# Chapter 6

## Biomechanical Analysis of Vertebrate Skeletal Systems

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121

121

## I. Introduction

This laboratory presents the *structure-function* concept, certainly one of the most important recurring themes in biology. The skeletal system (and associated muscular-nervous system) of a species represents natural selection's "best" efforts in producing an arrangement of jointed levers to deal with the physical stresses imposed by the environment and allow the total behavior required of that species. Another major objective is to examine some of the "rules of the game" with which natural selection has had to deal. Specifically, Newton's laws of motion and force and their impact on the evolution of skeletal systems are considered. Upon completion of the laboratory, students should understand the physical concepts of torque, work, and mechanical advantage, and their application in analyzing skeletal systems from a structure-function viewpoint.

This laboratory was developed in response to the recognition that students lack much understanding for how vertebrate skeletal systems function and why they have evolved into their present diverse forms. That the bumps, ridges, and depressions on bones have significance in the attachment of muscles and their functioning in lever systems escapes most students as they examine a skeleton. That the diversity of form in vertebrate skeletal systems is understandable from a function viewpoint and can be studied and explained using simple concepts from physics are important ideas not usually appreciated by the undergraduate student. We have developed these exercises to help students gain some experience with the physical realities that govern the evolution of skeletal systems.

These exercises can be used in a standard, instructor-led laboratory session, as they have been used at Siena College and Lycoming College and for six years in the introductory biology laboratory course at Cornell University. The exercises could also be adapted for use in an autotutorial format. This laboratory topic would be appropriate in various biology courses, including introductory biology, zoology, comparative vertebrate anatomy, and evolution. In conjunction with this laboratory, we assign the article by Hildebrand, "How Animals Run" (1960).

## II. Student Materials

### Introduction*

Vertebrates and arthropods have shown remarkable plasticity of design in successfully adapting to aquatic, terrestrial, and aerial life. Unquestionably, one major factor contributing to each group's success has been the independent evolution of skeletal systems (the endoskeleton of vertebrates and the exoskeleton of arthropods) organized as a series of jointed levers operated by

*Adapted from Chapter 13 in the laboratory text *Investigative Biology*, Glase *et al.* 1980 specific muscles. Analysis of the mechanical properties of skeletal systems (or parts thereof) can yield much biologically relevant information on the characteristics and potentials of movement in the animal as a whole. Such analyses are particularly useful in evaluating the structure/function relationship of animals with regard to locomotory or feeding behavior.

Before beginning your analyses of certain vertebrate skeletal units, it will be useful to recall the basic laws governing motion and force (courtesy of Sir Isaac Newton, *circa* 1675).

I. A body remains at rest (or moves at a constant velocity) unless a force acts upon it.
II. A force gives a body an acceleration in the direction of the force which is directly proportional to that force and inversely proportional to the mass of the body.
III. If body A exerts a force on body B, body B exerts an equal and opposite force on body A.

When expressed in biological terms, Law I states that if an animal (or parts thereof) is at rest relative to its environment, it can only be set in motion by the application of a force, and consequently, if an animal is to move by its own unaided efforts, it must elicit a force against its external environment. Law II states that when an animal elicits from its environment an external propulsive force, the velocity imparted to the animal is directly proportional to the magnitude of the force and the period of time during which it acts; at the same time, it is inversely porportional to the animal's mass. Law II obviously has implications when considering the amount of muscular force necessary to move heavy and light objects of equal size. Translated into biological terms, Law III can be expressed by saying that when subjecting its body to a forward propulsive force, an animal must simultaneously exert an exactly equal but opposite backward force against its external environment. The animal moves forward because the environment resists the movement of the fins, legs, or wings relative to the body.

With respect to the third law, it is useful to consider its application to muscular action in general. A typical skeletal muscle has three basic areas. The muscle's ends (origin and insertion) are usually attached to some skeletal part (e.g., bone or cartilage via tendons). The *origin* is attached to a stationary bone and is therefore relatively non-movable, whereas the *insertion* is attached to a more movable part. The enlarged center section of the muscle (*belly*) contains many muscle cells (*fibers*), which contract and pull the *bone* attached to the muscle's insertion. When a muscle develops tension, the force that it exerts on the bone at its insertion is exactly equal in magnitude, and opposite in direction, to that which it exerts on the bone at the muscle's origin. It should be noted that the final movement caused by muscular contraction is determined not only by the origin and insertion of the muscle, and the type of bone joint, but also by the *antagonistic* muscle group. Muscles typically work in antagonistic groups. For example, one muscle group (*biceps* group) causes an upward movement (flexion) of the forelimb, and an antagonistic group (*triceps* group) causes a downward movement (extension) of the limb.

All bone/muscle systems are machines. A machine is a mechanism that transmits force from one place to another, usually also changing its magnitude. It is useful to designate any force applied to a machine as an *in-force* ($F_i$), and any force derived from a machine as an *out-force* ($F_o$). In the body, in-forces are applied by the pull of tendons or tensed ligaments resulting from muscle contraction; useful out-forces are ultimately derived at the teeth, feet, digits, and elsewhere. For the most part, we will consider only simple machines having one in-force and one out-force.

**Bone/Muscle Systems As Lever Machines**

An in-force may be transmitted to an out-force by a crankshaft, hydraulic device, pulley, lever, or some other mechanism. Most feeding and locomotor systems of the body transmit forces by levers, and only these will be considered here. A *lever* (Figure 6.1) is a rigid structure, such as a crowbar or bone, that transmits forces by turning (or tending to turn) at a pivot or fulcrum.

Our childhood experiences with seesaws can help us better understand the functioning of lever systems. Successsful use of a seesaw depends on its being balanced with respect to the two participants. In order to obtain a balanced seesaw, the two individuals (A and B) must adjust their positions from the fulcrum in accordance with their body weights. Let's consider why this is true. In Figure 6.1, $F_A$ and $F_B$ are the forces exerted on the lever by the weight of individuals A and B, respectively. Each force is spaced from the fulcrum by a segment of the lever called a *lever arm* or *moment arm*. The distance separating A from the fulcrum is A's lever arm, or $S_A$. B's distance from the fulcrum is the lever arm $S_B$. $F_A$ causes the lever to turn in a counterclockwise direction. $F_B$ causes it to turn in a clockwise direction. A measurement of the turning power that a force exerts on a lever system is called torque (T) and equals the magnitude of the force times the length of its lever arm. Individual A creates a counterclockwise torque on the lever equal to $F_AS_A$. B's torque is clockwise in direction and equal to $F_BS_B$. In general, if $F_AS_A > F_BS_B$, the lever rotates in the direction of $F_A$; when $F_AS_A < F_BS_B$, the lever rotates in the direction of $F_B$. A lever is said to be in a state of equilibrium when the algebraic sum of all the torques acting upon it equals zero. That is, a lever is in equilibrium when the sum of all the torques that produce counterclockwise rotation equals the sum of all the torques that produce clockwise rotation. This general statement is called the *law of the lever:*

At equilibrium, *counterclockwise torque = clockwise torque,*

or

$$F_AS_A = F_BS_B$$

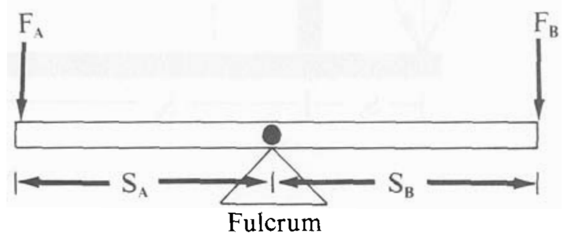


**Figure 6.1.** A simple lever system (see text for discussion).

Therefore, in order to obtain a balanced seesaw, the two participants must adjust their positions from the fulcrum so that the clockwise and counterclockwise torques they produce are equal. If both individuals are of about the same weight, then they should be about equal distances from the pivot in order to achieve a balanced lever system. That is, if their weight forces are equal ($F_A = F_B$), then their lever arms must also be equal ($S_A = S_B$) if the clockwise and counterclockwise torques are to be equal ($F_AS_A = F_BS_B$). Clearly, if individual A is heavier than individual B ($F_A > F_B$), then A's lever arm must be proportionately less than B's lever arm if $F_AS_A$ is to still equal $F_BS_B$.

