lateral view. Like other ceratopsids, but unlike more primitive ceratopsians and most other ornithischians, the pubis and ischium can move together as a unit. As the rectus abdominis (RA) muscle contracted, it would have pulled the pubis and ischium forward; as the ischiocaudalis contracted it would have pulled the two bones back. This motion is most similar to the breathing system in [ birds | mammals | crocodilians | ancestral archosaurs ].

10) B is the pelvis of the hadrosaur Corythosaurus. Its pubis (like those of many advanced ornithopods) was able to rotate slightly outward. When the iliopubic muscle would contract, the pubis would move slightly to the sides. On the drawings to the left, label which of the two dorsal (overhead) views shows the pelvis during inspiration, and which in expiration.
11) Other than advanced ornithopods and ceratopsids, the pelvic elements of ornithischians are immobile. If mobile pelvic elements exist to help increase the oxygen flow, and an increased oxygen flow is an indication of higher metabolic rate, this suggests that the metabolic rates of advanced ornithopods and ceratopsians was [ greater | the same | slower ] than other ornithischians.

Extra Credit) What is another lines of evidence for a different metabolism in ceratopsids and hadrosaurids relative to other ornithischians? (Consider the jaws).

12) Below is a cervical (neck) vertebra of the ceratosaur *Carnotaurus*. Labels A, C, D, and E indicate openings into the vertebral bone. Similar openings are found in all theropods, and in sauropods. Given the phylogenetic position of birds and the nature of the bird respiratory system, what might the openings in theropod bones indicate about theropod respiration?

**Part IV: Dinosaur Respiration (Noses)**

There is more to breathing than lungs. As physiologist John Ruben has pointed out, endotherms (with their rapid rate of breathing) risk drying out their lungs unless they can recapture moisture during expiration. In mammals this is achieved by a large complex system of nasal turbinates (bony scrollwork supporting soft tissues that capture outgoing moisture and humidify incoming air). Birds have smaller nasal turbinates, which are part of a more complex system of air sacs in the skull. Incidentally, the avian antorbital fenestra is one region in which such an air sac fits. The antorbital fenestrae of all dinosaurs (and other archosaurs) are presumed to have held such an air sac. Additionally, the skulls of theropods (and coelurosaurs in particular) show that many of the other additional air sacs were present in these dinosaurs.

As an animal size increases, it needs an increasingly large surface area to collect moisture in order to maintain wet lungs. Let’s see if there is evidence for this in dinosaurs. On the next page are a series of skulls from small and large representatives of some of the major groups of dinosaurs:
13) In these pairs of dinosaurs, the nares of the larger dinosaurs are proportionately [ smaller | the same | larger ] than in their smaller relatives.
Illustrators long thought that these large nostril openings meant that there were large nostrils. However, new studies show that the actually fleshy nostril was restricted to the very front of the nostril opening.

14) What might have been the function of the rest of the nares chamber?

Part V: Scaling and Thermoregulation

Some thoughts about aspects of scaling and thermoregulation: Although not all dinosaurs were giants, many were quite large. Several workers have observed that this attribute of dinosaurs might have some bearing on issues of the warm-blooded/cold-blooded debate.

Metabolism, food requirements, and the like are related to the mass of an animal (i.e., how much living tissue is present). On the other hand, the ability to exchange gasses, to lose or gain heat, etc., is related to the surface area (i.e., how broad a surface is present inside the lungs, or on the skin). How do mass and surface area change, as organisms get larger?

Let us consider an organism that has the dimensions of a cube. A small cube has a length on any side of 1, a surface area of 6 (6 sides of area 1x1), and a volume of 1 (1^3). Examine the table below:

<table>
<thead>
<tr>
<th>Length</th>
<th>Surface Area</th>
<th>Volume</th>
<th>Surface Area/Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6</td>
<td>1</td>
<td>6:1</td>
</tr>
<tr>
<td>2</td>
<td>24</td>
<td>8</td>
<td>3:1</td>
</tr>
<tr>
<td>3</td>
<td>54</td>
<td>27</td>
<td>2:1</td>
</tr>
<tr>
<td>4</td>
<td>96</td>
<td>64</td>
<td>3:2</td>
</tr>
<tr>
<td>10</td>
<td>600</td>
<td>1000</td>
<td>3:5</td>
</tr>
</tbody>
</table>

15) As size increases, the surface area/volume ratio [ gets smaller | stays the same | gets larger ].

16) The surface area/volume ratio gives us an indication of easy or difficult it is for animals to exchange heat with the outside world (to lose it or to soak it up). The higher the SA/V ratio, the easier it is to exchange heat with the outside world. Larger dinosaurs were thus [ less insulated | the same | more insulated ] from the outside world.

Extra Credit) The daily variation in temperatures of (hypothetical) large ectothermic dinosaurs be more like typical smaller modern [ homeotherms | poikilotherms ].

Name:________________________
Part VI: Bone Isotopes

Yet another approach in interpreting the physiology of extinct is the use of oxygen isotope variations ($\delta^{18}O$) from bone. These measurements estimate the variation of in temperature over time in an animal while it was alive. Questions 17-19 refer to the data table below. These data are taken from the femora of several dinosaurs and a varanid (monitor) lizard from the upper part of the Two Medicine Formation of the Late Cretaceous of Montana. When not specified, the specimen in question is a fully-grown adult.

Note: The higher the $\delta^{18}O$ value, the higher the variation in body temperature over time.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>$\delta^{18}O$ Variation (%)</th>
<th>Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daspletosaurus (Tyrannosauridae)</td>
<td>0.45</td>
<td>4000</td>
</tr>
<tr>
<td>Hypacrosaurus (Lambeosaurinae)</td>
<td>1.00</td>
<td>5000</td>
</tr>
<tr>
<td>Hypacrosaurus, hatchling (Lambeosaurinae)</td>
<td>0.95</td>
<td>5</td>
</tr>
<tr>
<td>Montanaceratops (Leptoceratopsidae)</td>
<td>0.90</td>
<td>150</td>
</tr>
<tr>
<td>Achelousaurus, juvenile (Centrosaurinae)</td>
<td>0.50</td>
<td>50</td>
</tr>
<tr>
<td>Orodromeus (Hypsilophodontia)</td>
<td>0.60</td>
<td>20</td>
</tr>
<tr>
<td>Varanid lizard (NOT A DINOSAUR!)</td>
<td>2.95</td>
<td>15</td>
</tr>
</tbody>
</table>

Some paleontologists suggest a model of gigantothermy in dinosaurs. In this model the fact that as size increases the surface area/volume ratio decreases suggests that very large animals should have stable body temperatures even if they were ectotherms.

17) Do large dinosaurs in the data set seem to have small variations in $\delta^{18}O$ compared to the (presumably ectothermic) varanid lizard?  [ Yes | No ]

A test for the gigantotherm model would be to look at smaller dinosaurs. If dinosaurs were strictly ectothermic, small adult and young dinosaurs would be much too small to be gigantothermic, and should have $\delta^{18}O$ values similar to those of similar sized ectotherms. Look again at the data set above.

18) The small dinosaurs have $\delta^{18}O$ values which are [ all smaller than | about the same as | all larger than ] that of the varanid lizard.

19) Circle the phrase below which best describes the situation above:
   a. The data are consistent with a model of growth heterometabolism, with endothermic juveniles and small dinosaurs, but gigantothermic adults of the large taxa.
   b. The data are consistent with a model of dinosaurs fully endothermic from hatching into adulthood.
   c. The data presented here cannot distinguish between the models in a or b.