Lab 8 - Vertebrate Functional Morphology

Objectives:

1. **Learn basic concepts involved in getting vertebrate organisms from one place to another**
2. **Become proficient in determining aspects of an organism's identity, evolutionary relationships and ecology from its physical form**

Textbook Reference Pages: pp. 717-718, 722-737 and 1017-1020

If you have ever watched a PBS television special about dinosaurs, you've probably seen paleontologists Robert Bakker and Jack Horner. What is remarkable about these scientists is that not only can they identify a species of dinosaur from a single fragment of bone, but they can also construct a likely scenario for the kind of habitat in which the animal lived, how it captured prey, and how it reproduced.

In this laboratory exercise, you will have the opportunity to play paleontologist in the Natural History Museum. Rather than have you identify a species from a single piece of bone and then reconstruct how it lives, however, we will ask you to do the analysis in reverse. The specimens on display in the Museum have already been identified for you. Even if you've never seen a live sabre-toothed tiger or woolly mammoth before, you can probably imagine how they lived. Thus, the question is, what clues do you use to reconstruct each animal's lifestyle: that is, what skeletal features, or adaptations, tell you what the animal does? For a sabre-toothed tiger, the answer is easy: its sharp claws and prominent fangs suggest that it was a carnivore, preying on other vertebrates. Other clues, however, may be more subtle. For example, both the horse and the lion inhabit open country habitats. The horse is adapted for running (Figure 1). Although they are capable of short sprints, lions are mostly walkers (Figure 2). The limb bones of these animals, which tell us something about what they do, reveal these characteristics.

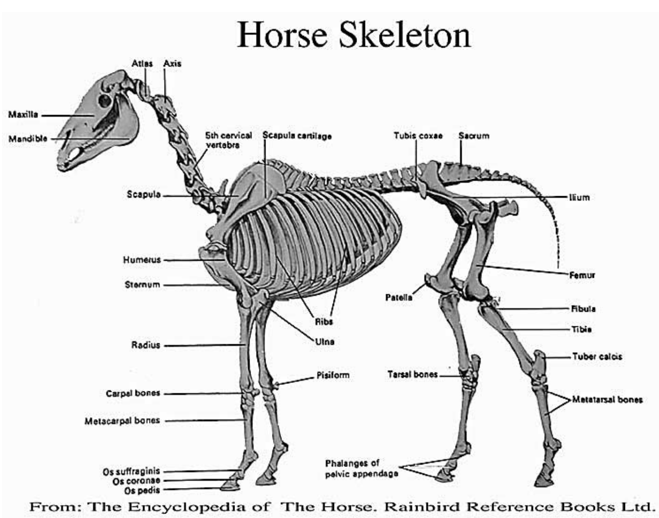


Figure 1. Horse skeletons

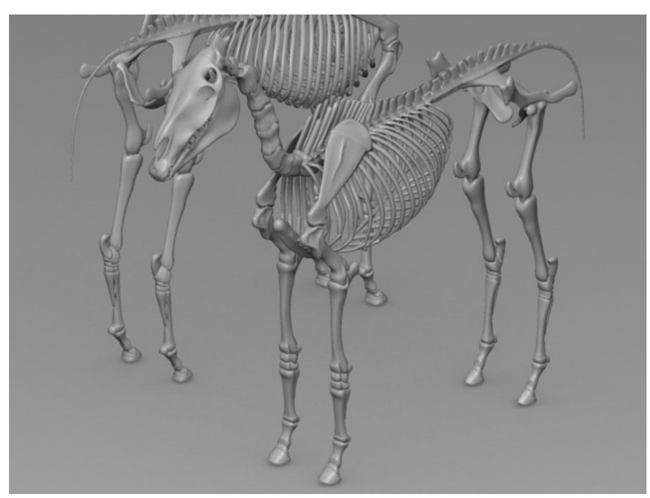
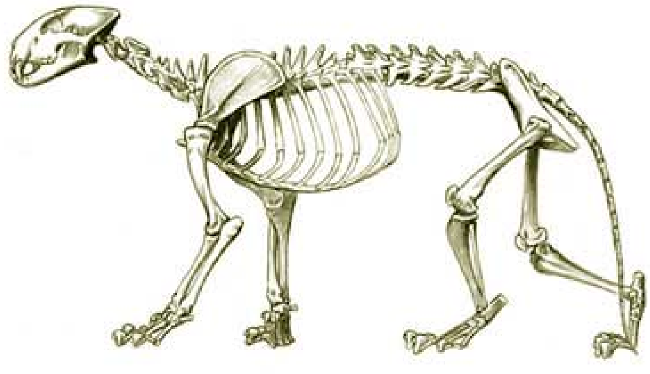


Figure 2. Lion skeletons.



The branch of biology dealing with the form and structure of vertebrates is called **vertebrate morphology**. In studying the form and structure of vertebrates, however, most biologists are interested in knowing not just what these structures are, and how they differ between species, but also how they **function**.

Deducing how an animal lives from a single piece or group of bones is not always an easy task. It helps to think of an animal as a machine that works through the action of bones and muscles. The bones form the frame of the machine, analogous to the metal tubes that form the frame of a bicycle. The muscles (and the ligaments and tendons that connect them to the bones), supply the power to run the machine and move its parts, the bones. When viewed in this way, how the bones of an animal operate for locomotion, feeding, and other activities can be understood by borrowing a few concepts from physics and engineering.

When a muscle contracts, it produces a **force**. Force is the product of mass times acceleration. For our purposes, it is okay to disregard units and consider force to be a push or pull that causes motion. The force created by a contracting muscle has a **magnitude** that is proportional to its cross-sectional area: the force generated by Arnold Schwarzenegger when he flexes his biceps has greater magnitude than the force generated by Woody Allen. In addition, forces have **direction**: when Arnold or Woody flexes their biceps, the force of the muscle contraction raises the forearm in the direction of the head.

Now, imagine a muscle just lying on a table by itself. If the muscle was to contract, it would shorten and lengthen, but it wouldn't go anywhere. This is where the frame of the machine, or skeleton, comes into play: the skeleton provides a series of firm, hinged segments, that together with muscles, are necessary for locomotion and other activities. The arrangement of these bones and muscles dictates how the machine operates.

For example, consider two bones lying parallel to one another, connected by a muscle in their middles (Fig. 3A). When the muscle contracts, it shortens, pulling the two bones towards each other. Note, however, that there is no forward or backward motion. Now, consider the arrangement shown in Fig. 3B. In this case, the two bones are connected to each other at one end, by a pivot (or screw, to maintain the analogy to machines). When the muscle contracts, the lower bone is pulled backwards. The arrangement of bones and muscles in Fig. 3B is representative of the limb systems of many vertebrates. The vertebrate body takes the system one step further, though. Usually, the upper bone is firmly anchored to the spinal column via the pelvic or thoracic girdle (depending upon whether we are dealing with hindlimbs or forelimbs, respectively). When the muscle contracts, the lower bone swings backward, contacting the ground. Because the limb system is connected to the spine, the resulting force generated by contact of the limb with the ground propels the animal forward.