Now let's consider how levers are used as machines in the vertebrate skeletal systems (Figure 6.2). A typical skeletal lever system involves two bones: bone 1 serves as the actual lever upon which forces are exerted; bone 2 provides the fulcrum about which bone 1 can turn. A muscle inserted on bone 2 at a distance from the fulcrum contracts, producing the in-force ($F_i$) on the lever system. The in-lever arm ($S_i$) is the distance separating $F_i$ from the fulcrum. The muscle's effort produces a clockwise in-torque ($T_i$) which equals $F_iS_i$. Where bone 1 contacts the environment an out-force is developed. The distance separating $F_o$ from the fulcrum is the out-lever arm ($S_o$). The out-torque ($T_o$) equals $F_oS_o$. Since $F_i$ transmitted through $S_i$ produces $F_o$ transmitted through $S_o$, in all cases $T_i$ and $T_o$ are equal in *both magnitude and direction.*

$$\textit{in-torque} = \textit{out-torque}$$

$$F_iS_i = F_oS_o$$

$$T_i = T_o$$

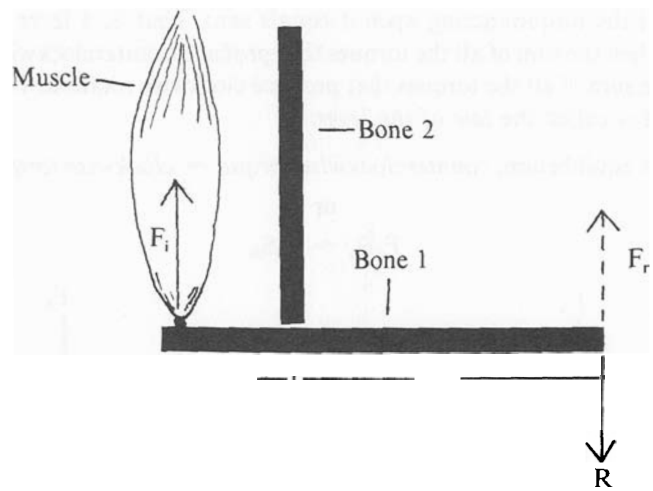


**Figure 6.2.** A skeletal lever system (see text for discussion).

$F_o$ can now be used to move against some environmental resistance (R) such as a weight. As the muscle contracts and $F_i$ increases, $F_o$ also increases proportionately. Newton's Third Law states that as force is applied by the lever system against R, an equal (in magnitude) and opposite (in direction) force is applied by R against the lever system. $F_r$ increases directly with $F_o$ and sets up a counterclockwise torque equal to the $F_rS_o$ that keeps the lever system in equilibrium. As predicted by the law of the lever,

at equilibrium, *clockwise torque* = *counterclockwise torque,*

or

$$F_iS_i = F_rS_o$$

However, when $F_o$ equals the force required to move R, bone 1 moves in a clockwise direction and the lever system has done useful work.

It is important that the student of biomechanics be able to solve the equation for the law of the lever for any of the variables, and to understand the relation of each to the others. If more than two forces tend to turn the same lever, then the net direction of rotation is determined by comparing the sums of all the clockwise and the counterclockwise torques.

The three recognized classes of lever, together with examples of their occurrence in the body, are illustrated in Figure 6.3. When examining the illustration it is important that you do not attempt to memorize diagrams, but learn to identify the pivot and the in- and out-forces. The distinction to be drawn between them is one concerning the relative position of the points of application of the in-force or "effort" (i.e., the muscle force operating the lever) and the "load" or "resistance" which the out-force has to *balance* if it is to hold the lever arm steady, or has to *overcome* if it is to start the lever doing useful work. In levers of the first class, the input and output forces are applied on opposite sides of the fulcrum, whereas in levers of the second and third classes, they are applied on the same side of the pivot point. The class of lever employed often depends upon the type of movement intended. For example, all three types of levers may be found in the movements of the foot. Tapping the toes involves the use of a first class lever; standing on the toes involves a second class lever when we focus on the action of the calf muscle; and lifting a weight with the foot involves a third class lever when we consider the action of the muscles located on the front of the leg. A vast majority of the levers of the body are of the third class. First class levers are few, but are still more numerous than the second class levers. Can you think of some reasons why this is true?

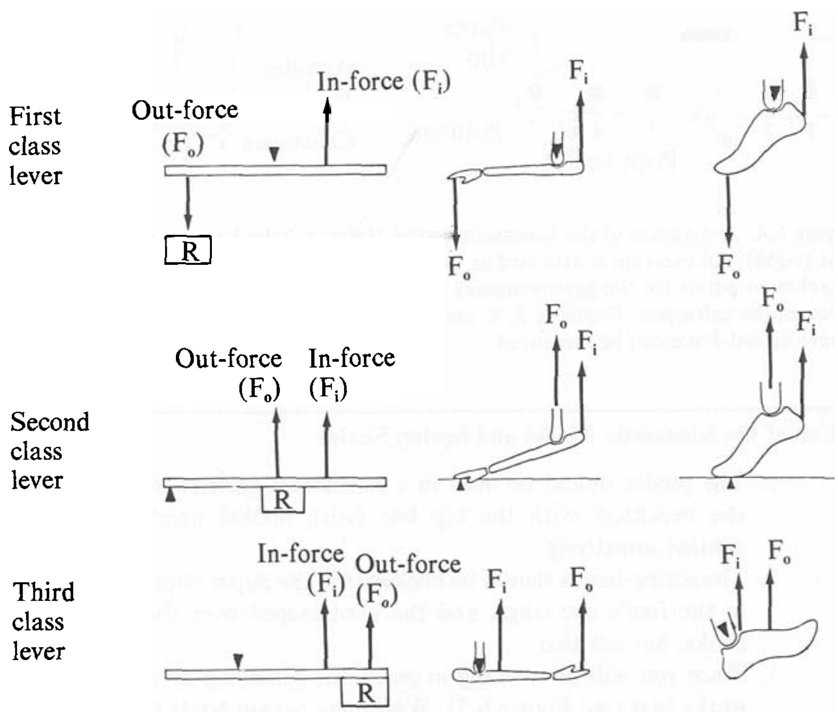


**Figure 6.3.** Illustration of three classes of levers as found in the movements of the arm and foot. R represents the resistance, against which the out-force is applied and the fulcrum is at ▲. (Adapted from M. Hildebrand: Analysis of Vertebrate Structure. Copyright © 1974 by John Wiley and Sons, New York. Reprinted with permission.)

## The Kinematic Model

1.* The physical model that you will use in these exercises is called a kinematic model, because kinematics is the study of motion, and we are ultimately concerned in this laboratory with understanding the basis for movement in organisms. Initially, consider the simple lever system of the kinematic model (Figure 6.4). Identify the components $F_i$, $S_i$, $F_o$, and $S_o$.

