other valleys in the Catskills,[8] however, it was partly filled with debris by the continental glacier, so that now the Saw Kill, for the first five miles of its course, has cut its way through a moraine of varying height, 70 ft. at Shady, and 40 ft. half a mile below its source. This fact is clearly shown by the character of its bed, which is strewn with huge bowlders of bluestone, sandstone and conglomerate, together with smaller ones of granite and quartz, the harder ones still showing the marks of glacial action.

Echo Lake[9]

Echo Lake, the only considerable body of water near Overlook, is clearly of glacial origin. It is a shallow pond, about three hundred yards long by two hundred wide, and about eighteen feet deep in the deepest part, situated in the angle formed by the Plattekill and Overlook Mountains, just at the base of the high ridge connecting them. Across this deep valley, the moraine forms a huge natural dam which holds back the water of Echo Lake. The lake is thus bordered on three sides by high wooded ridges; while on the west, extending out over the moraine, is a swamp larger than the lake itself.

As is to be expected from its situation, Echo Lake is apparently decreasing in size rather rapidly. The swamp on its western side is slowly invading its waters. On this side, too, the lake is being narrowed by the action of its outlet, the Saw Kill, in cutting back through the Glacial drift which forms its bed. The pitch of the Saw Kill, which falls 1200 feet in the first four miles of its course, together with the floods mentioned above, makes this erosion relatively rapid.

In addition to this cutting away on its lower side, the lake is being rapidly filled in from above. The silt and leaf mold washed from the steep mountain ridges above the lake are deposited in the still water, and the amount of this material is very considerable. On the north and east this deposit forms a bed extending into the lake for more than two hundred feet and reaching a depth of four or five feet. Here the deposit is, to a considerable extent, protected from further action of the water by a dense growth of the yellow pond lily, *Nymphæa advena*, for which the fine silt and leaf mold furnish a favorable substratum. The combined effect of these agencies in reducing the size of the lake is so great as to make it probable that, at no very distant date, Echo Lake will be obliterated.

Washington, D. C.

[8] John C. Smock: "On the Surface Limit or Thickness of the Continental Glacier in New Jersey and Adjacent States." Am. Jour. Sci., vol. 25, pp. 339-350. 1883.

[9] Also known as Sheu's Lake.

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NOTES ON THE PRINCIPLES OF QUADRUPEDAL LOCOMOTION AND ON THE MECHANISM OF THE LIMBS IN HOOFED ANIMALS

By William K. Gregory

CONTENTS

Introduction

The movements and locomotive mechanisms of animals were the subject of a classic work by Borelli in 1680, entitled "De Motu Animalium . . ." The chief pioneers of modern research were the brothers Weber (Eduard and Wilhelm), authors of "Die Mechanik der menschlichen Gehwerkzeuge," Göttingen, 1836. Marey, the author of the handbook on "Animal Mechanism"[1] (1874), invented elaborate apparatus for analyzing and graphically recording the movements of the limbs of men and animals, while more recently the mathematics of human locomotion have been developed by O. Fischer and others. General reviews of animal mechanics and of human locomotion are given by Marey,[2] Haycraft[3] and Luciani.[4] A very able analysis of the mechanism of locomotion in the horse is given in "The Horse in Motion," by J. D. Stillman,[5] while the extensive series of photographs by Muybridge[6] record the actual positions of the limbs and body assumed in motion by ungulates and other animals.

None of the above mentioned works considers the subject from the evolutionary point of view. Ryder,[7] and especially Cope,[8] pointed out certain adaptations in the feet of ungulates, such as the reduction of the digits in the "Diplarthra" and the so-called displacement of the metacarpals, and Cope used these observations in his argument for the hypothesis of the transmission of acquired characters. He also made the following very important observations:[9]

"In animals which leap, the distal segments of the limbs are elongated; in those which do not leap, but which merely run or walk, it is the proximal segments of the limbs which are elongated.

"Animals which run by leaping are divided into those which run and leap with all fours, as Diplarthra, and those which run and leap with the posterior limbs only, as the jerboas and kangaroos. In both types, the distal segments of the hind limbs are elongated, and in the Diplarthra, those of the fore limb also.

"Animals which do not leap in progression (elephants, Quadrumana, bears) are always plantigrade and have very short feet but elongate thighs and mostly tibias."

[1] 12mo. London, 1874.
[2] *Op. cit.*
[3] E. A. Schäfer: Text book of Physiology. Edinburgh and London. pp. 228-273, 1900.
[4] Physiologie des Menschen . . . Ins Deutsche übertragen and bearbeitet von Dr. Silvestro Baglioni und Dr. Hans Winterstein . . . Siebente Lieferung. Jena, 1906.
[5] Executed and published under the auspices of Leland Stanford, 4to, Boston, 1882.
[6] Animals in Motion . . . Third Impression 4to, London, 1907.
[7] Am. Nat., vol. 11, p. 607. 1877.
[8] "The Mechanical Causes of the Development of the Hard Parts of the Mammalia." Journ. of Morphology, vol. 3, pp. 137-290. 1889.
[9] *Ibid.*, p. 151.

Cope neglected to follow up the important mechanical and adaptive corollaries of these facts. He merely drew the very questionable inference that "those elements which receive the principal impact in progression are those which increase in length [in phylogeny]."[10]

In his paper on "The Angulation of the Limbs of Proboscidia, Dinocerata, and other Quadrupeds, in Adaptation to Weight," Osborn[11] concluded that

"The straightening of the limb [in the Dinocerata, Proboscidia, etc.] is an adaptation designed to transmit the increasing weight through a vertical shaft. Correlated with it are the shifting of the facets into the direct line of pressure and the alteration of their planes from an oblique to a right or horizontal angle with relation to the vertical shaft."

Gaudry,[12] in describing the limbs of extinct South American ungulates, endeavored to show how the pose of these animals could be inferred from a study of the facets,—an idea which had been previously advanced by Osborn.[13] Gaudry also designated as "rectigrade" the pose of elephants and similar heavy forms which stand with straightened limbs and toes, resting the weight chiefly on the pad.

The marked contrasts in the limbs and musculature between the slow-moving heavy-bodied ungulates and the slender swift-footed or cursorial types in various phyla, constitute a subject which will be discussed in considerable detail in the monograph on the Titanotheres by Professor Osborn. At his suggestion, the following notes, forming a part of the present writer's studies on this subject, are now published, together with some of the drawings which have been made by Mr. Erwin S. Christman, under the direction of the writer, for the monograph above mentioned. The writer is also indebted to Dr. W. D. Matthew for valuable criticisms and suggestions.

Limbs regarded as Compound Levers

The simple principle that the limbs of quadrupeds are compound levers and that the relative lengths of the upper, middle and lower segments are adapted to specific loads, muscular powers and speeds, although well understood by students of human and equine locomotion, has apparently not hitherto been applied to elucidate the adaptive contrasts between cursorial and "graviportal"[14] ungulates.

[10] *Loc cit.*
[11] Am. Nat., vol. xxxiv, pp. 89-94. 1900.
[12] "Fossiles de Patagonie. Les Attitudes de quelques Animaux." Ann. de Paléontologie, tomei.
[13] "Patriofelis and Oxyæna restudied as Terrestrial Creodonts." Bull. Amer. Mus. Nat. Hist., Vol. 13, pp. 270, 271. 1900.
[14] This word has been invented by Professor Osborn to describe the conditions in heavy-bodied animals with long proximal and short distal limb segments.

Evolutionary Stages of Quadrupedal Locomotion

In the Stegocephalian stage of quadrupedal locomotion, the short limbs were held widely outward from the body, the humerus and femur were very short and the feet were spreading and flat. Crawling was effected in part by a sharp downward pull of a proximal segment (humerus or femur), thus tilting the body upward on the same side and throwing the weight on the opposite foot. The long axis of the body was meanwhile thrown into alternate lateral curves, the advancing fore limb being on a convexity, the advancing hind limb on a concavity.

In the late reptilian or early mammalian stage, the feet were brought around partly under the body, the elbow and knee began to be drawn in, the scapula was rotated backward as the coracoid lost its connection with the sternum, and the body became well raised off the ground. According to a hypothesis advanced elsewhere by the writer,[15] this process was associated with the acquisition of climbing, or semi-arboreal, habits, structural vestiges of which remain in the partly divergent first digit and many other characters of early Eocene mammals.[16]

The Lower Eocene ancestors of the various orders of ungulates had probably all long since passed through these earlier stages of quadrupedal terrestrial locomotion, and at that time many of them had perhaps become more or less digitigrade. The primitive "Protungulates," *Meniscotherium*, *Periptychus*, *Pantolambda*, may give us some idea of what the several ancestors of the subungulate series (Hyracoidea, Embrithopoda, Proboscidea, Amblypoda) may have been like. They also preserve apparent traces of arboreal ancestry in the relatively short, spreading hands and feet, long limb bones, the humerus with large entocondyle and entepicondylar foramen, the undiminished power of pronation and supination of the forearm and many other characters. The Basal Eocene *Euprotogonia*, the ancestor of the Condylarth *Phenacodus*, with slender subunguligrade feet, represents a more advanced stage of evolution, in the direction of the Perissodactyls.