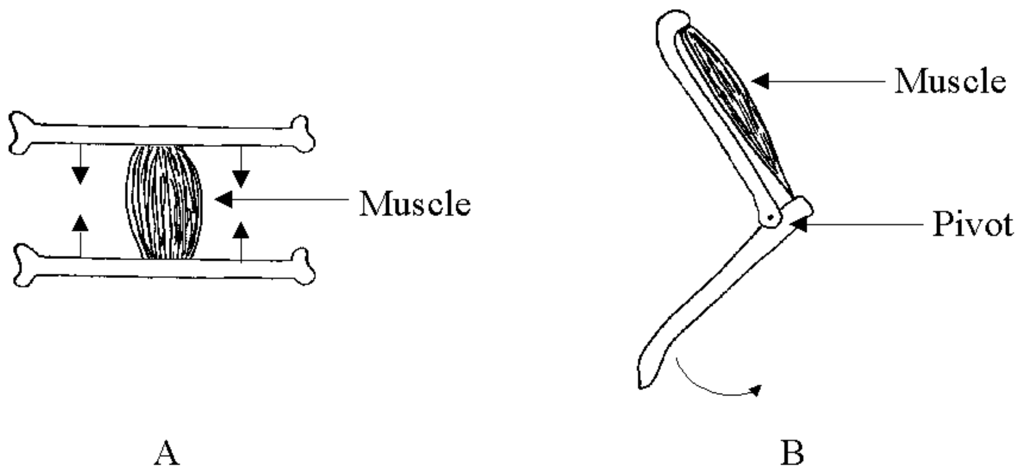


Figure 3: How pivots contribute to the directionality of motion in bone-muscle systems

Two forces are actually at work here: the input force of the contracting muscle, and the output force of the limb striking the ground. In morphology and engineering, any input force applied to a bone or machine is referred to as an **in-force** (**F_i**), and any output force generated from a bone or machine is an **out-force** (**F_o**). In the vertebrate body, in-forces are applied by the pull of tendons, ligaments or muscles, by gravity, and by external loads; out-forces are ultimately derived at the teeth, feet, hands, digits, or elsewhere. The bone-muscle system, then, is simply a machine that transmits force from one place to another.

In vertebrates, in-forces are usually transmitted to out-forces via levers (this is certainly the case for most feeding and locomotory systems). A **lever** is a rigid structure -in our case, a bone- that transmits forces by turning, or tending to turn, at a pivot. Both the in-force and the out-force are spaced from the pivot by a section of the lever called the **lever arm**. The **in-lever** (**l_i**) extends from the in-force (usually the attachment site of the muscle) to the pivot, and the **out-lever** (**l_o**) extends from the pivot to the out-force (e.g., the teeth, a foot, etc.) (Figure 4).

The product of a force times its lever are is called a **torque** (**t**). Torque is the ability of a rotating element -in this case, our pivot- to overcome resistance. When $F_i l_i > F_o l_o$, the in-lever rotates in the direction of F_i; when $F_i l_i < F_o l_o$, the out-lever rotates in the direction of F_o. When $F_i l_i = F_o l_o$, the system is in equilibrium, and there is no motion.

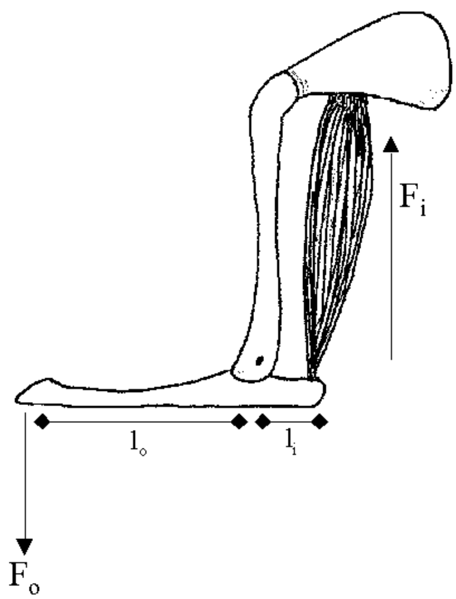


Figure 4: In-forces, out-forces, and lever arms

Although the preceding discussion may seem like a lot of mathematical mumbo-jumbo, the equations have their usefulness. For example, imagine you are "God", and you want to construct a digging mammal. For an animal that digs, it would be nice to produce a large out-force at the foot when the triceps muscles contract. Because $F_o = F_i l_i / l_o$, it can be seen that there are three ways to do this: increase either F_i or l_i, or decrease l_o. Adaptations of the forelimbs of diggers, in fact, include all three of these options.

Putting These Principles to Practice: Overview of the Lab

In this laboratory exercise, you will examine vertebrate specimens representative of three skeletal systems: 1) the skull, 2) the limbs, and 3) the spine. For each of these three systems, we have selected species adapted for different lifestyles. You will study how these adaptations are expressed in the animals' skeletal morphology. When necessary, the various bones will be identified for you, but for the most part, do not worry too much about memorizing the names of bones. Focus instead on how these bones function and are adapted for the animal's lifestyle.

All students should meet in the Biology 18 lab in the Life Sciences Building at 2 PM on their scheduled lab day for a short pre-lab discussion. The class will then be split in two, and we will then walk to the new Natural History Museum Building. Half the class will first examine skeletons of extinct species in the Natural History Museum, while the other half of the class will start by studying smaller, extant specimens in the Conservation Lab on the ground floor. The two student groups will switch areas at approximately 3:45 PM.

We ask that students work in pairs to answer the worksheet questions on pp. 17-22 of this handout while in the Museum building. If students need more time to look at the skeletons, you can revisit the public Museum collection anytime between 11-4 on Tuesday-Sunday. Digital images of most of the specimens in the Conservation Lab (which will not be open outside of formal lab hours) will be posted on Blackboard. **The completed worksheet is due at the beginning of lab next week.**

I) The Vertebrate Skull

A. Carnivore vs. Herbivore Skulls

Examine the skulls on display in the biology laboratory. One set of skulls are from **carnivores**, animals that eat other animals; the other set are from **herbivores**, animals that eat plant material. Can you tell which is which? Without reading any further, jot down on a piece of paper the features you used to distinguish the two animals.

Most likely, you probably distinguished the two animals by their teeth. Carnivores typically have sharp, pointed teeth for killing and holding prey: the **canines** of dogs and cats are good examples, but other vertebrate carnivores (crocodiles, pike, Gila monster, dolphins) also have sharp, conical teeth. Birds lack teeth, but the sharp points of the bills and talons of hawks and eagles serve a similar function.

The teeth posterior to the canines of your specimen (a cat or dog) are the **premolars** and **molars**. Molars tend to be larger than premolars, and to have more cusps and roots, but the distinction isn't always obvious. For this reason, premolars and molars often are collectively referred to as **cheek teeth**. If you look closely, you will see that the cheek teeth of your carnivore differ in appearance from the incisors and canines. Such a dentition in which the teeth differ in appearance is **heterodont** (= different + tooth), in contrast to **homodont** (same + tooth), where the teeth are all similar in appearance.