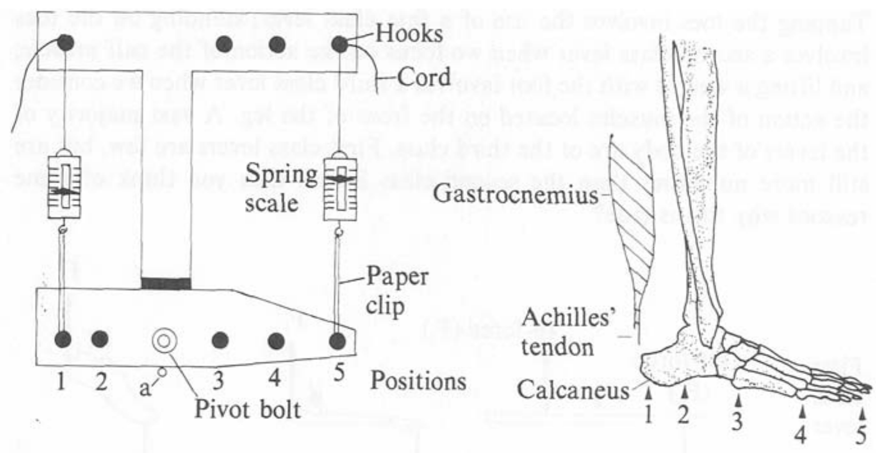


**Figure 6.4.** A diagram of the kinematic model (left) and the human lower leg and foot (right). An eye-ring is attached at position"a". Positions 1 and 2 represent attachment points for the gastrocnemius muscle, whose contraction produces an in-force on the calcaneus. Positions 3, 4, and 5 represent points on the front of the foot where an out-force can be measured.

**Use of the Kinematic Model and Spring Scales**

1. The model should be used in a horizontal position relative to the benchtop, with the top bar (with hooks) firmly braced against something.
2. The spring scales should be hooked into the paper clips attached to the foot's eye rings, and the cord looped over the top bar hooks, but not tied.
3. Since you will be working in pairs, the following arrangement works best (see Figure 6.5). While one person holds the model down by the "leg" piece and also holds stationary the scale attached to position #3, 4, or 5, the other person applies force on the other scale, attached to #1 or 2, by pulling its cord. The

*Note: Answers to important questions in the following section and sample data collected with the model are included in III. INSTRUCTORS' MATERIALS

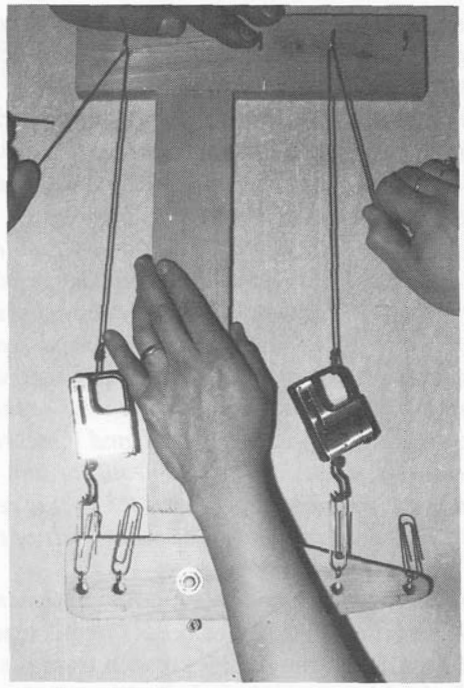

**Figure 6.5.** The suggested arrangement of two individuals manipulating and making measurements with the kinematic model.

magnitude of this in-force is measured by the lefthand scale. The righthand scale measures the out-force magnitude. Measurements should be made while keeping the foot roughly perpendicular to the leg.

4. Frictional resistance within the scales and at the pivot joint are the main sources of error. In making measurements these can be minimized as follows: (a) be sure that the pivot bolt is only loosely attached; (b) while watching the righthand scale, pull on the left-hand scale until the desired weight force (2 pounds) is just reached on the righthand scale. Slowly release tension on the lefthand scale until the indicator on the righthand scale is *just* affected. The reading on the lefthand scale represents the best measurement of the in-force required to produce a 2-pound out-force.

a. *With the spring scales attached to positions 2 and 3, verify that the "foot" is stationary relative to the "leg" (i.e., it is at equilibrium) only when the two forces exert equal but opposite torques about the axis of the joint.*

b. *Is this true for any angle formed between foot and leg?*
c. *Is the magnitude of the force necessary for producing a balancing torque at position 2 changed if the force exerted on the front of the foot is moved to insertion point 4? Are the torques (F × S) still equal? Rulers are available to measure distances.*
d. *Next, examine the compression forces developed at the pivots (points of articulation) of skeletal lever systems. To do this, remove the pivot bolt at the ankle joint and attach a third scale to the eye-hook ("a" in Figure 6.4). While one person firmly holds stationary both the "leg" and the upper two spring scales (lefthand scale attached to position #1 or 2, righthand scale attached to position #3, 4, or 5), the other person pulls down on the third scale. Simultaneously read all three scales. The third scale measures the compression force ($F_c$) that $F_i$ and $F_r$ develop at the pivot point. Recall that when the lever is in equilibrium, $F_o = F_r$. What is the relationship between $F_c$, $F_i$, and $F_r$? Is this relationship still observed if $F_i$ and $F_r$ are applied at other positions on the model? Try it!*

2. *Now consider the kinematic model in relation to the anatomy of your own leg/ankle/foot (Figure 6.4).* Positions 1 and 2 represent two possible points of insertion of the Achilles tendon from the gastrocnemius muscle into the heel bone (calcaneus). Positions 3, 4, and 5 represent points along the foot where forces are exerted, corresponding to positions at the proximal and distal ends of the metatarsal bones, and the ends of the toes, respectively. Alternatively, positions 3, 4, and 5 can be considered the ends of feet of different lengths.

   The purpose of walking is to propel the body forward, and although walking involves the muscles and joints of the whole body, the foot provides the pivot about which the body turns. That is, although the force exerted by your weight acts at the same point (the ankle joint) as you take a forward stride when walking, the fulcrum shifts forward, as does the foot's distribution of body weight (see Figures 6.6 and 6.7.)

   *Examine Figure 6.6 and attempt a stride yourself (a stride is from heel-strike to heel-strike by the same foot). Try to identify how many of the lever classes are involved (see Figure 6.3). At what point(s) along the stride does the gastrocnemius counteract the weight force?*

   For the foot of the walking human, all the parameters of the lever law are variable: both $S_i$ and $S_o$ change as the fulcrum changes position; $F_o$ varies during the stride as the distribution of total body weight is shifted from one foot to the other; $F_i$ varies as $F_o$, $S_i$, and $S_o$ vary. In actuality, because the model cannot duplicate the variable positioning

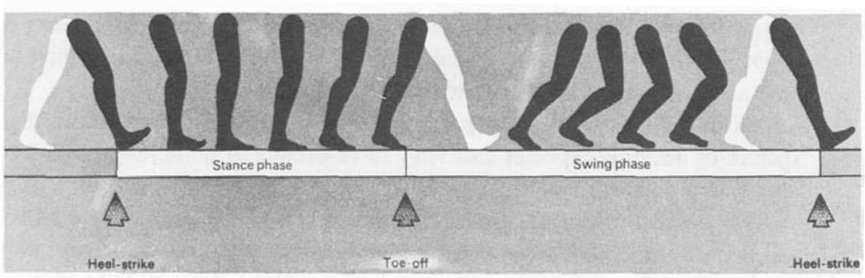


**Figure 6.6.** The striding sequence. The sequence starts as the right leg (black) swings in front of the body and the heel makes contact with the ground. Body weight is progressively distributed from the back to the front of the foot until it is borne by the toes (principally the big toe). At this moment the left leg (white), which has been swinging forward ready to take its turn in the walking cycle, hits the ground in the heel-strike position. The right leg, with a final strong propulsive drive (the toe-off), breaks free and starts to swing forward for the next step; and so it goes on, and the ground is covered by a smooth, rocking, heel-toe motion of one foot after the other. (From J. R. Napier: Primate Locomotion. Copyright © 1976 by Oxford University Press, Ely House, London. Reprinted with permission of Carolina Biological Supply Company.)