Factors of long-distance Travelling Power in Ungulates

The primitive ungulates of the Lower Eocene were doubtless surrounded by environmental conditions which set the premium of survival upon improvements in long-distance travelling power and in speed. These improvements have been attained in various ways and in the most

[15] "The Orders of Mammals," Bull. Amer. Mus. Nat. Hist., Vol. 27, p. 226, 1910.

[16] Matthew: Arboreal Ancestry of the Mammalia, Amer. Nat., Vol. 38, 1904, pp. 811-818.

diverse lines of evolution,—in the elephant no less than in the antelope. The general factors of long-distance travelling power may be grouped broadly under the headings: (A) Endurance and (B) Speed.

A. Endurance

Endurance may be measured either by (1) the length of time an ungulate can keep in motion without rest or refreshment, or by (2) the amount of reserve strength left after a stated expenditure of energy, or by (3) the relative quickness of recuperation. Endurance increases with practice. As metabolism increases, the muscles, lungs, heart and other organs of the thorax become stronger and larger.

More rapid metabolism requires more food and larger digestive apparatus. Although the Lamarckian hypothesis in its crude form is very probably untenable, it is a fact that herbivorous animals have longer and heavier digestive tracts than carnivores. Moreover, as fast as the dentition has become adapted for the harder, less nutritious kinds of food, the digestive apparatus must have become more complex and much heavier.

While the enlarging thorax and abdomen have made available a great increase in energy, they have caused an even more rapid increase in total weight.

With increasing total weight, the internal and external resistance to be overcome in locomotion also rises, and hence the margin between the total energy available and the energy required in progressing a given distance is lessened. In other words, endurance, the first great factor of long-distance travelling power, is directly proportional to the efficiency of the adaptations for minimizing the waste of energy.

Adaptations for minimizing waste of energy

Higher efficiency in locomotion has doubtless been attained, first, by advantageous modifications of the organs of propulsion (such as are described below), secondly, by improvements in the supporting framework, thirdly, by improvements in the methods (*a*) of conserving the inertia of forward motion, (*b*) of taking up shock, (*c*) of preventing dislocation and (*d*) of minimizing lost motion.

Momentum.—The shocks and strains to which the locomotive apparatus is subject vary with the momentum of the body in motion. Hence as momentum is the product of mass by velocity, the shocks and strains experienced by heavy animals in rapid motion are very great, and devices for lessening them become conspicuous.

Propulsion and the center of gravity.—"Perfect quadrupedal locomotion," says Stillman,[17] "requires uniform support to the center of gravity (of the whole animal) and continuous propulsion by each extremity in turn." In walking and running, by the straightening or extension of the limbs, the center of gravity is raised and thrown in advance of the centers of support. The body thus falls forward, the center of gravity describing a curve of greater or less convexity, the forward motion being accelerated by the thrust of the propelling limb.

The first shock of the downward fall in the running horse is taken up by the forwardly stretched and slightly bent hind limb (Fig. 1) placed beneath or in advance of the center of gravity; the gradually stiffening muscles of the thigh and back checking the downward momentum (Stillman, p. 91). The rearing muscles thus come into play and serve to let the fore part of the body down gently.

Dislocation of the fully extended forelimb in landing is prevented partly by (*a*) the crutch-like action of the limb itself (which is slung from the converging fibers of the serratus magnus attached to the top of the scapula) and by (*b*) the contraction of certain muscles of the shoulder, neck and back (Stillman, pp. 61, 62, *et seq.*). To these arrangements and conditions, Stillman attributes the absence of the clavicles in the horse.

The center of gravity in the smoothly trotting horse describes a relatively flat trajectory, whereas in the "bounding" movement, or gallop, the center of gravity ricochets and the trajectory consists of a series of cycloids of marked convexity. This mode of locomotion, while very rapid for short distances, is too wasteful for heavy-bodied animals, which require a relatively flat trajectory and a maximum saving of inertia.

Sinuous movement of the body in running.—By the bending backward of the pelvis, first on one side and then on the other, the thrusts of the femora are brought more nearly into line with the anteroposterior axis, while wrenching of the pelvis is prevented by the contraction of the longissimus dorsi of the opposite side (Stillman, p. 36). By this means also, the length of the stride is directly increased. The same sinuous motion of the body is associated with the "figure-of-8" movement of the limbs noticed by Pettigrew.[18]

In this connection may be noted also the devices for avoiding "interference" of the limbs (*e. g.*, "stifle action" of the iliacus, preventing the knee from striking the abdomen; oblique trochlea of the astragalus carrying the advancing foot around its fellow of the opposite side). Dislocation

[17] *Op. cit.*, p. 87.

[18] Animal Locomotion, p. 39. 12mo. New York, 1874.

is provided against not only by the ligaments, but also by the metapodial keels, by the grooved trochlea of the astragalus, by the cnemial crest of the tibia, etc.

Spiral configuration of limb bones and of articular surfaces.—Goodsir, Pettigrew[19] and others have shown that the articular surfaces of the elbow, ankle and calcaneo-astragalar joints are spirally warped surfaces which act after the manner of screws. The limbs as a whole also are twisted levers with the ridges and muscles arranged spirally. "This arrangement," says Pettigrew, "enables the higher animals to apply their traveling surfaces to the media on which they are destined to operate at any degree of obliquity so as to obtain a maximum of support or propulsion with a minimum of slip. If the traveling surfaces of animals did not form screws structurally and functionally, they could neither seize nor let go the fulcra on which they act with the requisite rapidity to secure speed, particularly in water and air."

Lost motion.—Lost motion through backward slipping of the foot upon the ground is provided against in the horse by the form and details of the hoof, and in the elephant by the plantar pads.

Pendulum action of the limbs.—The brothers Weber held that in rapid locomotion the limbs swing freely as pendula, but Marey and later investigators, according to Luciani,[20] hold that the natural swing of the leg is very largely damped and controlled by the flexor muscles. In favor of the view that there is some measure of analogy to the pendulum, we observe that in the horse, the center of gravity of the limb, corresponding to the "bob" of a pendulum, is relatively proximal in position, and this is associated with rapid oscillation of the limb, whereas in the elephant, the center of gravity of the limb is farther down the shaft, and here we have a slower oscillation of the limb. It will be observed that while the body is moving forward, the propelling limb is moving backward, and its own backward momentum, due to weight alone and to the pull of the extensors, must be overcome by the forward pull of the flexor muscles and by the forward pull of the body as a whole. Hence the heavier the limb, the greater the force expended in overcoming and reversing the momentum of each limb at the end of each stride.

SPEED

The speed of a quadruped or biped in motion is measured by the product of the length of the stride into the rapidity of the stride.

[19] Animal Locomotion, pp. 23-24, 28, 29. 1874.

[20] *Op. cit.*, p. 126.

The diverse adaptations in the limbs, considered as compound levers, are related to either or both of the factors, "length of stride" and "rapidity of stride."

LENGTH OF STRIDE

Length of limb.—Length of limb is the first factor of length of stride. It is generally proportional to height at the shoulders and hips. Length of limb has been attained in cursorial animals by lengthening the lower and middle segments of the limb, in graviportal animals by lengthening especially the proximal segments of the limb.

Angle of stride.—Angle of stride is the second factor. It is measured by the arc described by the lower end of the femur or humerus in swinging from the position of extreme extension to that of extreme flexion. A wide angle of stride not only lengthens the stride, but also enables each limb, first, to be placed in turn below or beyond the center of gravity in order to secure more continuous support for the center of gravity, and, secondly, it enables the propelling limb to exert its propulsive effort for a relatively long period.

Acceleration increment of stride due to ballistic power of limbs.—Those portions of the stride that are due simply to the length of the limb and to the angle of the stride might, if determined, be illustrated by moving the inert limbs of a dead animal suspended in the air. In the slow walk of a biped, the successive positions of the legs might for our purposes be represented by a series of inverted V's (/\/\/\/\/\/\ ) with the lower ends touching. Each /\ represents a single step and two successive /\'s represent a stride. In the rapidly moving animal, however, the stride receives a very considerable increment, due to the impetus imparted by the propelling limb and to the forward motion of the body as a whole, which carries the forwardly moving foot to a position far in advance of its own unaided reach. This "acceleration increment," as it may be called, increases with the velocity of the movement and is proportional to what we may designate the ballistic power of the limb. This ballistic power may be defined as excess propulsive power over and above that which is necessary to move the limbs as stilts and to support the weight of the body; it is expended in lengthening the stride. Ballistic power and the acceleration increment of the stride are measured by the length of time at least three of the feet are off the ground together during a single stride of a quadruped running at full speed. In Fig. 1, representing an elephant in rapid motion (ambling), it will be observed that three of the feet are never off the ground at the same instant; whereas Stillman's Figs. 2-10 show a galloping horse in which at least three of the feet are

off the ground at once in seven out of nine phases of one stride. The same figures show that the elephant has three feet on the ground together during five-sixths of one stride, and during the remaining sixth the body is supported by one fore foot and the opposite hind foot, whereas the horse in question never has three feet on the ground together during the stride there pictured. Thus it will be seen that the "acceleration increment" of the stride and the ballistic power of the limbs are at a maximum in cursorial animals and at a minimum in graviportal animals. The "acceleration increment" will no doubt increase also with the potency of the psychic motive and of the neural stimulus (cf., p. 282).