In carnivores, the cheek teeth tend to be blade-like and better suited for cutting and shearing than for piercing and killing. In fact, a distinguishing feature of carnivores are the **carnassials**: the upper fourth premolar and the lower first molar on each side of the mouth are enlarged, and oriented to form a powerful shearing mechanism (like scissors) for cutting and tearing apart flesh. The carnassials perform so well in cutting up flesh that the remaining cheek teeth of carnivores often are small or reduced in number, especially in cats. (Cats also supplement their teeth with horny projections on their tongue that enable them to rasp flesh from bones; you can check this out by letting a cat lick your hand).

Now examine the teeth of an herbivore [a rodent (probably a porcupine), or a lagomorph (a rabbit)], depending upon what specimens are on loan from the museum. Note that the canines are entirely absent. Instead, the anterior teeth -in this case, the **incisors-** are specialized for shearing off leaves, gnawing on wood, or cropping grasses. In many herbivores, such as rodents and rabbits, these teeth are ever-growing.

The cheek teeth of herbivores differ from those of carnivores, too. Note that they are large and flat, and are more like the premolars and molars of humans. The large, flat, cheek teeth of herbivores act like a mortar and pestle to pulverize and grind-up vegetable matter. Because there is only one kind of job to do, the teeth are all very similar to one another; that is, the premolars have come to resemble molars. The broad cheek teeth provide lots of surface area for acting on plant matter. But in order to grind and macerate effectively, a folded surface is superior to a smooth surface. Consequently, the cheek teeth of herbivores bear numerous ridges and infoldings on their occlusal surface that aid in grinding food. Although these ridges are visible in your lab specimens, they are most pronounced in large herbivores, such as elephants and horses (Figures 5 and 6).

Figure 5. Horse skull.

Figure 6. Elephant skull.

The continual grinding of plant matter puts a lot of wear on teeth. Accordingly, the cheek teeth of herbivores are large and heavy, and have numerous roots for support (this is true for humans, too: your molars have more roots -4- than your incisors or canines -1). In addition, in some mammals, such as horses and elephants, the teeth have long roots, and as the exposed part of the tooth wears down, the roots rise higher and higher in the jaw and bone fills in behind them. Eventually, nothing remains except the roots buried within the gums, and the animal starves to death. In other herbivores, such as rabbits and some rodents, the cheek teeth are ever-growing.

The prominent space between the incisors and cheek teeth of your specimen is the **diastema**. The diastema is characteristic of all herbivorous mammals. The evolutionary reasons for the diastema are unclear, but are probably related to the fact that the incisors and cheek teeth of herbivorous mammals do not operate simultaneously. When a beaver gnaws wood with its incisors, its lower jaw is pushed forward, and the cheek teeth do not touch each other. Likewise, when a rabbit chews, its incisors do not touch. Possibly, the diastema allows the teeth of each system to move in ways that would not be possible if the two systems operated simultaneously. In addition, such an arrangement probably reduces wear on each system. Many herbivorous mammals swallow food and then regurgitate it continuously throughout the day for more chewing (i.e., "chewing the cud"). Having the snipping system -that is, the incisors- rub against each other while the animal is chewing its cud would only wear them down at a time when the incisors are serving no useful function.

At this point, we've looked at different kinds of teeth, but we really haven't discussed how these teeth work. To return to our machine analogy, the teeth are where the out-force is applied. Can you identify the out-lever and in-lever, and the locations of the muscles supplying the in-forces? The answer to this question is easier than it seems. Moreover, the answer provides an answer to another question: why the skulls of herbivores and carnivores look so different.

To determine the out-lever and in-lever, you must first find the pivot. Looking at the *complete* skulls of the herbivores and carnivores, you can see that there is only one pivot, the point at which the lower jaw (= **lower mandible**) articulates with the skull (this articulation point is referred to as the **mandibular condyle**). The out-lever, then, is the distance from the mandibular condyle to the teeth. (Note that the length of the lever differs for the anterior and posterior ends of a row of teeth: how do you think that might affect an animal's feeding?)

Locating the in-lever(s) is a bit more difficult. Let's start with the carnivore. If you examine the lower mandible of a dog or cat, you will see that it has a prominent process at its posterior end, rising high above the mandibular condyle (refer to Figs. 7 & 8). This process is the **coronoid process**, and it is the attachment site for the **temporalis muscle**, which represents over half of the "closing" power of a carnivore's jaws [muscles that draw two bones, such as the lower mandible and skull, towards each other are called **adductor muscles** (ad = to); muscles that draw two bones away from each other are called **abductor muscles**)]. The in-lever for the temporalis, then, is the distance from its point of attachment on the coronoid process to the mandibular condyle. The temporalis muscle originates from the **braincase** and **sagittal crest** (the ridge along the dorsal surface of the skull, which is reduced in the cat, but more prominent in dogs and wolves). Note the enormous surface for muscle attachment afforded by the braincase: given that the force generated by a contracting muscle is proportional to its cross-sectional area, the jaw of a carnivore has considerable closing power. You also will see on the skull of the dog and cat a large, belt-like bone, extending posteriorly from the snout (or **maxillary** region) to the lower part of the braincase, around and over the coronoid process of the lower mandible. This bone is the **zygomatic arch**, which forms the lower rim of the eye socket (or **orbit**). The zygomatic arch, and in some cases, parts of the maxilla and orbit, are the point of origin for the **masseter muscle**, which inserts on the lower mandible in the depression below the coronoid process. The masseter also helps to close the lower jaw, and also stabilizes its articulation. Note that from its point of insertion on the lower jaw to its point of articulation at the coronoid process, the in-lever of the masseter actually is opposite the in-lever of the temporalis. On the ventral part of the braincase on each side posterior to the lower mandible are two bulges, the **tympanic bulla**(e) that protect the internal ears. At the very rear of the bulla on each side is a small projection, the **paroccipital process**. This is the point of origin of the **digastric muscle**, which inserts on the ventral surface of the lower mandible, and opens the jaw. Based on the size of the paroccipital process, do you think that the digastric muscle is larger or smaller than the temporalis muscle? How do these size differences relate to the functions of the two muscles?

Turning now to our herbivore, you can see that it, too, has a lower mandible that articulates at a mandibular condyle (Fig. 8). Note, however, that unlike the carnivore, the coronoid process (the in-lever of the temporalis muscle) is very short, barely rising above the mandibular condyle; in some herbivores, such as the rabbit, it is absent. Similarly, the posterior part of the braincase has a smaller surface area for muscle attachment than the braincase of the carnivore. In contrast, the posterior portion of the lower mandible -the point of insertion of the masseter muscle- is very broad, and the distance to the mandibular condyle (the in-lever of the masseter) is much greater than in the carnivore. The points of origin of the masseter -the zygomatic arch, the orbit, and the maxilla- also are very broad. Given these differences in skull morphology, which muscle -the temporalis or the masseter- do you think has the more prominent role in closing the jaw of an herbivore?