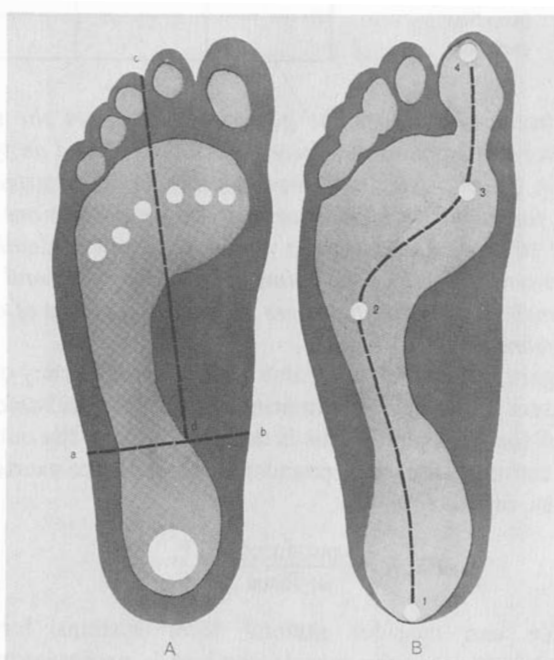


**Figure 6.7.** A diagram showing distribution of weight in the human foot. When individual is motionless (left), the foot divides its load (one-half the body weight) between the heel and ball, along axis A-B, and equally on both sides of the C-D axis. When striding (right) the load is distributed smoothly from *1* through *4*. (From J. R. Napier: The Antiquity of Human Walking. Copyright © 1967 by W. H. Freeman and Co., San Francisco, California. Reprinted with permission.)

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of the fulcrum, *the kinematic model functions only as a first class lever*. The in-force can be applied to either position 1 or 2 (see Figure 6.4) and produce an out-force at position 3, 4, or 5.

3. Let us now consider the four parameters of the lever law for different species of animals. Species can vary in reference to bone lengths and insertion points of muscles.
   a. *For a species with its gastrocnemius inserted at position 1, measure the muscle forces required to cause a 2-pound out-force to be exerted at positions 3, 4, and 5. Enter these data in Table 6.1.*
   b. *For a species with its gastrocnemius inserted at position 2, measure the muscle forces required to cause the 2-pound out-force at positions 3, 4, and 5. Enter these data in Table 6.1.*

**Table 6.1.** The force exerted by gastrocnemius ($F_i$) to produce a constant out-force of 2 pounds ($F_o$) at position 3, 4, or 5.

| | | *$F_o$ at Position* | | |
|---|---|---|---|---|
| | | 3 | 4 | 5 |
| *Gastrocnemius insertion position* | 1 | | | |
| | 2 | | | |

   c. *At what position does the gastrocnemius exert the most force to produce the 2-pound out-force? The least? Based on your results in section 1d, estimate the compression force ($F_c$) exerted on the pivot point for each of the in-force and out-force positions in Table* 6.1. *What structural adaptations would be useful in dealing with these compression forces at the points of articulation in real skeletal lever systems? What material covers the actual surfaces of articulation in a vertebrate?*

4. We can gain insight into the force conversion efficiency of the leg/foot lever system by roughly estimating the *force mechanical advantage* (FMA) of the "machine". This is done by dividing the out-force (in this case the constant force of 2 pounds) by the in-force exerted by the gastrocnemius, or:

$$\text{FMA} = \frac{\text{out-force}}{\text{in-force}} = \frac{F_o}{F_i}$$

*Note:* We can consider skeletal lever systems force-efficient if FMA $>$ 1.0, because the muscle involved is producing more out-force than the in-force it generates. If FMA $<$ 1.0, the skeletal lever system is force-inefficient in that the out-force is less than the in-force that the muscle generates. With FMA = 1.0, the muscle neither gains nor loses mechanical advantage since $F_i = F_o$.

*a. From your measurements above, calculate the FMA for a species with its gastrocnemius inserted at position 1. Enter these data in Table 6.2. Do the same for a second species with its gastrocnemius inserted in position 2.*

**Table 6.2.** The force mechanical advantage at various gastrocnemius insertion positions and output force positions.

| | | $F_o$ at position 3 | $F_o$ at position 4 | $F_o$ at position 5 |
|---|---|---|---|---|
| *Gastrocnemius Insertion Position* | 1 | | | |
| | 2 | | | |

*b. In each case, at what point along the foot is the greatest FMA observed (i.e., position 3, the proximal metatarsals; position 4, the distal metatarsals; or position 5, the toes)? Does this agree with your experience with your own leg and foot? To answer this, suspend one leg in mid-air, and pull up with a rope at points along the foot corresponding to positions 3, 4, and 5. While contracting your gastrocnemius, use the tension developed on the rope as an estimate of the out-force magnitude produced by the muscle at these positions on the foot. Does your leg/foot lever system "agree" with the kinematic model? Are these results understandable in terms of the "law of the lever"?*

*c. Which of the two species (species 1 = gastrocnemius inserted in position 1; species 2 = insertion at position 2) has the greatest force mechanical advantage?*

5. The maximum "effectiveness" of a particular muscle/bone lever system is achieved when the distance moved by the muscle is small compared to the distance moved by the "business end" of the bone (the end of the moment arm moving the "load"). Speed mechanical advantage (SMA) equals the distance moved by the business end of the bone (B) divided by the distance of muscle contraction (M), or:

$$\text{SMA} = \frac{\text{B}}{\text{M}}$$

Note that M is equivalent to the distance moved by the heel bone at the muscle's insertion point.

*a. To obtain estimates of SMA, we need to measure the arcs described by points corresponding to the two muscle insertion positions and the three foot lengths. The arcs can be made by placing the model on a sheet of paper and, with five pencils positioned in holes located along* *the foot, move the foot through the full extent of its rotation. Also, carefully mark the position of the pivot point. Carefully measure these arcs, to the nearest mm, and also the lever arms for all five points (see Figure 6.8). $M_1$ and $M_2$ are the contraction distances for gastrocnemius muscles inserted at distances $S_1$ and $S_2$ from the pivot. $B_1$, $B_2$, and $B_3$ are the movements of the ends of feet of lengths $S_3$, $S_4$, and $S_5$, respectively.*

Results similar to the following should be achieved.

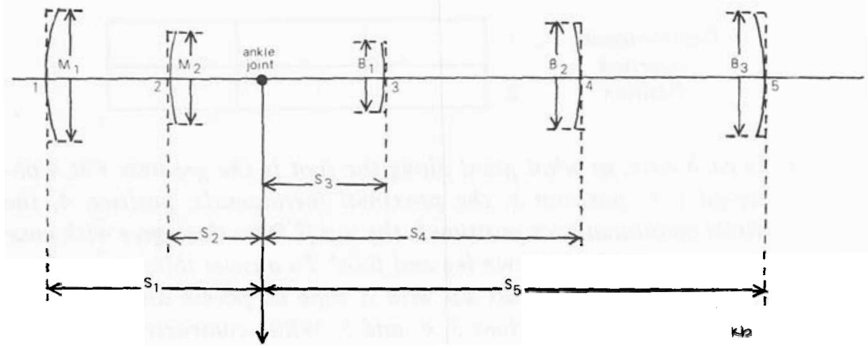



**Figure 6.8.** Diagram showing the relationship between the lever arms ($S_1$-$S_5$) at various position (1—5) in a simple lever system, and the distance of muscle contraction ($M_1$-$M_2$) and bone movement ($B_1$, $B_2$, $B_3$) at these positions.