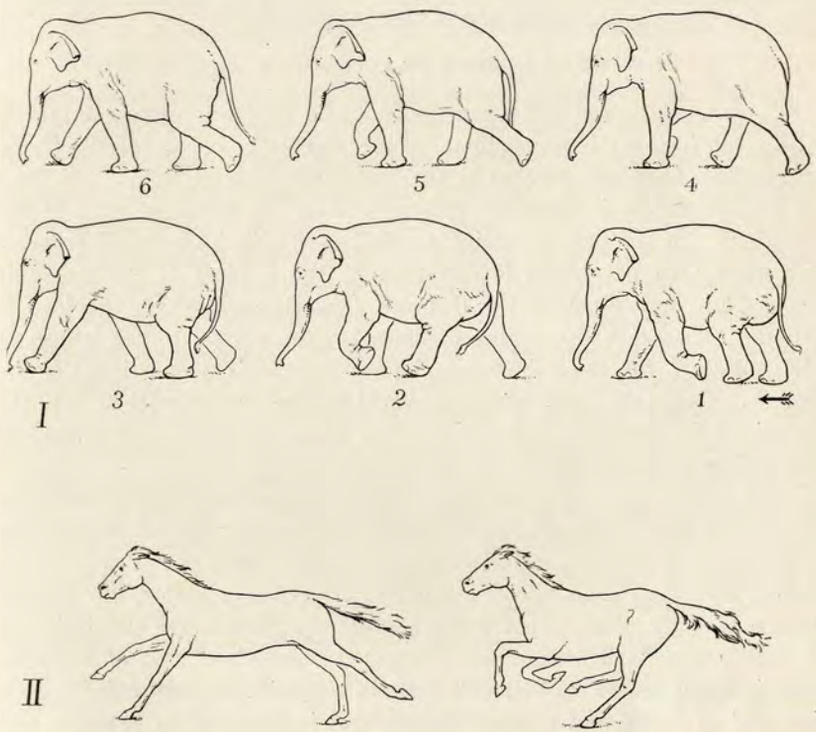

FIG. 1.—*Graviportal and cursorial modes of locomotion contrasted in the amble of the elephant (I) and gallop of the horse (II)*

I after Muybridge; II after Stillman

In brief, the factors of length of stride are (1) length of limb, (2) angle of stride, (3) acceleration increment.

RAPIDITY OF STRIDE

Rapidity of stride, the second major factor of speed, is determined by the rate of oscillation of the limbs, especially of the proximal segments. The conditions determining rapidity of stride are discussed below (p. 281).

MECHANICAL AND PHYSIOLOGICAL RELATIONS OF POWER AND SPEED IN THE LOCOMOTIVE APPARATUS

CONTRACTILE FORCE OF LOCOMOTIVE MUSCLES

The contractile force of a muscle (*i. e.*, its ability to overcome inertia at a given instant) is proportional to the number of its contractile fibers, when these fibers are parallel to the direction of contraction. The force of such a muscle is therefore proportional to the sectional area of the muscle.[21] In the case of weights lifted vertically by isolated muscles, the work (W) performed is measured by the product of the muscular force (F), multiplied by the distance (D) through which the load is lifted[22] ($W = F \times D$). This distance is proportional to the length of the muscle,[23] for the "shortening" of a muscle is proportional to its length. Hence the total work performed will be proportional both to the length of the muscle and to its sectional area, and hence to the mass or the weight of the muscle.[24]

The work performed by a long muscle is greater than that of a shorter one of the same sectional area.[25] Long and slender muscles such as the sterno-mastoid and the sartorius of man exert a small power over a long range; short and thick muscles such as the pectoralis major, the glutæus maximus or the temporalis develop a relatively great power multiplied by a short range.[26] The contractile force of muscle per unit of sectional area is much less in cold-blooded than in warm-blooded animals.[27] It is lessened by disuse and extreme fatigue and is increased by exercise, and hence is dependent upon the nervous system and general systemic conditions.

The contractile force is inversely proportional to the number of connective tissue fibers mingled with the striped muscle fibers. Hence muscles grade into tendons and ligaments. When a muscle is stretched,

[21] HAYCRAFT in Schäfer's Text book of Physiology, p. 242.
[22] *Ibid.*, p. 245.
[23] *Ibid.*, p. 244.
[24] *Ibid.*, p. 246; also Marey, p. 62. 1874.
[25] HAYCRAFT, p. 246.
[26] MAREY, p. 62.
[27] HAYCRAFT, p. 243.

it serves partly as a ligament. All muscles *in situ* are stretched to a certain degree, and thus act as ligaments.[28] "Over extension" of the muscle is prevented by the inextensible connective tissue fibers.[29] According to Stillman,[30] the length of the muscles cannot be increased by exercise, otherwise the tension necessary to prompt action would be lost.

The contractile force is highest when a muscle is stretched to its full "physiological length" (that is the greatest length it ever assumes during life). As shortening takes place, the contractile force becomes less and less (Haycraft).[31]

Contractile force and speed of movement augmented by "hold and let go" arrangements.—Fick and Helmholtz showed[32] that the greatest force and velocity of contraction are developed when the movement of the muscle is checked during the initial stages and when the resistance is suddenly diminished.

Amount of contraction.—The shortening of individual muscles is in general proportional to their length when in repose, but different investigators give somewhat different estimates. "While Weber described a muscle as shortening 70 per cent. of its length, when unweighted, more recent observers incline to put the shortening at 20 to 30 per cent. of its length" (Haycraft).[33] Marey[34] estimates "the mean shortening of a muscle while contracting, when it is not detached from the animal," as "about a third of its length when in repose." Bishop's estimate is one-fourth (Stillman, p. 31). "When the fibers are not parallel, but obliquely set, as in the gastrocnemius, we have a greatly extended transverse area of muscular fibers, which act therefore very powerfully, though, on account of their short length, they can exercise their pull but a comparatively short distance" (Haycraft).[35]

THE "ANGLE OF INSERTION" AND THE PRINCIPLE OF THE PARALLELOGRAM OF FORCES

In Fig. 2 (I), let AC represent a rod free to rotate around the point A in the direction CC′; let BD represent a contractile spring fastened at D, inserted on AC at B and forming the angle ABD (a). Assume that the length of BD is proportional to its contractile force; then from

[28] *Ibid.*, p. 245.
[29] *Ibid.*, p. 242.
[30] *Op. cit.*, p. 32.
[31] *Op. cit.*, p. 242.
[32] HAYCRAFT, *op. cit.*, p. 248.
[33] *Op. cit.*, p. 244.
[34] *Op. cit.*, p. 62.
[35] *Op. cit.*, p. 242.

the principle of the parallelogram of forces, we may resolve BD into two forces, the first AB acting in the direction of the rod AC and tending to press AC against its fulcrum A, the second component BR acting at right angles to the first and tangent to the arc of rotation BB′. The first component AB may be called the "centripetal component," the second BR may be called the "rotation component." In Fig. 2 (II), the contractile spring *bd* is of the same length as before, but the angle of

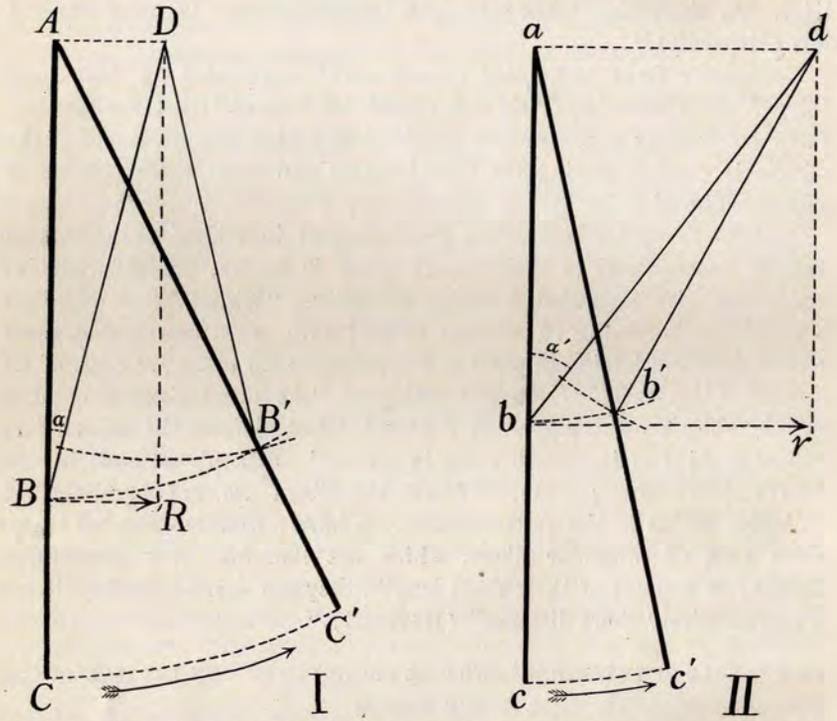

FIG. 2.—*Diagram illustrating the direct relation of the angle of insertion (a, a′) to the "rotation component" (BR, br) and the inverse relation of the angle of insertion (a, a′) to the "centripetal component" (AB, ab) and to the speed of the insertion point (proportional to BB′, bb′).*

insertion *abd* (*a′*) is increased; then the centripetal component *ab* will be less than AB, but the "rotation component" *br* will be greater than BR. Accordingly as the angle of insertion increases, the pull *across* the shaft becomes more direct, while the pull *along* the shaft decreases; in other words, the rotation component varies directly, the centripetal component inversely, with the angle of insertion.