Finally, compare the eye sockets, or orbits, of carnivores and herbivores, especially their position. The eyes of carnivores generally face anteriorly, whereas the eyes of herbivores often face laterally. How do you think these differences in the orientation of the eyes relate to the lifestyles of a carnivore and an herbivore?

Figure 7a: Some features of the skull and mandible of a wolf (from Hildebrand, Analysis of Vertebrate Structure, 4th edition).

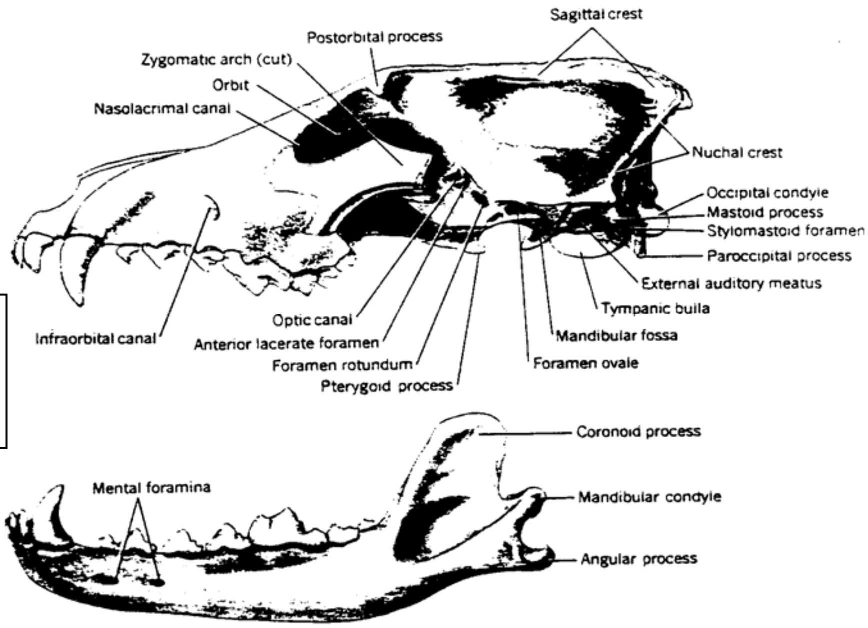


Figure 7b: Relations of the skull and mandible of a wolf to various muscles (from Hildebrand, Analysis of Vertebrate Structure, 4th edition).

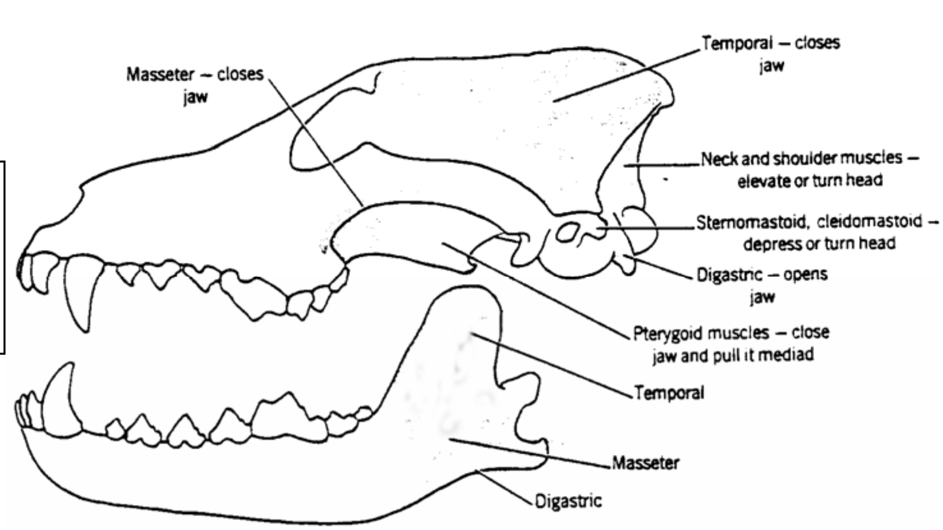
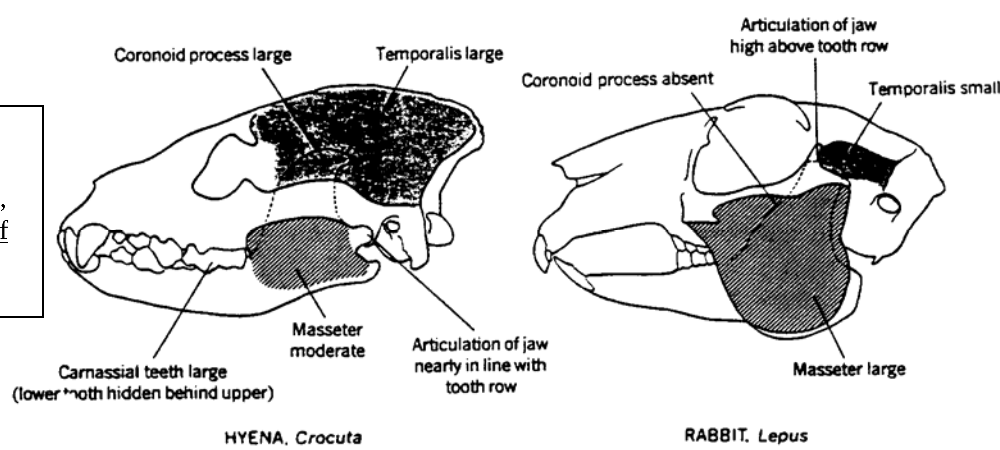


Figure 8: contrast between the jaw mechanics of a carnivore (left) and an herbivore (right), (from Hildebrand, Analysis of Vertebrate Structure, 4th edition).



II) The Limbs

A. Overview

The limb bones of vertebrates are used for a variety of locomotory activities, such as walking, running, climbing, or digging. Whether an animal is adapted for one activity or the other often can be deduced from the length and thickness of the limb bones, and especially from their lengths relative to each other. Read through the following section, and try to decide for which activities the different limb systems on demonstration are adapted. Also, take some time to familiarize yourself with the different limb bones.

Examine the human skeleton and palpate the limb bones on your own body. Starting with the bones closest to your body (Fig. 9), the bones of your arm are the **humerus**, **radius** and **ulna**, **carpals** (wrist bones), **metacarpals** (hand bones), and **phalanges** (finger bones). The corresponding bones of your leg are the **femur**, the **tibia** and **fibula**, the **tarsals** (ankle bones), the **metatarsals** (foot bones), and the **phalanges** (toe bones). Think about the activities that you perform each day with your limbs and consider how their structures are especially suitable for these activities.

The bones of the **pectoral (shoulder) girdle** and the **pelvic girdle** attach the upper and lower limbs, respectively, to the axial skeleton. What bones make up each of these girdles? Locate them on the human skeleton and palpate these bones on your own body. Why do think that dislocated shoulders are so much more common than dislocated hips?