Calculate the following speed mechanical advantages from your measurements:

$\frac{B_1}{M_1} =$ $\qquad$ $\frac{B_2}{M_1} =$ $\qquad$ $\frac{B_3}{M_1} =$

$\frac{B_1}{M_2} =$ $\qquad$ $\frac{B_2}{M_2} =$ $\qquad$ $\frac{B_3}{M_2} =$

Note: We can consider skeletal lever systems speed-efficient if SMA $>$ 1.0, since the muscle is moving the bone's end through a greater arc than its own contraction distance. If SMA $<$ 1.0, the lever system is relatively speed-inefficient since the distance moved by the muscle is greater than the movement of the other end of the bone caused by its contraction. With SMA $=$ 1.0, the muscle neither gains nor loses mechanical advantage since the contraction distance equals the bone movement.

How do the above SMA values compare with:

| | | |
|---|---|---|
| $\frac{S_3}{S_1} =$ | $\frac{S_4}{S_1} =$ | $\frac{S_5}{S_1} =$ |
| $\frac{S_3}{S_2} =$ | $\frac{S_4}{S_2} =$ | $\frac{S_5}{S_2} =$ |

*Why should a relationship exist between SMA and the corresponding lever arm ratios? Compare the SMA values for the two muscle insertion positions and foot lengths.*

b. *How does the SMA of a species with its gastrocnemius inserted at position 1 compare with that of a species whose muscle insertion is at position 2?*

c. *Suppose we examine two species whose gastrocnemius muscles insert at an equal distance from the axis of rotation, but whose feet are of different lengths. Which species would have the greater SMA?*

d. *What part of your foot contacts the ground when you want speed (as in running)? Does your leg/foot lever system agree with what would be predicted from your measurements with the kinematic model?*

6. The *work* of a muscle (W) is equal to the force exerted by the muscle (F) times the distance moved by the muscle (M), i.e., the amount of shortening during contraction. Thus, if muscles A and B exert equal forces, but muscle A contracts by 1cm and muscle B by 2 cm, muscle B has done twice as much work as A.

   *Using your data on the muscle force ($F_i$) needed to produce a 2-pound out-force (Table 6.1) and your data on distances moved by muscles at positions 1 and 2 ($M_1$ and $M_2$; section 5), calculate the work performed by muscles ($W = F \cdot M$) at positions one and two in the skeletal lever system. Enter these data in Table* 6.3, *expressed as centimeter pounds.**

   Are these data reasonable?

**Table 6.3.** The work (centimeter pounds) performed by muscles at insertion positions 1 and 2 on the "calcaneus bone".

| | | $F_o$ at Position 3 | 4 | 5 |
|---|---|---|---|---|
| *Gastrocnemius Insertion Position* | 1 | | | |
| | 2 | | | |

**Ideally both measurements should be in metric units. We deviate from this because the only economical spring scales we could obtain measure force in pounds.*

7. How does the FMA compare with the SMA at the various points along the foot/leg lever?
   OF WHAT CONSEQUENCE IS THIS IN PREDICTING THE PROPERTIES OF SKELETAL DESIGN FROM LOCOMOTORY CHARACTERISTICS??

**Analysis of Articulated Vertebrate Skeletons**

Now that you have developed some insight into the physical considerations important in the evolution of endoskeletal systems, you have the opportunity to apply this knowledge to a variety of organisms. The article by Milton Hildebrand ("How Animals Run") should provide some additional background information. The articulated skeletons of a number of different vertebrates: man; fish; frog; snake; turtle; bird; cat; salamander; etc.; are available for study.

*Select one of the specimens for detailed analysis.* Note that you are *not required* to learn the names of the bones for a particular skeleton; bones are named on the figures simply for the purpose of orientation and comparison between organisms. *Carefully examine the lengths and arrangements of the skeletal bones. Also note the prominent "bumps" and "knobs" on each of the bones. These protuberances serve as attachment points (origins and insertions) for the skeletal muscles. Consider what you know about the locomotory and feeding behavior of the species you are studying and the biomechanical principles you have just learned.* For example, a mammal that digs needs to produce a large out-force ($F_o$) at the forefoot when the triceps contracts. Since $F_o = F_iS_i/S_o$, the animal can increase $F_o$ by increasing $F_i$ or $S_i$ or decreasing $S_o$.

What bone movements are necessary to produce the *simple behavioral movements typical of the organism you are examining?*

How would you arrange the skeletal muscles in your animal to produce these movements? Be specific!

**Stimulation of a Frog Skeletal Muscle**

Another method useful in studying the relationships between skeletal systems, muscle arrangements, and movement is to directly stimulate an intact muscle and observe its effects on the animal. *Obtain a frog that has been doubly pithed. Remove the skin from a fore- and hindlimb.* A layer of external connective tissue (fascia) is evident on the surface of each muscle. *With the handle of a dissecting needle, carefully free the gastrocnemius muscle along its entire length. Be careful not to break the origin or the insertion.* In the frog, the gastrocnemius has its origin on the distal end of the *femur* and on the *triceps femoris* muscle. It inserts by the *tendon of Achilles,* which runs along the ankle, to the side of the foot. *Free the Achilles tendon from its* *fascia and note the extreme length of the insertion.* The antagonist of the gastrocnemius is the *tibialis anticus longus,* which is on the front of the calf. *Your teaching assistant will aid you with the electrical stimulation of the muscle preparation.*

*Examine the other muscles of the frog.* What changes in the orientation of the frog's bones are implemented by contractions of the muscles you examine?

Attempt to understand the integrated contraction of muscle groups necessary to enable the frog to turn around, walk, jump, or swim.

**Examination of an Exoskeletal Muscle System**

Arthropods, with exoskeletons, have their muscles attached to the inside of the skeletal system. Would the same mechanical principles that you observed in reference to vertebrates also hold for an arthropod? *Observe the arthropod on demonstration, and* diagram *in the worksheet an exoskeleton lever system with an* extensor *and* flexor *muscle correctly positioned and labeled.*

## BIOMECHANICS

WORKSHEET

Name ______________________

Lab day and time ______________________

Lab instructor's name ______________________

You are now in a position to predict and analyze the properties of leg/ankle/foot lever systems in vertebrates which have become modified during the course of evolution for: (1) producing powerful pushing forces vs. (2) providing rapid locomotory movements.

1. Diagram the foot/leg lever of an animal that has evolved maximum force mechanical advantage (FMA).

2. Diagram the foot/leg lever of an animal that has evolved maximum speed mechanical advantage (SMA).

3. Can one animal show skeletal and muscle adaptations for maximizing *both* force *and* speed at the same time? Why and how?

4. Can animals functionally convert their leg/foot lever systems from high force to high speed systems? How? Give an example.

5. Estimate the SMA for the gastrocnemius/foot lever systems of the three vertebrates shown in the Hildebrand article, using their lever arm ratios. Do these SMA values agree with predictions for these organisms in terms of their requirements for "force" and "speed" efficiency? Show your calculations.

6. Diagram an exoskeleton lever system with a labeled extensor and flexor muscle shown and an arrow indicating the direction of movement during flexion.

## III. Instructor's Materials

### A. Suggestions for an Introduction to the Laboratory

Our general approach to teaching this laboratory has involved a "learn-by-doing" strategy. That is, we do relatively little pre-lab lecturing but, rather, directly involve the students with the materials. Although the written student materials (see previous section) and the article by Hildebrand (1970) should initially provide adequate background for student understanding of this laboratory sequence, it is useful to review several simple concepts. First, since we will be treating skeletons as the simple lever systems that they are, applying some simple concepts from physics will have relevance and give some insight into their evolution. Second, it will be useful to discuss the following terms [with reference to a see-saw (Figure 6.1) to give some added relevance]: in-force, out-force, in-lever arm, out-lever arm, torque, and the "law of the lever". With these basic ideas discussed, students can begin work, although it will be necessary to also present the concepts of *mechanical advantage* and *work* later in the session. As data are collected, the instructor leads a consideration of it, making explicit its biological implications, and helps students answer the questions posed in the laboratory handout. The following section provides suggestions for this phase of the laboratory session.