Applying this to Fig. 6, II, we see that in the horse, the muscles figured are inserted at more open angles of insertion (α, β, γ) than in the mastodon or elephant and that their rotation components are therefore relatively greater, the centripetal components relatively less.

The foregoing principles were worked out independently by the writer, but Luciani[36] gives similar principles for human locomotion. He states that not all of the muscular force is available for the movement of the skeleton, that this is only the case when the insertion of the muscle on the bone reaches almost a right angle, as in the case of the masseters, which can exert their whole strength in pressing the lower jaw against the upper jaw. He says that generally, owing to the conditioning form of the skeleton, the muscle is attached more or less obliquely, so that the direction of its fibers makes a more or less acute angle with the long axis of the bone. In all these cases, a great part of the total force of the muscle is lost as regards movement. In every case, however, whatever the form of the muscle or the size of the angle of insertion may be, by resolving the total pull into its components, in accordance with the law of the parallelogram of forces, one can determine how much of the total pull is expended in the movement of the bone, assuming the other bones to be stationary. Luciani[37] also shows that the more acute the angle of insertion is, the smaller will be the component of rotation, and the nearer the angle of insertion approaches a right angle, the greater will be the component of rotation.

Relations of speed of movement and angle of insertion.—Returning to Fig. 2, we see that if DB contracts to DB′, the point of insertion will move from B to B′. If now the angle of insertion be increased to *a′* and *db* (equal to DB) contracts to *db′* (equal to DB′), then the point of insertion moves only through *bb′*, which is less than BB′. If the contraction time as well as the distance be constant, then B will move faster than *b*; that is, when the rate of contraction and length of muscle are constant the speed of the insertion point varies inversely with the angle of insertion.

It is also evident that if the angle of insertion and other factors remain constant the speed of the distal end of a long bone will increase as the point of insertion is moved toward the head of the bone. (Because BC will be larger.)

Variableness of the rotation component.—From Fig. 2, it will be seen that the angle *ab′d* is somewhat greater than *abd*, that is, both the angle of insertion and the rotation component increase as the muscle contracts.

[36] Physiologie des Menschen, Siebente Lieferung, p. 115.
[37] *Ibid.*, p 116.

"MOMENT OF RESISTANCE" AND "DIMINISHING LOAD"

In every lever, whether of the first, second or third order, the "power" and the "resistance," acting along parallel lines, but in opposite directions, are in equilibrium when the power multiplied by its effective distance from the fulcrum is equal to the resistance multiplied by its effective distance from the fulcrum. The "effective distance" is measured by a line passing through the fulcrum and perpendicular to the line of direction of the force. The product of a force multiplied by its effective distance from the fulcrum is called its "moment."

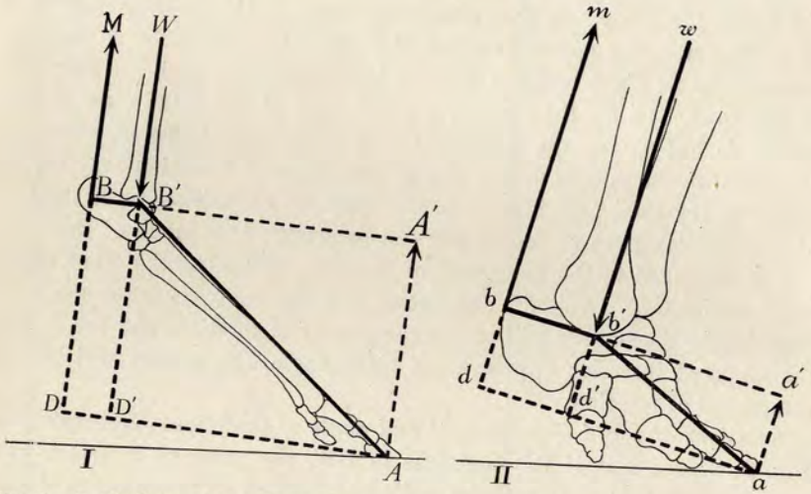

FIG. 3.—*I. Hindfoot of an extremely cursorial type (Neohipparion) showing at the instant of greatest extension of the foot a low moment of power of the calf muscles ($M \times BB'$) and a very high moment of resistance ($W \times B'A'$) of the pressure of the tibia upon the ankle.*

II. Hindfoot of an extremely graviportal type (Mastodon) showing at the instant of greatest extension of the foot a much higher moment of power of the calf muscles ($m \times bb'$) and a relatively lower moment of resistance ($w \times b'a'$) of the pressure of the tibia upon the ankle.

In Fig. 3, I, it would appear natural to assume that the point A, on the ground, is the fulcrum, and that the "resistance" is the pressure of the tibia upon the ankle joint at B′, while the "power" is the contractile force of the muscles of the calf, applied at B. Similarly, Eduard Weber[38] described the human foot as a lever of the second order and gave for the relations of the forces and movements of the foot in raising the

[38] Cf. HAYCRAFT, *op. cit.*, p. 251.

weight of the body a formula which translated into the terms of our Fig. 3 would be as follows:

$$M \times BA' = W \times B'A'$$

But Knorz, Henke, Ewald and others, as quoted by Haycraft (*loc. cit.*), showed that the effective distance of the muscular force M is not BA′, but BB′, and that we should rather conceive the foot as a lever of the first order with the pivot at B′, the "power" at B and the "resistance" (offered by the reaction of the ground upon the foot) at A. In that case, the moments around B′ are as follows:

$$M \times BB' = W \times B'A'$$

Hence, other things being equal, the longer the foot, the greater will be the moment of resistance to be overcome by the muscles of the calf.

If the angle B′AD′ be increased, as when the foot assumes a more vertical position, the effective distance B′A′ decreases; that is, the moment of resistance decreases as the foot becomes more vertical. In other words, the "load" diminishes as the calf muscles contract. It has been shown by Fick and others (quoted by Haycraft, *loc. cit.*, p. 246) that when the force of muscular contraction is opposed to a diminishing moment of resistance, the muscle is capable of performing more total work (force × distance) than when the resistance is constant. Consequently, the diminishing resistance, conditioned by the raising of the foot, enables the calf muscles to perform their work under the most favorable conditions.

SUMMARY OF MECHANICAL AND PSYCHIC FACTORS IN POWER AND SPEED

The speed of the distal end of a "long bone" of the limbs will depend upon (1) the nearness of the point of insertion of the principal muscles to the joint or axle, (2) the smallness of the angle of insertion of the muscles, (3) the position of the muscle fibers with reference to the long axis of the muscle, and (4) the speed of contraction of the muscle itself. If a long muscle and a short muscle were isolated for experiment, it might prove that the short muscle would contract faster than the long one, but, in nature, a single movement of a long bone is produced by the simultaneous and coördinated action of muscles of varying length. Thus, in the act of extending the whole arm from the fully flexed position, the relatively short, broad thoraco-scapular and scapulo-humeral muscles contract in the same time as do the relatively long extensors of the forearm, irrespective of their lengths. The speed and force of contraction naturally depend partly upon the strength of the stimulus and partly on

the resistance to be overcome.[39] The end result, as it were, determines the rate of contraction of the coördinated muscles. The effective regulation and correlation of muscular action is obviously an extremely complex function of the peripheral and central nervous systems. The force and speed of contraction of a given set of muscles in a living animal at a given moment are determined not only by many mechanical factors, of which a few have been mentioned above, but also by the whole psychic constitution of the animal and by the psychic effectiveness of the exciting "motive."

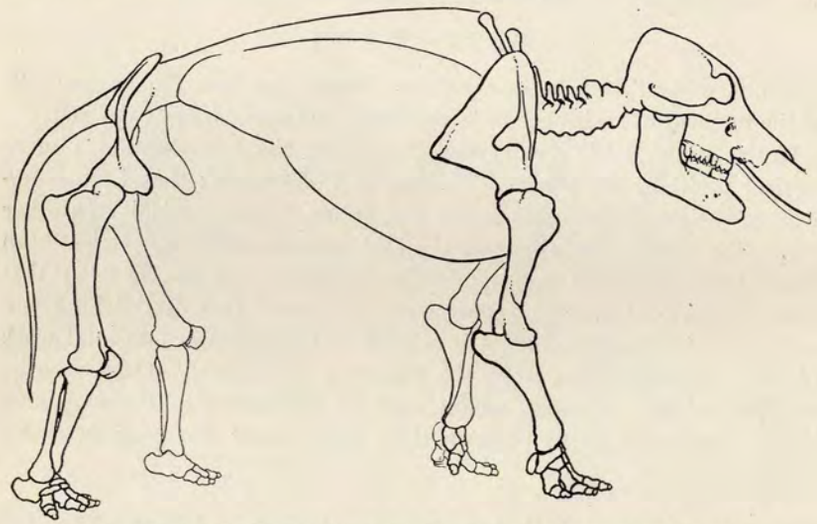

FIG. 4.—*"Graviportal" adaptations for the walk and amble in the Mastodon*

APPLICATION OF THE FOREGOING PRINCIPLES TO THE STUDY OF THE LIMBS OF UNGULATES

FUNCTIONAL SIGNIFICANCE OF THE ANGULATION OF THE LIMBS

As noted above (p. 269), the straightness of the limbs in the Proboscidea and similar heavy-bodied animals was interpreted by Osborn in 1900 as "an adaptation designed to transmit the increasing weight through a vertical shaft." While this is no doubt an incidental advantage of the straightness of the limbs, it is probably not the chief teleological "object." From a consideration of the mechanical principles governing the use of the limbs as compound levers (see pp. 278-281) and

[39] J. BURDON SANDERSON, in Schäfer's Text Book of Physiology, Vol. 2, p. 363, 1900.

from a comparison of the photographs (Fig. 1) of an ambling elephant and of a galloping horse, it seems probable that the straightness of the limbs in graviportal animals has been evolved *pari passu* with the short rectigrade feet and with an ambling even gait, in combination with a long stride of minimal acceleration increment (p. 274). Conversely, the bent or angulate character of the limbs in the horse and other cursorial animals is correlated in part with the very long, slender unguligrade feet and with a bounding galloping or trotting gait, in combination with a long, very rapid stride of maximal acceleration increment.