As we saw earlier, limbs are levers. The bones of your forearm, the **radius** and **ulna**, articulate with the **humerus** at the elbow. In fact, when you bang your elbow, your are in reality banging the proximal end of your ulna (the **olecranon process**); the olecranon process serves as the in-lever for the muscles that extend your forearm. The out-lever is the length of the ulna

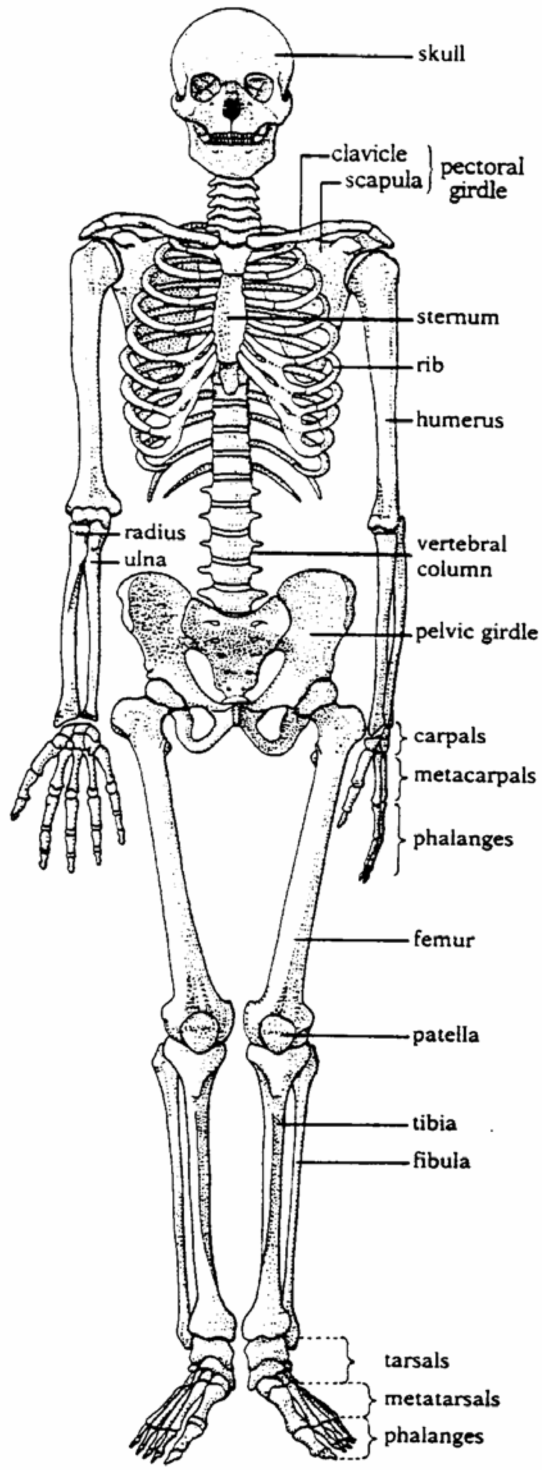


Figure 9. The human skeleton.

from the pivot to its distal end.

B. Diggers vs. Runners

Consider an animal that digs, such as a shrew or a mole (Figure 10). For such an animal, it would be desirable to exert a lot of force at the tips of the claws of its forepaws, in order to break and remove hardened earth. Recall that $F_o = F_i l_i / l_o$. Hence, our mole can increase the force at its claws by increasing the in-force (the size of its muscles), by increasing the length of the in-lever (the olecranon process), or by shortening the length of the out-lever (the ulna).

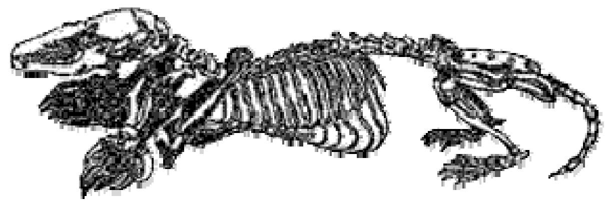


Figure 10. Mole skeleton.

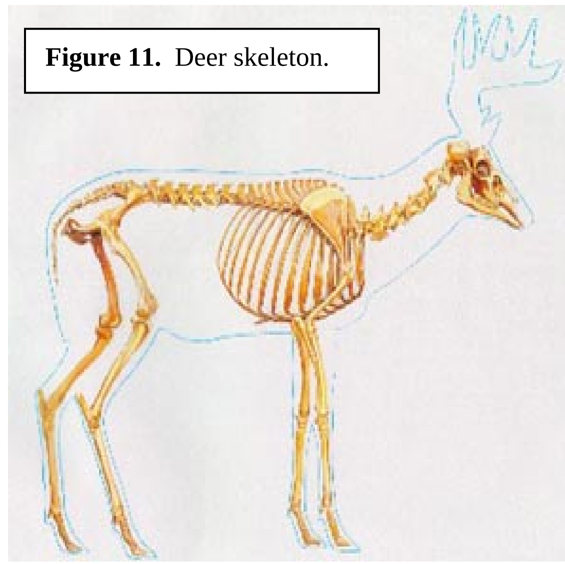


Figure 11. Deer skeleton.

Now consider an animal that runs, such as a deer or an antelope (Figure 11). For such an animal, force is not as important as speed (**velocity**). The out-velocity of a limb, v_o, is related to the in-velocity, v_i and in- and out-forces, by the equation: $v_o = v_i l_o / l_i$. Note the difference in the arrangement of variables when calculating out-velocity as compared to when calculating out-force. Hence, for a runner, out-velocity can be increased by increasing the speed at which muscles contract (v_i), by *decreasing* the length of the in-lever, l_i (the olecranon process), and by *increasing* the length of the out-lever, l_o (the ulna).

To put it another way, the ratio l_o/l_i for running animals tends to be much larger than corresponding ratios for digging animals. When referring to skeletons, then, the radius and ulna of runners tends to be longer than the humerus (and likewise, the corresponding bones of the hindlimb, the **fibula** and **tibia**, tend to be relatively longer than the **femur**). For digging animals, these relationships are reversed. Note the trade-off, here: an animal can become a better digger, but it may have to do so at the expense of its running ability, and vice-versa. Such trade-offs are common in living organisms, and explain why natural (or sexual) selection generally does not push a character to extremes.

The bones of runners and diggers exhibit other adaptations characteristic of the two activities. For runners, speed is increased by increasing the length of the out-lever, i.e., by lengthening the stride. One way to do this is to increase the lengths of all the limb bones relative to the rest of the body; compare the legs of a horse or cheetah to the legs of a bear or pig, for example. This increase in limb length does not occur equally across all the limb bones, however: the distal limb bones (the metacarpals, radius and ulna and the metatarsals, tibia, and fibula; the carpals and tarsals do not change) tend to be relatively longer than the proximal limb bones (the humerus and femur). Changing the way the foot strikes the ground also can increase length of stride. Humans walk on the ground flat-footed, and have **plantigrade** feet (= sole + walking). Carnivores walk on what is equivalent to the ball of the human foot, and have **digitigrade feet**. Ungulates (horses, antelopes, etc.) walk on their toenails, and have **unguligrade** feet (hoof + walking).