*Note:* The work with the kinematic model introduces students to essential concepts. The other sections of the article (Analysis of Skeletal Systems and Stimulation of Frog Muscles) are extensions of this work and allow students to use some of the concepts developed with the model. The instructor can decide on the amount of emphasis to place on these sections. Our experience shows that about two hours is required for a thorough session doing the exercises with the model and discussing the results. About one hour can be productively devoted to the skeletal system analysis or stimulation of frog muscle groups.

### B. Suggested Laboratory Activities Involving the Kinematic Model; Answers to Questions Posed in the Student Materials

After a brief review of the physical concepts (as outlined in the preceding section), students should receive their kinematic models (one model per student pair) and begin the procedure section of the student materials.

Answers to questions posed in the procedure section of the student materials are as follows:

1. a. Equilibrium in a lever system occurs when all opposite torques about the joint's axis are equal. Since the moment arms from the axis to positions #2 and 3 are equal, the forces required to produce equilibrium should be approximately equal.

b. Yes. They should verify this.

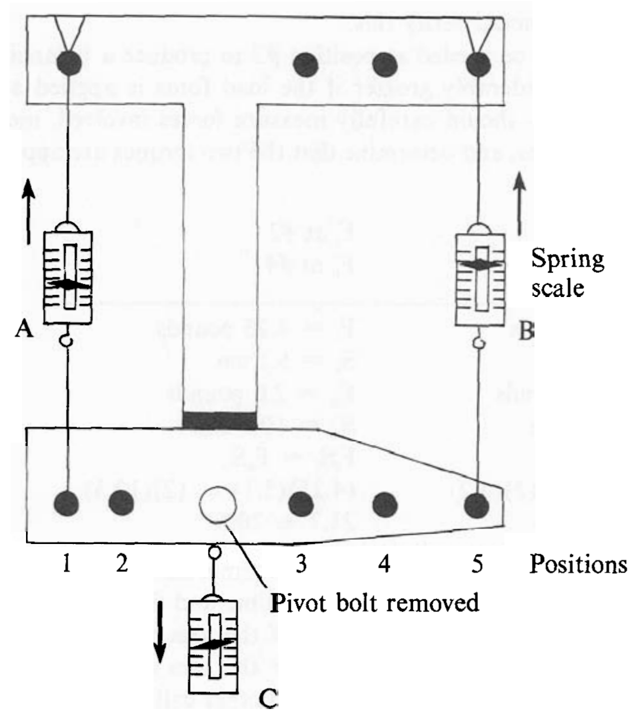
c. Yes. The force needed at position #2 to produce a balancing torque will be considerably greater if the load force is applied at position #4. Students should carefully measure forces involved, measure the moment arms, and determine that the two torques are approximately equal.

| $F_i$ at #2<br>$F_o$ at #3 | $F_i$ at #2<br>$F_o$ at #4 |
|---|---|
| $F_i$ = 2 pounds | $F_i$ = 4.25 pounds |
| $S_i$ = 5.1 cm | $S_i$ = 5.1 cm |
| $F_o$ = 2 pounds | $F_o$ = 2.0 pounds |
| $S_o$ = 5.2 cm | $S_o$ = 10.3 cm |
| $F_iS_i = F_oS_o$ | $F_iS_i = F_oS_o$ |
| $(2)(5.1) \approx (2)(5.2)$ | $(4.25)(5.1) \approx (2)(10.3)$ |
| $10.2 \approx 10.4$ | $21.7 \approx 20.6$ |

d. This exercise demonstrates that the compression forces developing at points of articulation (i.e., base of tibia and fibula) are equal to the *sum* of the forces on either side of the axis producing equilibrium. Thus, with a person's weight over the toes and a balancing force generated by the gastrocnemius and other calf muscles, the compression force generated on the ankle joint may be several times the person's weight. Of course, there are two ankle joints, each bearing only one half the total. This also explains why the articulating ends of limb bones are enlarged and strengthened (you might point this out later when they are examining skeletons). The following diagram should clarify the arrangement of three scales in this exercise.

The easiest way to make measurements is to place the model flat with three scales in position and *with the bolt removed*. While one person firmly holds the upper part of the model down, the other person pulls on the lower scale (C) and reads the three forces generated. $F_c = F_i + F_o$.

2. With reference to Figure 6.3, the comparison between the kinematic model and the leg/ankle/foot system should be evident.




3. a. See the following data (in lbs).
   b. See the following data (in lbs).

| | | $F_o$ at Position 3 | 4 | 5 |
|---|---|---|---|---|
| *Gastrocnemius Insertion Position* | 1 | 1.25 | 2.75 | 4.75 |
| | 2 | 2.00 | 4.25 | 7.25 |

   c. Position 5, for both species.

   Position 3, for both species.

   As indicated in Table 6.1 the force developed by the gastrocnemius to obtain equilibrium increases directly as the distance from the ankle joint axis to the force position increases. *Again, the compression forces which joints are subject to are equal to the sum of the forces on either side of the joint.* In the above example, with $F_i$ at position #1, and 2 pounds at position #3, the compression force would be

1.25 + 2.00 = 3.25 pounds. With $F_i$ at #1, and 2 pounds at #5, the compression force would be 4.75 + 2.00 = 6.75. Cartilage is located between the points of articulation of bones, particularly at joints subject to high compression forces. Because of the elasticity and compressibility of this material in comparison with bone, cartilage helps reduce wear and aids in the absorption of shock.

4. Mechanical advantage is here viewed as a relative measure of input versus output, or "what you get for what you give". Students will discover later, when they calculate muscle work output, that you don't get something for nothing! If a species evolves to maximize force mechanical advantage, a proportional decrease in speed mechanical advantage is simultaneously accrued, and vice versa.

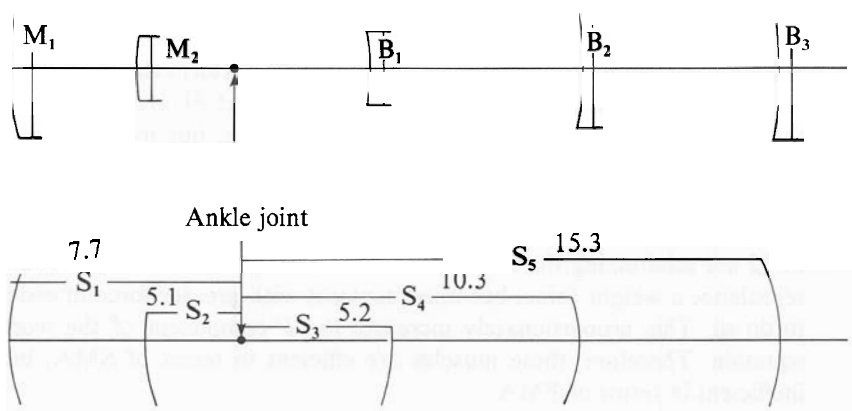
a. See the following data.

| | | $F_o$ at Position | | |
|---|---|---|---|---|
| | | 3 | 4 | 5 |
| *Gastrocnemius Insertion Position* | 1 | 1.60 | 0.73 | 0.42 |
| | 2 | 1.00 | 0.47 | 0.28 |

b. Greatest FMA is achieved with $F_o$ at position #3 for both species.

c. The species with its gastrocnemius inserted at position #1 has the greatest FMA.

5. a. It is important to carefully mark the location of the pivot bolt when making the tracings, since this is needed to determine the moment arms. The following measurements, in cm, and calculations are typical of those collected with our models.