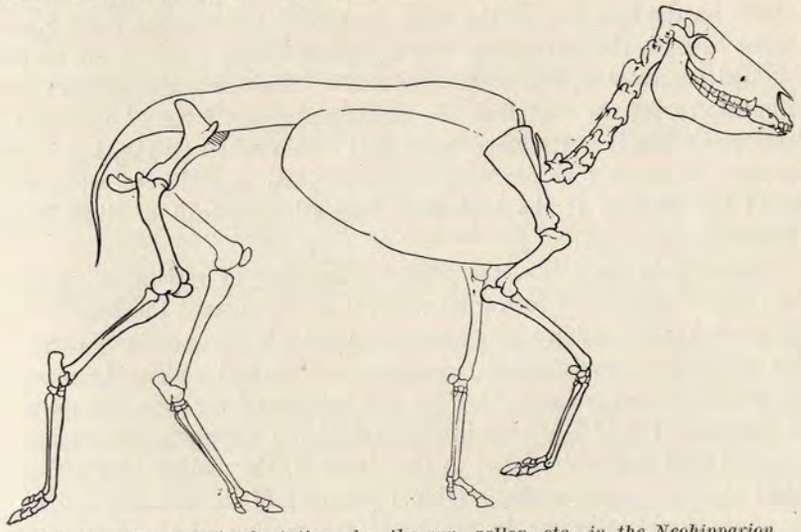

FIG. 5.—*"Cursorial" adaptations for the run, gallop, etc., in the Neohipparion*

In other words, the use and structure of the feet have been the teleological dominants which have determined the diverse modifications in the musculature, proportions and angulation of the proximal segments of the limbs, just as in early stages of aquatic adaptation in reptiles (*e. g.*, Thalattosuchia, Nothosauria, etc.) the aquatic habits are reflected more clearly in the feet or distal segments rather than in the proximal limb segments.

MECHANICS OF THE FOOT IN GRAVIPORTAL AND CURSORIAL FORMS

Comparing the structure and function of the graviportal and cursorial types of feet, we see (Figs. 3 and 4) that, in the elephant, the very massive gastrocnemius and soleus muscles are attached at a wide angle to the massive calcaneum, while the foot itself is very short. In the position shown in Fig. 3 (II) and as compared with conditions in the horse, this

gives a relatively high moment of power (proportional to bb') to the calf muscles and a relatively low "moment of resistance" (proportional to $b'a'$) to the great pressure of the shaft of the limb upon the astragalus. A considerable part of this "moment of resistance" is also subtracted by the supporting effect of the great pad of elastic tissue underneath the foot. No doubt the specimen from which Fig. 3, II, was drawn should have been mounted with the feet more nearly vertical; this would greatly shorten $b'a'$ and further increase the advantage of $m \times bb'$. As the plantar pad is raised from the ground, more weight is thrown on the toes, but, at the same time, they are brought further back almost beneath the astragalus, thus reducing $b'a'$ to a minimum, so that the load decreases as the muscles contract. This arrangement not only compensates for the fact that the greatest absolute force of a muscle is developed when it is stretched to its full psysiological length, but it also permits the muscle to perform a greater total quantity of work than would be the case if the load were increasing instead of diminishing (p. 280).

Similarly, in the horse, the greatest "moment of resistance" is when the foot is fully flexed forward (which is at the instant the foot touches the ground); the action of the extensor muscles is thus suddenly checked; this conditions physiologically a corresponding and sudden increase in the available energy (p. 277). By the raising of the heel the moment of resistance ($W \times BA'$), as in the case of the elephant, also decreases, *i. e.*, the load diminishes; but in the elephant, the motion of the foot is relatively slow and the acceleration increment of the stride (p. 275) is therefore slight, whereas in the horse the motion of the foot is very rapid, and the acceleration increment (through the high velocity imparted to the relatively light body by the spring-like extension or opening of the angles at the stifle, hock, fetlock and pastern) is very great, so much so that at least three of the feet are off the ground during a great portion of the time. In brief, short feet (as in the Proboscidea) slightly bending at the ankle, raise a heavy load through a short distance with a minimal acceleration increment of the stride; long feet (as in the horse), sharply bending at the ankle, throw a smaller load a long distance, with a maximal acceleration increment.

Metatarso-femoral ratios.[40]—That in cursorial animals the hind foot is long as compared with the femur, while in graviportal animals the

[40] The investigation of limb- and arch-form and proportions, and especially the establishment and significance of definite ratios between the limb segments, were suggested by Professor Osborn and taken up conjointly by him and the writer in the Eocene section of the Titanothere Monograph; the following observations on limb ratios are in part a preliminary publication of the joint results attained.

reverse is the case, is shown by the table of ratios, Plate XXXIV, and especially in the following examples:

$$\text{Ratio} : \frac{\text{Length of metatarsal III}}{\text{Length of femur}}$$

Graviportal		*Mediportal*		*Subcursorial*		*Cursorial*	
Coryphodon...	.14	Rhinoceros	.37	Eohippus...	.50	Equus.....	.78
Uintatherium .	.10	Palæosyops	.21	Tragulus....	.56	Antilope....	1.00
Mastodon.....	.11			Mesohippus.	.57	Odocoileus..	1.00
Elephas.....	.13						
Brontotherium	.20						
Toxodon.....	.17						

These ratios definitely prove the connection between the mode of locomotion and the length of the middle metatarsal as compared with the femur. The wide differences in the metatarso-femoral ratio, ranging from .10 in extreme graviportal forms to 1.00 and upward in cursorial forms, are partly bridged over in the mediportal and subcursorial types, and even more completely in a fifth group including certain primitive ungulates, the Condylarths, in which $\frac{\text{Mts. III.}}{\text{F.}}$ ranges from .43 to .31.

Perhaps the most important facts to keep in mind in comparing these and similar ratios (below) are that the ancestral Placentals probably had relatively short hands and feet and long limb bones (p. 270), but that there was doubtless a considerable range of variation in this respect even as far back as the Upper Cretaceous epoch. We are unfortunately unable to follow the ratios through approximate phyletic series except in a few cases (especially Titanotheres, Equidæ, Rhinocerotidæ), but, in every case, we can feel sure that the precise ratios attained in the end-forms are conditioned largely by the nature of the ratios in the stem-forms of each family.

Thus, the exceptional shortness of the feet in the Amblypoda is conditioned by the fact that this group, as represented by *Pantolambda*, had comparatively short feet before gigantism was developed. *Hyrax* is another example of a small form with very short feet, and from some such forms the Proboscidea probably arose.

Besides those phyla which had short feet in the ancestral forms and which merely emphasized this feature, there are many phyla which started from animals with feet of moderate length and later shortened up the feet to a considerable extent. Thus in the Titanotheres, the oldest and most primitive form (*Eotitanops*) has a metatarso-femoral ratio of about .34, which is not far from that of other early Perissodactyls, but

in the collateral descendants of *Eotitanops*, we observe a relative shortening of the digits, correlated with increasing body size and straightening of the knees, so that $\frac{\text{Mts. III.}}{\text{F.}}$ drops from .34 through .31 and .30 in the Middle Eocene genera to .28, .26 and even .20 in the gigantic *Brontotherium*. Again, in the Rhinoceroses, the oldest, smallest and most primitive forms have a foot of moderate length ($\frac{\text{Mts. III.}}{\text{F.}}$ = .43-42), but by progressive relative shortening and broadening, the ratio drops to .24 in *Metamynodon*. In the Hippopotami, which are probably descended from animals proportioned about as in *Oreodon* (with an index of .38), gigantism and aquatic habits have brought about a reduction of the index to .26. Similarly in the Toxodonts, the smaller and more primitive forms had relative long, slender feet, while in the gigantic *Toxodon* $\frac{\text{Mts. III.}}{\text{F.}}$ falls to .17.

In those groups in which the most primitive known members had already attained a slender foot, with reduced side toes, gigantism is unable to effect a complete approximation to the graviportal type. Thus, in the bisons, which are undoubtedly descended from slender-footed forms having a metatarso-femoral ratio not less perhaps than .75, the sudden increase in size causes the ratio to fall but slightly (to .65). In the gigantic Irish elk, whose ancestors probably had a very high metatarso-femoral ratio (perhaps 1.00 or more), this ratio falls to .71.