There are additional ways runners increase the length of the out-lever. In runners, like a horse or cheetah, the **thorax** (rib-cage) is laterally compressed, and the **scapulas** (shoulder blades) are oriented on the vertical, flat against the sides of the animal, rather than horizontally across its back. These modifications bring the legs underneath the animal's body, rather than "splayed-out" to the sides. The **clavicles**, or collar-bones, which anchor the forelimbs to the chest, are often reduced in size or completely lost. This allows a running four-limbed animal (= **tetrapod**) to greatly extend its forelimbs, and increase length of stride.

Most large, running animals not only have long legs, but they have **slender** legs. There is a reason for this. If body size was to increase without altering body proportions, then the load on the limbs would increase faster than their capacity to provide support and power. This explains why an elephant cannot jump or gallop, and why some small animals, such as a fox, can sprint as fast as a horse, without sharing the horse's long, slender limbs. To increase speed while at the same time minimizing costs, large, running animals reduce the mass of their limbs in several ways. Muscles on the limbs are greatly reduced or absent, and are concentrated near the body of the animal. Bones, such as the ulna of the forelimb and the fibula of the hindlimb, may be reduced greatly reduced in size, or become fused to the radius or tibia, respectively. Fusion of limb bones not only reduces their mass, but it also makes the resulting limb stronger. This may explain why, in many running animals, the toes also tend to be reduced in number and fused.

In contrast to runners, digging animals display almost an exactly opposite arrangement of the proportions of limb bones. The out-levers of the forelimb tend to be short relative to the length of the in-lever, the olecranon process (= elbow), which increases the out-force at the animal's claws. Out-force also can be increased by increasing the in-force, i.e., the mass of muscles involved in flexing and extending the out-lever. Hence, limb bones of diggers tend to be broad and thick, as well as short, and bear projections and grooves for muscle attachment.

C. Leapers and Jumpers

Examine the skeletons of the cat and the hare to ascertain the skeletal adaptations in their limbs that enable these animals to leap (vertically) great heights. Questions to consider are where are the out-levers and the in-levers for the muscles that extend the limbs? Also, how has the pectoral girdle (e.g., clavicles and scapulae) in cats been modified to allow extension of the forelimbs?

D. Flyers

Examine the fore limbs of the vertebrates in lab that fly (e.g., birds and bats). How are their skeletons modified to support flight in each type of animal?

E. Swimmers

Study how fish are adapted to swimming by examining the living fish in the lobby and the fish skeleton in lab. Also, try to understand the origin of tetrapod limbs from studying the skeleton of the fish. Notice how the limbs are greatly reduced in animals such as the crocodile, which spend considerable time in water, as compared to the mammals studied above.

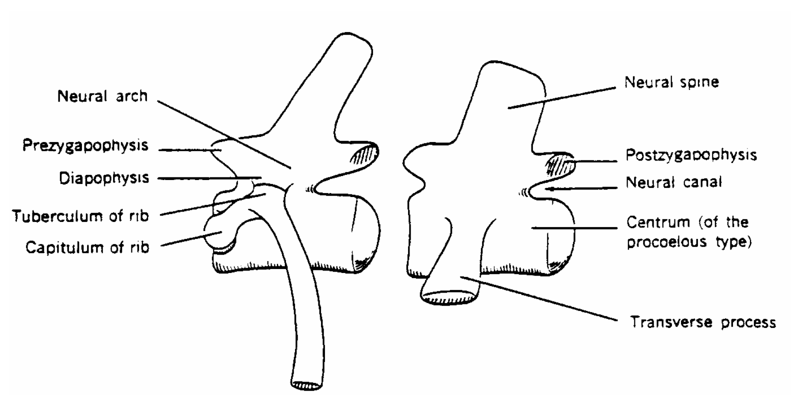
III) The Vertebral Column and Bony Thorax

A. The Vertebral Column (Spine)

You may already know that the spinal or vertebral column of vertebrates is the main support system of the body and that it protects part of the nervous system, the spinal cord. However, it may be less obvious to you that the vertebrae have a role in locomotion. In fact, it is often possible to identify not only the kind of vertebrate (fish, amphibian, reptile, bird, or mammal) but also the way the animal moves from a single vertebra.

Examine the vertebrae on display in the biology laboratory. The solid, spool-like, central portion forms the main part of the vertebra, the **centrum** (Fig. 12). Dorsal to the centrum is an arch-like structure, the **neural arch**. The opening within the neural arch accommodates the spinal cord. A **neural spine** may extend from the apex of the neural arch. In some animals, especially fish, a **hemal arch** and a **hemal spine** may project ventrally from the centrum. As its name implies, the hemal arch, when present, surrounds blood vessels. Centra also may accommodate the head (capitulum) of a rib either with a cavity or with a process (parapophysis or diapophysis). A process that extends out laterally from a centrum is a **transverse process**; transverse processes are usually on vertebrae lacking ribs. Adjacent vertebrae always articulate by their centra, and in tetrapods they also articulate by processes located on the neural arches, the **zygapophyses** (= joining + processes). The **prezygapophyses** on the anterior end of one vertebrae articulate with the **postzygapophyses** on the posterior end of the preceding vertebra. Prezygapophyses face upward and inward, whereas postzygapophyses face downward and outward.

Figure 12: Some features of vertebrae, left side views (from Hildebrand, Analysis of Vertebrate Structure, 4th edition).



The articulatory surfaces at the ends of the centra can provide clues as to the identify of the vertebrate and the kind of motion exhibited by its spine (Fig. 13). If each surface is concave, the centrum is said to be **amphicoelus** (= both + hollow). Amphicoelus centra allow limited motion in any direction, and are characteristic of bony fishes (examine the vertebrae the next time you have fish for dinner). Other kinds of centra have a bulge at one end and a depression at the other, the bulge of one fitting into the depression of its neighbor. **Procoelous** vertebrae have a concave anterior end and a convex posterior end, whereas **opistocoelous** vertebrae have the reverse, a convex anterior end and a concave posterior end. Joints between these types of vertebrae permit motion in any direction (except as modified by the zygapophyses), and they help prevent dislocation. Centra with flat surfaces are **platyan**. Platyan centra withstand compression and limit motion, unless provided with fibrous disks between the joints. Modern amphibians may have amphicoelous, procoelous, or opistocoelous vertebrae, whereas modern reptiles usually have procoelous vertebrae. The vertebral centra of mammals may be opistocoelous in areas requiring motion (e.g., the neck, or cervical vertebrae), but are often platyan (= acoelous) in areas requiring support (e.g., the lumbar or pelvic region). Birds have **heterocoelous**, or saddle-shaped, centra, **Heterocoelous** centra allow vertical and lateral motion, but prevent rotation around the spine.