$\frac{B_1}{M_1} = 0.68$ ; $\frac{B_2}{M_1} = 1.34$ ; $\frac{B_3}{M_1} = 2.00$

$\frac{B_1}{M_2} = 1.03$ ; $\frac{B_2}{M_2} = 2.03$ ; $\frac{B_3}{M_2} = 3.03$

$\frac{S_3}{S_1} = 0.68$ ; $\frac{S_4}{S_1} = 1.34$ ; $\frac{S_5}{S_1} = 1.99$

$\frac{S_3}{S_2} = 1.02$ ; $\frac{S_4}{S_2} = 2.02$ ; $\frac{S_5}{S_2} = 3.00$

Since the radius (the S's or moment arms) of a circle determines the length of the arc (the M's and B's), dividing $B_x$ by $M_y$ will produce the same quotients as that obtained by dividing $S_x$ by $S_y$. The concept is important since it allows us to calculate speed mechanical advantages for different skeletal units as moment arm ratios without the necessity of dealing with arcs. SMA is greatest with $F_i$ at #2 and $F_o$ at #5. SMA is least with $F_i$ at #1 and $F_o$ at #3.

b. Toes. Yes!

c. The species with its gastrocnemius inserted at position #2 has greater SMA than the species with its insertion at #1.

d. Species that, under *these conditions*, have longer feet will have greater SMA.

6. Consider the following data (in cm-lbs).

| Gastrocnemius Insertion Position | $F_o$ at Position 3 | 4 | 5 |
|---|---|---|---|
| 1 | 6.6 | 14.6 | 25.2 |
| 2 | 7.0 | 14.9 | 25.4 |

With a fixed weight force, muscles inserted at #1 perform the same work as muscles inserted at #2. Muscles with insertion at #1 are minimizing the *force* needed to counterbalance a weight force, but must contract through a greater distance, therefore proportionately increasing *M* in the work equation (F × M = W). These muscles are efficient in terms of FMA, but are less efficient in terms of SMA. Muscles with their insertion at #2 are minimizing the contraction distance required in order to counterbalance a weight force, but must contract with greater force in order to do so. This proportionately increases the *F* component of the work equation. Therefore, these muscles are efficient in terms of SMA, but inefficient in terms of FMA.

7. FMA *increases* and SMA *decreases* with an increase in the distance from the pivot point to the muscle's insertion. FMA *decreases* and SMA *increases* with an increase in the distance from the pivot point to the location of the weight force. *We would, therefore, predict that species requiring rapid locomotion should have their locomotory muscles inserted close to the pivot points of the leg joints and also that these species should have relatively long leg bones.* In reference to the first point, bony processes for the insertion of locomotory muscles (such as the calcaneus) should be relatively short. The reverse should be true for species not requiring rapid locomotion, but instead needing the ability to move heavy objects (such as their own weight). These animals should have long bony processes for muscle insertion and relatively short limb bones.

**C. Suggested Approach to Analysis of Articulated Vertebrate Skeletons**

In this part of the laboratory, students are asked to examine several different skeletal systems and consider the sizes, shapes, and arrangement of bones in reference to what they know about the feeding behavior and locomotory behavior of the animal. Extensive interaction with student groups during this section is required. Our laboratories usually have a minimum of five different vertebrate skeletal systems on display: (1) human, (2) frog, (3) cat, (4) chicken or pigeon, and (5) snake, bat, salamander, turtle, fish, or horse. As an aid to students in their comparison of different skeletal systems, supplemental diagrams of the main vertebrate bones are provided in their laboratory text or on posters in the laboratory.

Although we explain that attempts to apply mechanical principles to the body based only on an examination of skeletal systems must be done with caution, we ask students to consider a specific movement (i.e., walking, jumping) and speculate on what muscle arrangement would be required by the animal in order to perform the behavior. In addition, we explain that adaptations of the whole organism are involved in its locomotory ability. As discussed in Hildebrand, the speed of the cheetah depends not only on its long (digitigrade or "fingerwalking") feet, but also on a supple, flexible spine and rotational ability of the pelvic and pectoral girdles. In preparation for your discussions, the references listed in the bibliography, and specifically the book by Gans (1974), titled *Biomechanics—an Approach to Vertebrate Biology*, should be helpful.

A good approach to this phase of the laboratory is to assign student groups to the various skeletons and to ask them to prepare an end-of-the-lab presentation discussing adaptations shown by their skeleton in relation to concepts learned with the kinematic model. We have found that this approach stimulates students to thoroughly analyze their skeletal system and helps them link the physical concepts learned with the model to the biology of locomotion and feeding behavior.

### D. Electrical Stimulation of Muscles of a Skinned, Pithed Frog

This segment of the laboratory work can be very useful in helping students appreciate the complex, integrated action of muscle groups needed to produce simple movements. It can be done as a demonstration by the instructor in about 15–20 minutes or more actively involve students for one hour. One frog and stimulator per pair of students are adequate in the latter case. Because the muscles are bigger, larger-size frogs (at least 3 inches, snout-to-vent) make it easier to stimulate specific muscles without cross-stimulating adjacent muscles.

After the frog is doubly pithed, the skin should be carefully removed from one fore- and hind-leg. We use a Grass Instruments stimulator (model S5) but any similar square-wave stimulator is adequate. We have found that a stimulus of 10 to 40 volts (depending on the preparation) with a duration of about 10 milliseconds and a frequency of 10 pulses per sec is best. The stimulator can be used to determine the action of specific muscles (flexor, extensor, adductor, abductor) and to identify which muscles form synergist and antagonist groups relative to a bone lever system. A detailed examination of the actions of the many small muscles of the foreleg and forefoot are particularly impressive. Students should consult an articulated frog skeleton to understand where the muscles they stimulate have their origins and insertions and make predictions on their actions. To better see the action of a muscle when it is stimulated, hold the bone on which it has its origin in a fixed position. This will allow the muscle to produce maximum movement of the bone on which it inserts. Keep the frog well moistened with frog Ringer's solution (7.5 g NaCl, 0.35 g KC1, 0.21 g $CaCl_2$ in 1.0 liter water).

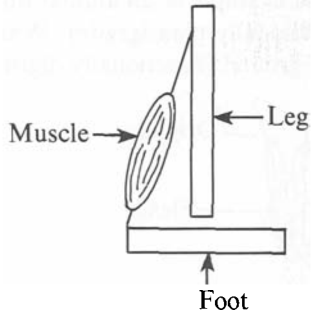
### E. Examination of an Exoskeleton Muscle System*

A preserved, dissected crayfish, lobster, or crab with some labeled extensor and flexor muscle groups is placed on demonstration. Good preparations can usually be made of the muscles in the abdomen and/or cheliped. For a comprehensive description of the biomechanics of chelipeds, see Brown *et al* 1979.

*(for methods to use in stimulating hindleg flexor and extensor muscles of a live grasshopper see the Chapter in this volume by Carlson, *et al*-eds. note).

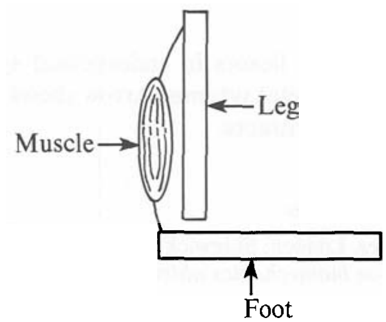
## IV. Biomechanics Worksheet Answers

1.




Long calcaneus
short foot

2.




Short calcaneus
long foot

3. Yes. In theory, by having two sets of muscles, each inserted on different parts of the same bone, one could have the "best of both possible worlds." In fact, this is quite common (see the article by Hildebrand and his discussion of the vicuna). The speed efficient muscle would have its insertion close to the joint. The force efficient muscle would be inserted at a greater distance from the joint. This arrangement allows "gear shifting."
4. The lever arms are measured directly from the figure in the Hildebrand article (1970).