The evolution of cursorial forms is also indicated by marked changes in the ratio under consideration. Thus, in the Equidæ, it rises from .53 in *Eohippus*, through .68 in *Mesohippus* to .99 in *Hypohippus*, reaching the extreme of 1.16 in the slender-limbed Upper Miocene horse, *Neohipparion*. In the relatively small and slender kiang, the ratio is still 1.00, but in the relatively heavy-bodied *Equus scotti* of the Pleistocene, the ratio is only .84, while in modern horses, we observe even in race horses a falling off of the index to .78, and in the stocky-limbed *Hippidion*, it drops to .72. Correlated with this fall in the length of the metatarsal III, we observe a straightening of the knee. These figures possibly may mean that the modern *Equus caballus*, on account of its great size, is somewhat less adapted to extreme cursorial locomotion than was the slender *Neohipparion* which closely paralleled the deer *Odocoileus*.[41] On the other hand, race horses seem to have comparatively long femora (*cf.* Stillman, p. 80) and cheetahs, hounds and other

[41] J. W. GIDLEY : Bull. Amer. Mus. Nat. Hist., Vol. 19, pp. 474-476. 1903.

forms that progress by bounding have quite long femora. In this connection, it must be remembered (p. 278) that a long femur, implying small angles of insertion of the principal extensors, gives relatively high speed of rotation of the insertion points, but low power for the rotation components. The long femur of graviportal forms has a wholly different meaning (p. 289).

Progressive reduction of the side toes in the Artiodactyla as in the Perissodactyla is accompanied by the elongation of the cannon bone (here represented by two coalesced digits, metatarsals III. and IV.) and by other cursorial adaptations. The primitive Artiodactyl foot with four complete side toes is represented in *Oreodon*, which has a ratio of .38. In *Sus* the ratio is .34, in the primitive four-toed camel *Eotylopus reedi* it rises to .52, in *Tragulus* to .66, whence it rises rapidly to 1.00 and more in the deer and antelopes, culminating in 1.35, an extreme figure, in the giraffe. In the giraffe, the development of great body size has not brought about any reduction in the length of the metacarpals, but, in correlation with the long neck, has even lengthened them.

Other adaptive contrasts in the feet.—There are other adaptive contrasts in the feet of graviportal and cursorial animals, as follows:

In graviportal forms, the astragalus is flattened down, for, when the weight of the body is raised, it is easier to force the tibia up a gentle slope than a steep one. No lateral keels are needed on the trochlear surface to prevent dislocation because of the breadth and spreading character of the tarsus and of the large size of the fibular malleolus. In cursorial animals, on the contrary, the curvature of the astragalar trochlear is steep and the range of movement wide; the trochlea keels help to keep the narrow tarsus in place.

With regard to the phalanges, in cursorial animals, the sharp bending at the fetlock and pasterns and the sudden straightening out of these joints under the pull of the powerful flexors of the foot greatly assists in projecting the body into the air (Stillman, *loc. cit.*, p. 89).

In graviportal animals, on the other hand, the terminal phalanges are reduced; the massive flexors of the foot raise the weight slowly and assist the animal in rolling from one foot to the other.

GRAVIPORTAL AND CURSORIAL TYPES OF TIBIA

Some of the tibio-femoral ratios $\left(\frac{T}{F}\right)$ given on Plate XXXIV may here be grouped as follows:

Graviportal

Uintatherium	.53
Coryphodon	.61
Pyrotherium	.56
Mastodon	.69
Elephas indicus	.60
Brontotherium	.54
Metamynodon	.58
Teleoceras	.57

Subcursorial or Primitive

Phenacodus primævus	.84
" wortmani	.97
Euprotogonia	1.01
Meniscotherium	.91
Procavia	.97
Hyrachyus	.95
Sus scrofa	.86
Eotylopus	.96

Mediportal

Palæosyops	.77
Rhinoceros indicus	.79
Tapirus	.80
Pantolambda	.76

Cursorial

Eohippus	1.00
Mesohippus	1.08
Neohipparion	1.17
Equus caballus	.92
" scotti	.88
Tragulus	1.09
Odocoileus	1.16
Gazella	1.25
Antilope	1.21
Antilocapra	1 23

These figures express the fact noted by Osborn, that, in general, graviportal forms have relatively a short tibia and long femur, while cursorial forms have a long tibia and short femur. It is highly probable that in the remote ancestors of all the Placental orders, the tibia was long, perhaps about as long as the femur. The primitive combination of long tibia and short feet is retained in *Meniscotherium, Hyrax* and to a less degree in *Euprotogonia, Phenacodus wortmani* and *Eohippus.* The steps through which the shortening of the tibia in graviportal animals has been attained may in some cases be discerned. Thus in the Amblypoda, the small and primitive *Pantolambda* has a tibio-femoral ratio of .76; in *Coryphodon,* this ratio falls to .61 and in the huge *Uintatherium* to .53; similarly in the titanotheres, the ratio drops from .77 in *Palæosyops* to .54 in the massive *Brontotherium.* In the Rhinoceroses, it falls from .95 (*Hyrachyus*) to .79 (*Rhinoceros*) and .58 (*Metamynodon*).

In the extremely cursorial lines, the long tibia of primitive mammals was usually lengthened slightly, but in the heavier members of cursorial phyla (*e. g., Equus, Bison*), we observe occasionally a falling off in the ratio.

The difference between the shortest graviportal tibia (*Uintatherium,* ratio .53) and the longest cursorial tibia (*Gazella,* 1.25) is much less extreme than in the metatarso-femoral ratios, which range from .11 to

1.35. There are also more ratios of intermediate type. Consequently, the tibio-femoral ratios taken alone do not always furnish a sure indication of the mode of locomotion.

From the viewpoint of adaptation, there are several plausible reasons why the tibia has not shortened to so extreme a degree as has the middle metatarsal. A short tibia implies a low knee joint and a long femur. A long femur, as stated below, is associated with a nearly vertical in-

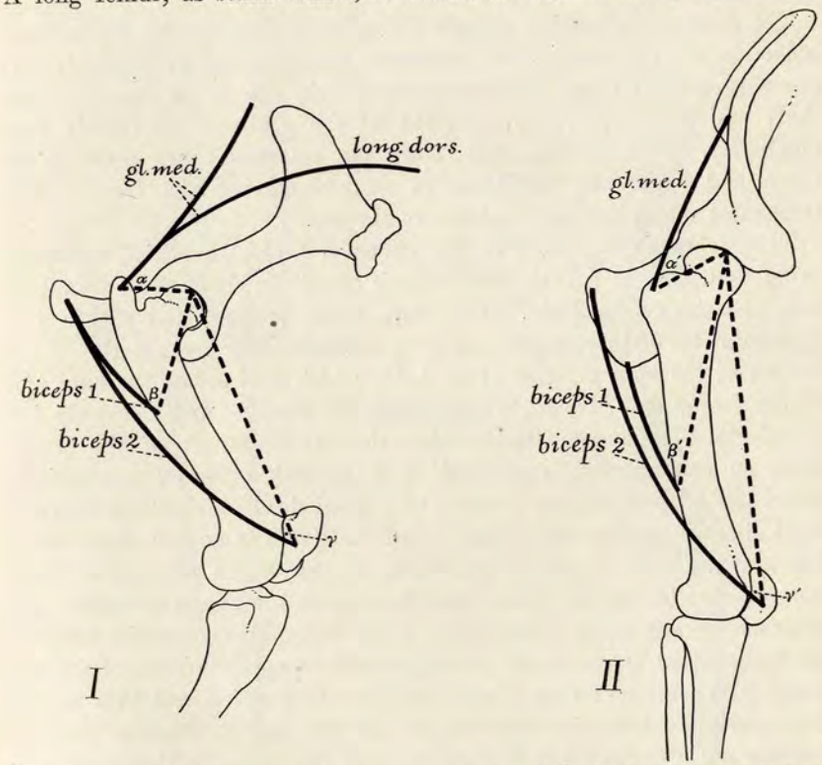

FIG. 6.—*Relations of certain extensor muscles to the pelvis and femur in the standing pose in (I) a typically cursorial form, the Horse, with relatively wide angles of insertion (α, β, γ), and in (II) a typically graviportal form, the Mastodon, with narrow angles of insertion (α′, β′, γ′).*

The heavy black lines represent the general directions of the muscles; the broken lines represent the radii of rotation of the insertion points.

nominate bone and with narrow angles of insertion of the principal long muscles (Fig. 6). The result of these small angles of insertion is that the long muscles exert a powerful pull in the direction of the shaft of the femur (p. 278 and Fig. 2), an arrangement favorable to the lifting and support of great weight (p. 290). The short tibia and

short foot, conditioning a low knee joint, also enable the very heavy animal to rise from the ground with comparative ease. At the same time, excessive shortening of the tibia (as in Ground Sloths) probably conditions very slow motion, which would be very disadvantageous to an animal that has to wander far in search of food.