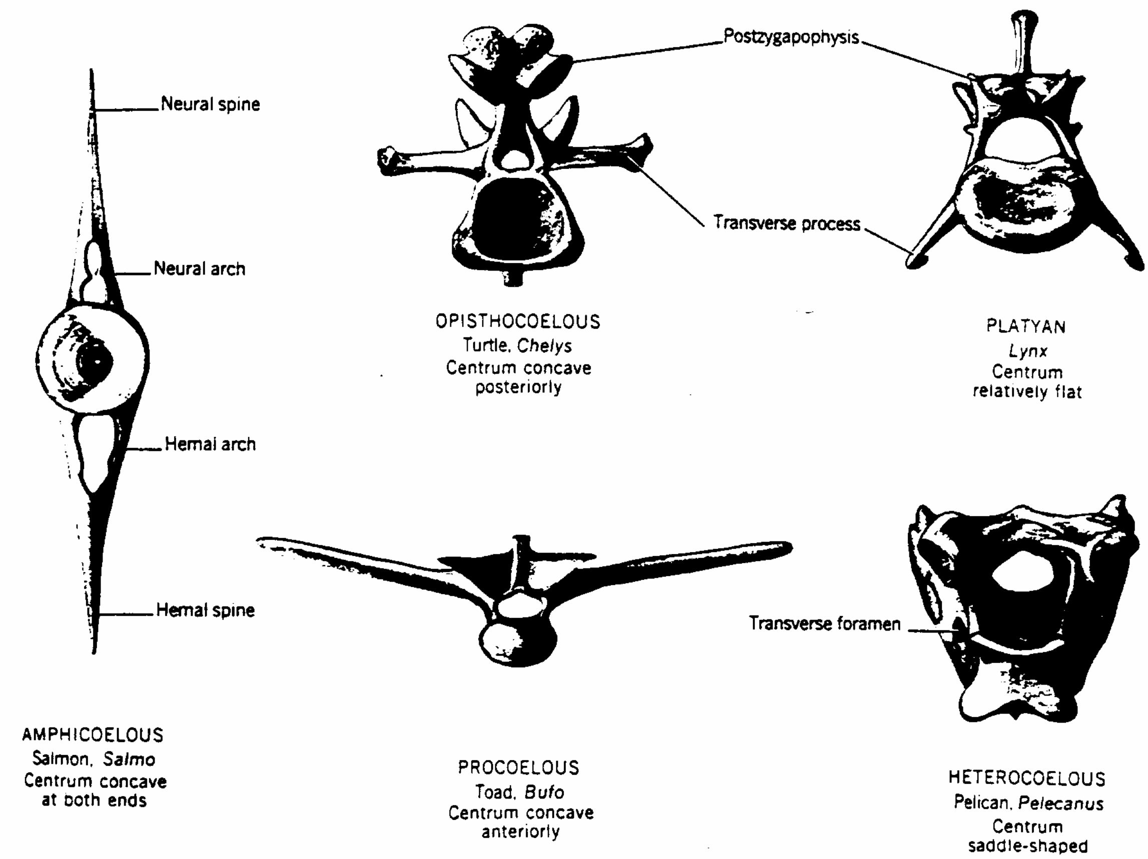


Figure 13: Vertebrae showing various shapes of centrum, and other features, as seen in posterior view (from Hildebrand, Analysis of Vertebrate Structure, 4th ed.).

Zygapophyses, in addition to the centra, also affect the direction of articulation of the vertebrae. If the zygapophyses are vertically oriented, that is, the postzygapophysis lies on top of the prezygapophysis, motion is restricted in the vertical, but not the horizontal, plane. If the zygapophyses are oriented horizontally (side-by-side), motion is restricted in the lateral plane.

Whether the spine flexes in the vertical or horizontal plane is characteristic of the different kinds of vertebrates. In fishes, this flexion tends to be in the horizontal plane, that is, from side-to-side (observe the fish in the tank in the Conservation Lab to verify that this is the case). If you've ever eaten fresh fish, you probably removed its bones as you ate. Most likely, the bones in question were the neural and hemal spines. The neural and hemal spines are the only processes on the vertebrae of fishes, and are located in the vertical plane. The neural and hemal spines provide attachment surfaces for the muscles that flex the spine. In contrast, if you examine the vertebrae of amphibians, reptiles, birds, or mammals, you will see that often, the neural and hemal spines are reduced in length (and may be absent altogether), and unlike fish, transverse processes are present. Moreover, rather than being of uniform appearances, the spines and processes on tetrapod vertebrae may differ in size and their direction of orientation. How do you think these differences in vertebral processes between fishes and tetrapods relate to their modes of locomotion, and why?

B. The Bony Thorax

The bony thorax consists of the **ribs**, **sternum** (breast bone) and **thoracic vertebrae**. These structures protect the soft tissues of the thorax (chest) – e.g., the lungs, heart and associated major blood vessels. The ribs also assist in breathing. The size of the rib cage can thus provide a rough estimate of the relative lung volume of each animal (which is a major factor in the level of metabolic activity that an animal can sustain). Compare the size of the thoracic cavities in the various skeletons and consider the metabolic demands of the daily activities of each type of animal.

The sternum of different vertebrates may be a single bone or consist of several bony elements in series. Which types of vertebrates lack a sternum? The sternum (breastplate) of birds has been greatly expanded to provide an increased surface area for the attachment of the flight muscles. Examine the sternum of the gull, with its very prominent ventral **keel (carina)**. The clavicles of birds are also fused together to form the **furculum** (e.g., the wishbone), which articulates with the breastplate and provides additional lateral attachments for the flight muscles.

Vertebrate Morphology Web Sites

Digital Morphology (a dynamic archive of information on digital morphology and high-resolution X-ray computed tomography of biological specimens)
http://digimorph.org/navcommon.phtml

Videos of Vertebrate Movement (Lizards and Snakes)
http://www.biology.uc.edu/faculty/jayne/videos.htm

Biologically Inspired Robotics Group (Salamander Locomotion)
http://birg.epfl.ch/page28707.html

Vertebrate Morphology Lab: Summary of Questions to Consider

General:

For any articulated skeleton, what can you infer about the ecology and evolutionary history of the animal (e.g., what special skeletal adaptations enable it to live the way it does)?

Vertebrae:

1. Where are the haemal arches and spines, centra (centrum, sing.), neural arches and spines in the fish vertebrae?
2. How do pre- and post-zygapophyses allow for dorsoventral movement (e.g., in the deer), lateral movement (in the snake) or both (in the cat)?
3. From what kinds of organisms are the vertebrae in the plastic boxes derived?
4. How do the differences in vertebral structure between fishes and tetrapods relate to their modes of locomotion? Why?