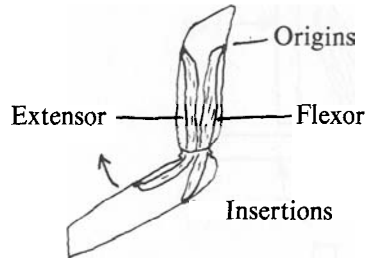
*SMAs:* Deer—$\frac{S_5}{S_1} = \frac{7.1 \text{ cm}}{1.2 \text{ cm}} = 5.92$

Dog—$\frac{S_5}{S_1} = \frac{4.5 \text{ cm}}{0.9 \text{ cm}} = 5.00$

Badger—$\frac{S_5}{S_1} = \frac{3.4 \text{ cm}}{0.9 \text{ cm}} = 3.78$

The deer, being a fast-running mammal, should possess limbs showing greater SMA. This would be true, to a lesser extent, for the dog. The badger, being a digging mammal, requires a certain amount of FMA and thus a reduction in SMA.

5. Yes, by varying the location of the fulcrum from directly under the ankle to the toes. The kangaroo is a good example of an animal that loafs and walks on the flat of its feet (functionally plantigrade). While running, only the tips of the toes touch the ground (functionally digitigrade).
6.




Note: The position of extensors and flexors in endoskeletal systems is reversed from their position in exoskeletal systems. Arrow shows direction of segment movement when flexor contracts.

**References**

Alexander, R. McN. *Animal Mechanics.* London; Sidgwick and Jackson; 1968.

*An interesting readable text on biomechanics which covers both vertebrates and invertebrates.*

Brown, S. C.; Cossuto, S. R.; Loos, R. W. Biomechanics of Chelipeds in some decapod crustaceans. *J. Zool.* Lond. 188:143–159; 1979.

*One of the few recent studies on the biomechanics of organisms with exoskeletons.*

Gray, J. *How Animals Move.* Cambridge, MA: Cambridge University Press; 1953.

*A classic review of animal locomotion. More elementary than his next book. (see below).*

Gray, J. How fishes swim. *Scientific American* 197(2): 48–54; 1957.

*A general comparison of swimming in fish, whales, and dolphins.*

Gray, J. *Animal Locomotion.* New York: W. W. Norton; 1968.

*An updated more comprehensive review of the application of mechanics to locomotion. Excellent source on fishes, amphibians, snakes and birds. Extensive bibliography.*

Gans, C. How snakes move. *Scientific American* 222(6): 82–96; 1970.

*An interesting description of locomotion without appendages.*

Gans, C. *Biomechanics, An Approach to Vertebrate Biology.* Philadelphia, PA: J. B. Lippincott Co.; 1974.

*Good review of principles. Mostly a detailed coverage of the biomechanics of locomotion and food gathering of reptiles, especially snakes.*

Glase, J. C. and Zimmerman, M. C. Mechanical analysis of vertebrate skeletal systems. Glase, J. C.; Ecklund, P. R.; Houck, M. A. eds. *Investigative Biology.* Denver, CO: Morton Publishing Co; 1980: 317–348.

*An introductory biology laboratory text with an investigative approach.*

Hildebrand, M. How animals run. *Scientific American* 202(5): 148–157; 1960.

*Especially good background material for this laboratory. Discusses adaptions of the skeleton and muscles that increase speed of running in mammals, notably horses and cats. We require our students to read this article before they come to the laboratory.*

Hildebrand, M. *Analysis of Vertebrate Structure.* New York: John Wiley and Sons; 1974.

*An excellent readable test in comparative anatomy. Contains eight chapters on locomotion of vertebrates.*

Napier, J. R. The antiquity of human walking. *Scientific American* 216(4): 56–66: 1967.

*Includes some of the classic photographs of human movement by the photographer Eadweard Maybridge.*

Napier, J. R. Primate locomotion. *Oxford biology Reader #41*. London: Oxford University Press: 1976.

*Available from Carolina Biological Supply Co.*

Pennycuick, C. Animal flight. *Studies in biology #33*. London: Edward Arnold Publ.; 1972.

*Good comparison of bird and bat flight.*

## APPENDIX I

### *Construction of the Kinematic Model*

The kinematic model is constructed from three pieces of $2\frac{3}{16}$″-x-¾″ pine (see Figure 6.9). Both the top and "foot" are 10″ long and connected by a 16¾″ "leg". The top is fitted to the "leg" by two nails after a $2\frac{3}{16}$″-x-⅜″ section is cut out. The "foot" is connected to the "leg" by a 1½″-x-¼″ bolt.

Five holes are drilled into the "foot" at a height of ¾″ and distances from the "heel" of ½″, 1½″, 5½″, 7½″ and 9½″, respectively. To allow mobility of the "foot" in the "ankle" region, a ⅜″-deep, "V"-shaped (1¼″ bottom, 3¼″ top) groove is cut from the back. The "toe" and "heel" ends of the groove are cut at angles of 30° and 20°, respectively. In order to fit the "foot", the lower end of the "leg" is rounded and a 3″-x-⅜″ piece cut from the front. When operational, five 2″ paper clips are fastened to the eye screws. To perform the exercises described in the laboratory, three Zebco De-Liar (Model 208; obtained from Fredon Wholesale Co., 1912 Teall Ave., Syracuse, NY 13206, phone 315-463-0464) fish weighing scales are required per model. The hook of a fish scale is connected to a paper clip and "force" applied by pulling on a piece of string connecting the scale to a hook in the top piece of the model. We recommend that each pair of students have access to a model.

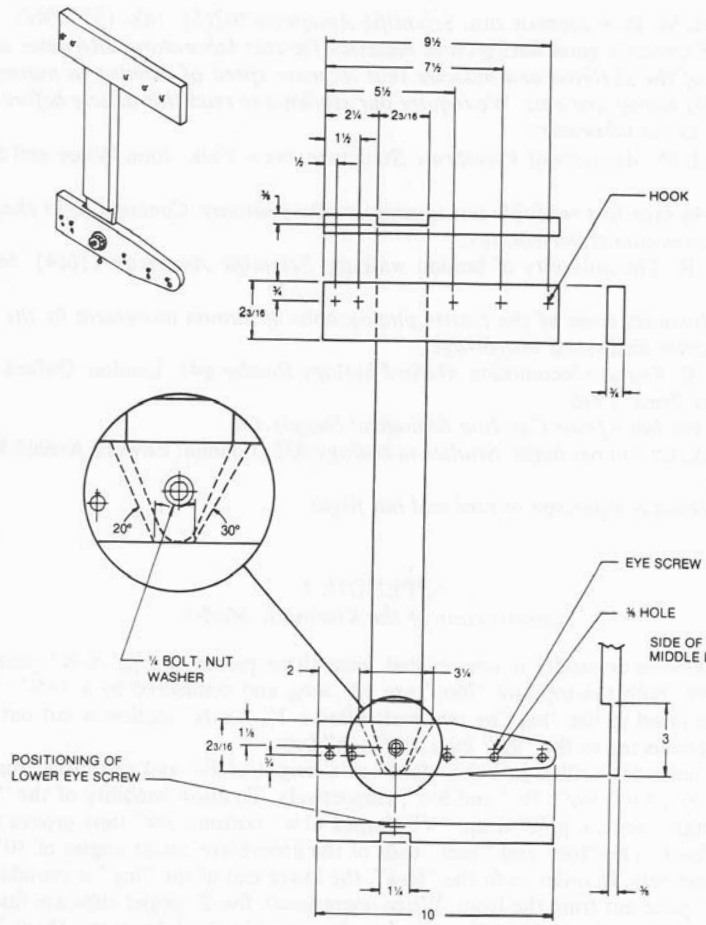



**Figure 6.9.** Plans for construction of the kinematic model.