GRAVIPORTAL AND CURSORIAL TYPES OF FEMUR

The femur of primitive animals (Creodonts, Condylarths, Stem Perissodactyls, etc.) is long, when compared with the size of the body. It has a prominent third trochanter situated in the upper fourth of the shaft and serving for the insertion of the glutæus superficials (seu maximus). This muscle arises from the enlarged tuber coxæ of the ilium and apparently functions as an adductor of the femur. The trochanter major projects high above the shaft.

These characters persist in the cursorial types, the chief difference being that here, as a rule, the femur is relatively short when compared with the size of the body. The short femur is associated with a subhorizontal innominate bone and with comparatively open angles of insertion of the long muscles (Fig. 6, I), which pull across the long axis of the femur and give high components of rotation and relatively low centripetal components (in the direction of the shaft of the bone). Such an arrangement, associated as it is with cursorial adaptations, seems less adapted for the support of a great dead weight than that noticed above in graviportal animals. In the standing pose, a sharp angulation at the knee conditions a tendency for the leg to collapse, which is counteracted by the stretching and tension of the opposing flexors and extensors of the thigh (Fig. 7). In the horse, these opposite tensions are transmitted by means of special tendons on opposite sides of the leg, which also serve to tie as it were the limb in position and thus relieve the muscles to a considerable extent. In graviportal animals, the long muscles are also stretched in standing and thus serve as ligaments, and since they are inserted at very narrow angles, their centripetal components are relatively high (p. 278).

In the femur of graviportal animals, the third trochanter is often reduced, absent or confluent with a long ridge running down from the great trochanter and situated well down the shaft. The functional meaning of this is possibly that the glutæus superficialis is less developed in graviportal animals, its place, perhaps, being usurped by the greatly enlarged glutæus medius. Again, it is conceivable that the third trochanter may have been crowded out, so to speak, by the enlargement of the powerful vastus muscles, which arise on the femur just above the

third trochanter and which are one of the chief muscles used in lifting the body at the hips. The great trochanter of graviportal animals is very broad and heavy, but is more or less sessile, not jutting up so much

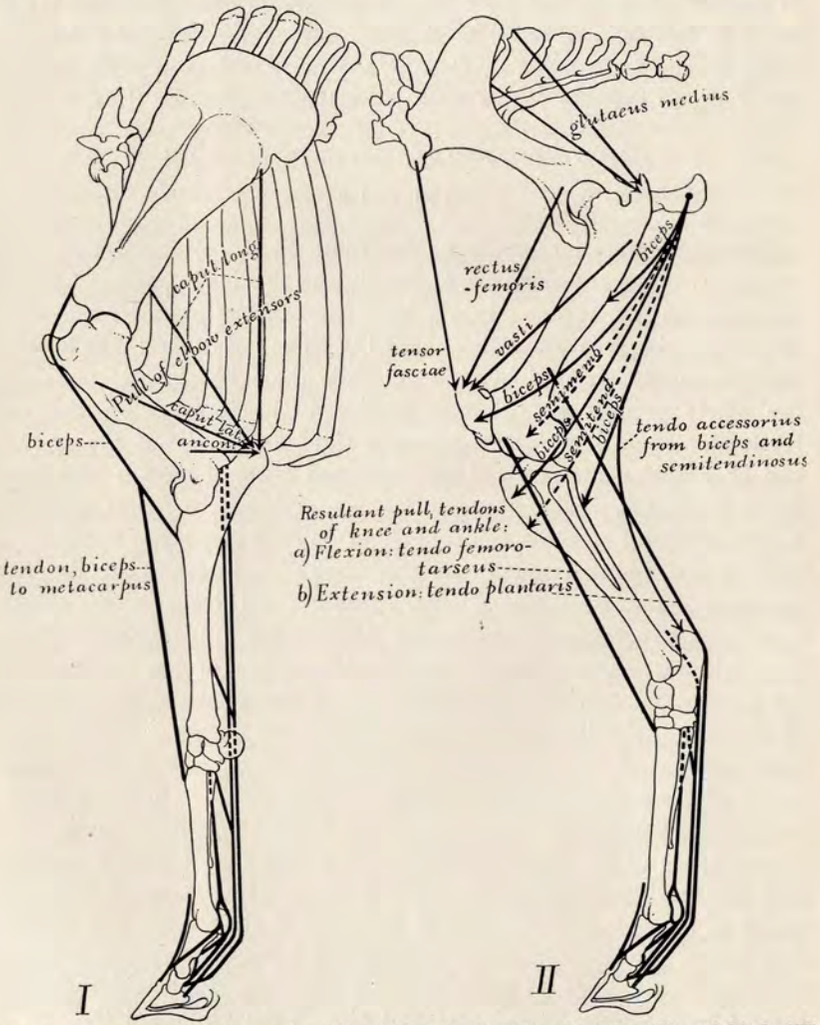

FIG. 7.—*The tendons and muscle-pulls which hold in place the fore- (I) and hind- (II) limbs of the standing horse*

After Schmalz

above the head of the bone. The reason is that the massive glutæus medius is inserted more upon the flat top and outer side of this projection than upon its anterointernal slope (Fig. 6, II), a fact correlated with the subvertical position of the ilium.

In brief, the long femur of graviportal animals serves for the attachment of long and very massive flexor and extensive muscles inserted at slight angles; it brings the knee joint well down below the belly, and it is further characterized by a very heavy sessile great trochanter and a more or less reduced third trochanter, located far down the shaft; the distal facets, as observed by Osborn, are more or less at right angles to the shaft, so that the femur rests subvertically upon the tibia.

GRAVIPORTAL AND CURSORIAL TYPES OF PELVIS

(Figs. 4-6)

The upper anterior border of the ilium in cursorial animals is concave, so that the anterior part of the glutæus medius is produced in front of the ilium and inserted into a long fossa in the posterior end of the fascia covering the longissimus dorsi.[42] The result is that these two muscles apparently pull in tandem, while the subhorizontal position of the pelvis permits the glutæus medius to be inserted on the great trochanter at an angle approaching a right angle. Thus the powerful and prolonged contraction of the combined glutæus medius and longissimus dorsi is exerted well across the long axis of the femur, producing a very powerful rotation component. Similarly the subhorizontal position of the ischium opens out the angles of insertion of the three branches of the biceps and of other extensors and flexors of the thigh.

In such progressively graviportal lines as the Amynodontinæ among the Rhinoceroses, we observe the transformation of the cursorial into the graviportal pelvis by the filling out of the anterosuperior concavity of the ilium, the broadening of the ilium and outward growth of the tuber coxæ and the increasing verticality of the whole pelvis. The result of these changes with regard to the muscles is that the glutæus medius is separated by a wall of bone from the longissimus dorsi, the insertion space of the glutæus medius and accessorius is greatly increased and the medius passes down subvertically on to the broad trochanter major of the femur; the angles of insertion of the flexors and extensors also lessen. Such graviportal adaptations have taken place independently in many lines of ungulates (Amblypoda, Proboscidea, Titanotheres, Amynodonts, Toxodonts) and also in the ground sloths.

[42] R. SCHMALTZ: "Atlas der Anatomie des Pferdes." Zweiter Teil: Topographische Myologie, Taf. 27 u. 28. 4to, Berlin, 1909.

GRAVIPORTAL AND CURSORIAL TYPES OF FORE LIMB

Much of what has been said above regarding the mechanical advantages of short hind feet in moving a heavy load or of long feet in throwing forward a light load applies also to the fore feet. The table of ratios (Plate XXXIV), however, shows that in both graviportal and cursorial types, the third metacarpal is usually longer in proportion to the radius than is the third metatarsal to the femur. The radius also is usually much longer in proportion to the humerus than is the tibia to the femur and the radiohumeral ratio responds less clearly to changes in mode of locomotion than does the tibiofemoral ratio. The adaptive reasons for these facts are not altogether clear, but they must be conditioned partly upon the marked differences in form and musculature between the shoulder girdle and the pelvis and upon the different situations of the fore and hind limbs with respect to the center of gravity of the animal. The relatively long metacarpals and long radius even of graviportal animals gives a very long reach to the fore arm, as shown in Fig. 1, I. In some graviportal animals, as in the Proboscidea, the humerus is much longer than the scapula, the elbow is widely exserted from the body and is turned outward in the back stroke, thus bringing the wrists well in. Interference is avoided by the sharp pronation of the radius, so that during flexion of the wrist the palm of the manus is turned partly outward. In this type of scapula, the backward extension of the posterior angle of the blade, as well as the length of the humerus, gives space for a very heavy caput longus of the triceps, which thus also secures a more direct upward pull on the olecranon. The postspinous fossa is located almost directly above the posterior part of the great tuberosity of the humerus, so that the pull of the infraspinatus muscle is nearly vertical. The tuber spinæ of the scapula is greatly enlarged, its upper border for the trapezius, its lower for the heavy deltoideus. In some other graviportal types (*e. g.*, *Toxodon*, *Rhinoceros*), the scapula instead of being broad and short is narrow and high, with vertically extended pre- and postspinous fossæ. In some cursorial types (*e. g.*, *Equus*), the scapula is also long, with rather narrow pre- and postspinous fossæ; in others (*e. g.*, Pecora), the scapula is fan-shaped, truncate at top, with prespinous fossa reduced and postspinous fossa much developed.