Limbs:

1. How does the structure of the out-levers of swiftly-running animals increase speed of the distal part of the limb? More generally, how does the bulkiness of the legs differ for runners relative to diggers and scrapers?
2. What bones contact the ground in plantigrade (human), digitigrade (cat) and unguligrade feet (horses)?
3. What makes the pectoral girdle of the cat distinctive?
4. How do the relative lengths of olecranon processes and out-levers differ in runner relative to scrapers and diggers?
5. What other leg bone has a process that looks and functions like the olecranon process, and why are the two different processes similar?
6. How is the gull skeleton adapted for flight?
7. Flying animals must have high amount of lift per unit weight (i.e., low wing loading). How was this problem solved for bats?

Skulls:

1. How do diastemas work (e.g., on the marmot skull) and why are they only found in some of the skulls?
2. Which animals are homodont? Heterodont?
3. How do grinding teeth (in porcupines, rabbits and marmots, and large ungulates) and shearing teeth (e.g., the carnassials in the lion, fox and dog) work?
4. Where are the out-levers and in-levers for the various jaws on display? How do they work?
5. Where are the attachments for the digastric muscles that open the jaws? How do they work?
6. Which muscles – the digastric or temporalis – are larger? How does this size difference relate to the respective functions of each muscle type.
7. What are the differences in function between the masseter and temporalis muscles, and why is the temporalis relatively more important in carnivores than in herbivores? How do the differences in the functions of these muscles depend on the point of insertion of the muscle relative to the pivot?
8. How and why do the orientations of the eye sockets in carnivores and herbivores differ?

Vertebrate Morphology Lab Worksheet

(This worksheet is due at the beginning of lab next week. Submit *one* worksheet per pair.)

Lab Day:______________________ Names: ____

Part 1. Natural History Museum Exhibits

1) For each of the following animals, note whether it has a plantigrade, digitigrade, or unguligrade foot. (4 points)

a) dire wolf:

b) mammoth:

c) horse (*Equus scotti*, wall on far side of stairs):

d) yourself:

2) Examine the spine (focusing on the thoracic-lumbar regions) of *Eryops megacephalon* (a primitive amphibian having a dog-like appearance) and *Edaphosaurus* (a reptilian dinosaur), located in the display case in the interior wall on the second floor. Compare them to the arrangement of the lumbar vertebrae of *Canis dirus* (the dire wolf) or *Smilodon californicus* (the saber-toothed cat), which are in the large display area on the main floor of the museum. When each of these animals walks, does its spine move from side-to-side or up-and-down? How can you tell? (Hint: look at the overlap of the pre- and postzygapophyses.) Are the arrangements of the limb bones of these animals consistent with your answers, and if so, how? (4 points)

3) Along the far side of the stairway leading up to the second floor of the museum is an exhibit that traces the evolution of horses from the ancestral forms, *Hyracotherium*, *Mesohippus* and *Merychippus,* to the modern horse, *Equus*. Identify <u>four</u> evolutionary changes in the skeletons of these horses that are adaptations for a running lifestyle, and briefly explain the structural or physiological advantages conferred by each. (4 points)

4) (5 pts) For each of the following animals in a-d, note whether it has homodont or heterodont dentition.

a) *Dunkleosteus* (an armored fish, or placoderm, located in the second floor display case along the internal wall):

b) *Carcharodon megalodon* (a primitive shark, several teeth of which are on display in the top Chondricthyans drawer, on the left wall as you enter the Museum):

c) *Tyrannosaurus rex* (skull, located on ground floor, to left of stairs):

d) *Smilodon californicus* (saber tooth cat):

e) Many morphologists consider heterodont dentition to be an evolutionary advantage for feeding. Provide an explanation for why this may be the case.

5) Look at the 'Herbivore and Carnivore' display case in front of the stairs leading up to the second floor. Then, examine the skulls of each of the following animals, and note whether the animal is a carnivore, an herbivore, or an omnivore. Explain why, based on an examination of each animal's teeth. For each animal, would you expect the temporalis or masseter muscle to have the more prominent role in closing the jaws? Why (e.g., what does the structure of the skull tell you about the relative sizes of these two muscles)? (3 points)

a) dire wolf:

b) *Mesohippus bairdi* or *Equus scotti* (in the horse display):

c) cave bear:

6) Long neural spines of vertebrae are typical of fishes, and serve as points of attachment for muscles used in swimming. In contrast, the vertebrae of mammals usually lack long neural spines (see the cave bear, for example). Some mammals, however, have relatively long neural spines on their thoracic (chest) vertebrae; look at, for example, the thoracic vertebrae of *Brontops tyleri* (a rhino-like mammal, on the bottom of the two-story Mammal Fossil Wall), the Irish Elk, the Mammoth, the Mastodon, and *Equus* (the horse) on display in the Museum. Can you explain why the neural spines of these mammals' thoracic vertebrae are so long? (2 points)

7) Neck length can vary tremendously in both birds and mammals: consider your neck and the neck of a giraffe or the neck of an owl as compared to the neck of an ostrich. Is the structural basis of an increase in neck length the same in birds and mammals? For help in answering this question, compare the number of cervical vertebrae in the neck of an owl (see Figure 1) with that of the moa on display in the bird case on the main floor of the museum. Then, compare the number of cervical vertebrae in the long neck of the Irish Elk or the giraffe camel (*Oxydactylus longpipes*, second from the top left on the Mammal Fossil Wall) to the number of cervical vertebrae in the much shorter necks of *Oreonotes gracilis* (upper left of the Mammal Fossil Wall) or *Hyracotherium* (horse panel). **Note**: the first rib is attached to the first thoracic vertebra, which is immediately posterior to the last cervical vertebra. (4 points)

List the number of cervical vertebrae in the

moa:
barn owl:
Irish elk or giraffe camel:
O. gracilis or *Hyracotherium*:

State your conclusion here:

Figure 1.
Barn owl

Part 2. Conservation Lab Specimens

1) The appearance of feathers was an innovative adaptation for flight. Describe three additional features of the gull's anatomy that make it especially well suited for flying. Please use correct anatomical names of pertinent structures. (3 points)

2) Are the wings of a bat and the wings of a bird homologous or analogous structures? Why? (2 points)

3) What are <u>three</u> features of the hind limbs of the rabbit that make it a good leaper? Hint: start by identifying the in-levers for extension and considering where the muscles that extend the limb attach to bone. Be as specific as possible in your descriptions, using anatomical names of bones or muscles whenever possible. (3 points)

4) Compare the vertebrae of the deer and the snake. Which vertebrae allow for more rotational motion of the spine? Support your answer by noting differences in the structures of the two types of vertebrae. Also, consider what structure passes through the neural arch of the vertebrae in a living animal and how the presence of this structure affects the degree of rotational motion that is allowed by the vertebrae in each animal. (3 points)

5) Describe <u>three</u> features of the forelimbs of moles that make them especially well suited for digging. Select from the following terms for your answer. You may also elect to use additional terms that are not listed below to support your answer. (3 points)

length of in-lever	humerus	olecranon
length of out-lever	triceps muscle	ulna

Score: ________/ 40 ⟶ **________ / 20 (final score)**