Regarding the relative power of the fore and hind limbs, many people think that in the horse, the hind limbs furnish much more than half of the locomotive power, but Stillman arrays cogent evidence[43] tending to

[43] *Op. cit.*, pp. 69, 79, 89.

show that the fore feet, drawn backward by the great pectoral triceps and powerful back muscles, contribute more than their share to the general result.

DIAGNOSTIC VS. CONVERGENT EVOLUTION VALUE OF LIMB RATIOS

From inspection of the table (Plate XXXIV), it will be seen that, allowing for imperfection of the fossil material and incompleteness of the series, the limb ratios have a certain degree of diagnostic value when taken in groups and that pure convergent evolution rarely brings about a close agreement in all four ratios at once.

The best cases of convergent evolution noted are as follows:

			Mts. III / F.	T. / F.	Mtc. III / H	R / H
Cursorial...	Perissodactyla	Neohipparion	1.01	1.17	1.16	1.30
	Artiodactyla	Odocoileus	1.00	1.16	1.05	1.12
Traviportal.	Edentata	Lestodon	.12	.51	.17	.60
	Amblypoda	Coryphodon	.14	.61	.19	.66
Mediportal.	Titanotheriidæ	Brontops robustus	.26	.55	.37	.82
	Amynodontidæ	Metamynodon	.24	.58	.39	.81
	Rhinocerotidæ	Teleoceras	.25	.57	.37	.78
	Toxodontia	Toxodon	.17	.56	.38	.77

The greatest extremes are found in the following:

Traviportal.	Amblypoda	Uintatherium	.10	.53	.19	.70
Cursorial...	Giraffidæ	Giraffa	1.35	1.18	1.42	1.60

COMPARATIVE TABLE OF LIMB RATIOS IN THE HOOFED MAMMALS.

Species.	Femur (F)	Metatarsal III (Mts. III)	Mts. III / F (F=1)	Tibia (T)	T / F (F=1)	Humerus (H)	Metacarpal III (Mtc. III)	Mtc. III / H (H=1)	Radius (R)	R / H (H=1)
Sus scrofa	248	86	**.34**	215	**.86**	208	77	**.37**	168	**.80**
Hippopotamidæ										
Hippotamus amphibius	498	130	**.26**	332	**.67**	395	152	**.38**	270	**.68**
Camelidæ										
Eotylopus reedi	148	78	**.52**	142	**.96**	118	68	**.57**	100	**.84**
Camelus arabicus	470	325	**.60**	400	**.80**	363	330	**.90**	455	**1.25**
Tragulidæ										
Tragulus napu	94	62	**.66**	103	**1.09**	74	42	**.56**	62	**.83**
Cervidæ										
Odocoileus hemionus	253	255	**1.00**	295	**1.16**	198	208	**1.05**	223	**1.12**
Cervus megaceros	430	350	**.71**	454	**1.05**	334	342	**1.02**	358	**1.07**
Bovidæ										
Gazella dorcas juv.	140	132	**.81**	176	**1.25**	93	134	**1.44**	118	**1.26**
Antilope cervicapra	183	183	**1.00**	223	**1.21**	133	180	**1.35**	168	**1.26**
Bison bison	369	243	**.65**	355	**.96**	290	198	**.60**	293	**1.01**
Antilocapridæ										
Antilocapra americana	210	218	**1.03**	260	**1.23**	164	213	**1.30**	202	**1.23**
Giraffidæ										
Giraffa sp.	466	630	**1.35**	550	**1.18**	435	618	**1.42**	698	**1.60**

e—Estimated.

COMPARATIVE TABLE OF LIMB RATIOS IN THE HOOFED MAMMALS.

Species.	Femur (F)	Metatarsal III (Mts. III)	$\frac{\text{Mts. III}}{\text{F}}$ (F=1)	Tibia (T)	$\frac{\text{T}}{\text{F}}$ (F=1)	Humerus (H)	Metacarpal III (Mtc. III)	$\frac{\text{Mtc. III}}{\text{H}}$ (H=1)	Radius (R)	$\frac{\text{R}}{\text{H}}$ (H=1)
	mm.	*mm.*		*mm.*		*mm.*	*mm.*		*mm.*	
CONDYLARTHRA										
Euprotogonia puercensis	105	45	.43	107	1.01	.....	.....	.....	.....	.....
Phenacodus wortmani	134	51	.38	{ 131 ? 138 *r*	{ .97 1.00 }	107	36	.65	89	.83
Phenacodus primævus	234	74	.31	198	.84	167	70	.42	146	.87
Meniscotherium terrærubræ	100	29	.29	91	.91	82	22	.27	58	.70
AMBLYPODA										
Pantolambda bathmodon	149	36	.24	114	.76	124	31	.25	82	.66
Coryphodon lobatus	423	62	.14	260	.61	363	70	.19	240	.66
Uintatherium (Dinoceras) mirabile	692	70	.10	360	.53	540	106	.19	380	.70
PYROTHERIA										
Pyrotherium (figd. by Gaudry)	622	.....	.....	351	.56	452	.....	.....	238	.52
PROBOSCIDEA										
Mastodon americanus	1,020 *e*	117	.11	705	.69	885	165	.18	670	.75
Elephas indicus	1,020	138	.13	618	.60	810	183	.22	685	.80
E. (Loxodonta) africanus	1,050	144	.13	755	.71	1,000	205	.20	870	.87
HYRACOIDEA										
Procavia sp	71	19	.26	69	.97	69	16	.23	46	.66
TOXODONTIA										
Toxodon sp.	577	101	.17	325	.56	387	147	.38	298	.77
EDENTATA GRAVIGRADA										
Hapalops sp.	150	18	.12	108	.72	130	22	.16	106	.80
Lestodon armatus	640	78	.12	330	.51	530	94	.17	325	.60
PERISSODACTYLA TAPIROIDEA										
Heptodon calciculus	175	75 *e*	.43	175	1.00	115	67	.58	114	.99
Tapirus americanus	262	108	.41	208	.79	205	106	.50	177	.86
Tapirus indicus	320	120	.37	258	.80	250	120	.48	228	.91
PERISSODACTYLA RHINOCEROTOIDEA										
Hyrachyus agrarius	254	110	.43	243	.95	197	93	.47	197	1.00
Hyracodon nebrascensis	267	114	.42	220	.82	202	114	.56	210	1.03
Rhinoceros indicus	495	180	.37	395	.79	385	186	.48	385	1.00
Teleoceras fossiger	408	105	.25	233	.57	305 *e*	114	.37	238	.78
Metamynodon planifrons	480	118	.24	280	.58	393	153	.39	320	.81
PERISSODACTYLA TITANOTHEROIDEA										
Eotitanops borealis	250 *e*	? 86	? .34	.....	.....	203	85	.41	.....	.....
Palæosyops major	433	137	.31	332	.77	.....	.....	.....	.....	.....
Palæosyops leidyi	370	110	.30	290	.78	325	? 113	? .34	235	.72
Palæosyops sp. (A. M. N. H. No. 12205	.....	.....	.....	.....	.....	? 340	106	.30	237	? .69
Limnohyops sp. (A. M. N. H. No. 11689	355 *e*	111	.31	285	.79	293	109	.37	228	.77
" " " " No. 11690	387	123	.31	283	.73	.....	.....	.....	.....	.....
Manteoceras manteoceras	? 390	.....	.....	272	.69	.....	.....	.....	.....	.....
Mesatirhinus petersoni, No. 11659	358	118	.33	283	.79	.....	.....	.....	.....	.....
Dolichorhinus hyognathus, No. 13164	386	119 *e*	.30	.....	.....	315 *e*	.....	.....	284	? .81
Titanotherium trigonoceros	770	220 *e*	.28	430	.55	620	240	.38	520	.83
Brontops robustus	812	212 *e*	.26	448	.55	608	230	.37	504	.82
Brontotherium gigas ♀ (518 A. M.)	780	200	.20	427	.54	528	214	.40	478	.90
PERISSODACTYLA HIPPOIDEA										
Eohippus sp.	162	82 *e*	.50	162	1.00	121	64	.53	110	.90
Mesohippus sp.	178	121	.68	193	1.08	136	92	.68	136 *e*	1.00
Hypohippus osborni	278	218	.78	277	1.00	205	203	.99	260	1.27
Neohipparion whitneyi	249	252	1.01	293	1.17	187	218	1.16	244	1.30
Equus kiang	313	277	.88	310	.99	237	238	1.00	302	1.27
Equus scotti	370	263	.71	330	.88	289	243	.84	342	1.18
Equus caballus (race horse)	392	288	.73	363	.92	305	240	.78	363	1.19
Hippidion neogæum	340	214	.62	305	.89	273	198	.72	287	1.05
ARTIODACTYLA										
Oreodontidæ										
Oredon culbertsoni	161	62	.38	142	.88	138	57	.41	113	.81
Suidæ										
Sus scrofa	248	86	.34	215	.86	208	77	.37	168	.80
Hippopotamidæ										
Hippotamus amphibius	498	130	.26	332	.67	395	152	.38	270	.68
Camelidæ										
Eotylopus reedi	148	78	.52	142	.96	118	68	.57	100	.84
Camelus arabicus	470	325	.60	400	.80	363	330	.90	455	1.25
Tragulidæ										
Tragulus napu	94	62	.66	103	1.09	74	42	.56	62	.83
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