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MATERIALS FOR A MEMOIR

ON

ANIMAL LOCOMOTION.

BY

HARRISON ALLEN, M.D.

Extracted from the "Report on the Muybridge Work at the University of Pennsylvania—The Method and the Result."

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MATERIALS FOR A MEMOIR

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ANIMAL LOCOMOTION.

BY

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INTRODUCTION.

THE writer has undertaken, at the request of the representatives of the University of Pennsylvania, a series of studies on animal locomotion. The subject has been approached from the point of view presented by instantaneous photography, and has been especially based on the results obtained by Mr. Eadweard Muybridge. He will also state that he is indebted to Professor Thomas Eakins for facilities afforded in studying the results of an experiment in the use of a modified form of Marey's wheel devised by him, in photographing the action of the horse in motion.

Many of the statements could have been deduced from data already accessible to the writer, but since he wrote the paper immediately after the inspection of the photographs his conclusions may be said to be based upon them. At the same time he has not hesitated to include materials not embraced by the photographs. Whenever practicable the study of a given series was carried on at the same time that the animal itself lay dissected before him. For example, when studying the photographs of the elephant, he had the good fortune, through the courtesy of Professor Huidekoper, to dissect the limbs of an elephant. He has also dissected the horse, the ox, the raccoon, the sloth, the skunk, the Virginian deer, and the domestic cat. In the course of the

investigation Prof. Horace Jayne extended many facilities. Mr. Edwin A. Kelley has kindly furnished a carefully prepared list of the names of the quadrupeds and birds; this appears in an appendix to the report. Mr. Kelley also gave valued assistance in the dissections.

To better inform himself on the subject of the gait of the horse, the author has observed the impressions made by the hoofs on a sand-beach. In this connection he desires to express his acknowledgments to Dr. M. H. Cryer for valuable assistance and suggestions.

The great delay that would be occasioned in the preparation of this essay by subjecting every statement based upon observation to the test of anatomical demonstration, caused the writer to remain content with making many of the conclusions rest upon the evidence presented by the phenomena recorded by the photographs. He is aware that such conclusions are not in all respects satisfactory. The several heads under which the appearances are discussed must be looked upon as themes which suggest research rather than summaries of work already done. It is hoped that the notes may stimulate some of his readers to attempt to confirm the writer's impressions and further to extend the application which can be made of the pictures to the important subject of animal locomotion.

The "materials" are so arranged as to make two main groups of notes,—those pertaining to the action of the limb when on the ground and those pertaining to the action of the limb about to leave the ground and when in the air. To these will be appended a short section on the human subject, on zoological considerations, and on flight. Occasional repetitions of statements of facts have been difficult to avoid in preparing the notes. The inconvenience arising from this defect has been in a measure overcome by the use of cross-references.

The Use of Terms.

It is necessary to propose the use of a few terms which will clearly express in a word a meaning which otherwise would require the employment of a cumbersome phrase. The words flexion, extension, abduction, adduction, pronation, and supination imperfectly express many animal movements. Thus no adequate word exists for the movement of the hand upward and downward

when the forearm is held in semipronation. Such a motion is of importance in describing the wing of the bird and the bat. The term *Planation* is here thought to be convenient, since it expresses the fact that the movement of the hand is in the plane of the flexor surface of the forearm. Planation includes both pronation and supination. *Contraplanation* as easily indicates a movement at an angle to the plane of the flexor surface of the forearm. It embraces flexion and extension, and is not especially demanded, except that a term which includes both flexion and extension as well as abduction, as used in the sense of abduction of the thumb, may be acceptable.

In like manner it has been found useful to employ terms for the different orders of the foot-falls.

Synchiry indicates that the right and left foot of a single pair act together. Thus in the canter, gallop, and the run, the horse moves all the feet synchirally. The movement of the lower limbs in man is also synchiral. The feet may act alternately or together.

In the strictest sense all mammalian limb-motions are synchiral, —*i.e.*, the right and left parts of a single pair move alternately. This motion is at its maximum in the trot, and at its minimum in the spring as performed by the kangaroo. The term is intended to apply to the act in which the feet succeed each other on the ground. The alternation of the right and left hind legs on the ground, while the fore legs are in the air, is a posterior synchiry; and in the same way the alternation of the fore legs on the ground, the hind legs being in the air, is an anterior synchiry. The rabbit appears to resort to synchiry as an alternation of the walk even in the slowest rate of movement; but, as a rule, it may be said that synchiry is an expression of a fast gait.

Asynchiry would naturally embrace the movements in which the feet act in combinations of hind and fore feet. But since these movements are varied and important, it has been thought desirable to substitute a positive term, and the word *heterochiry** is proposed. The walk, the trot, and the rack are heterochiral, since the fore foot is followed, not by its fellow, but by a hind foot. When the

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* While assuming the responsibility for this word the writer desires, at the same time, to say that it was suggested to him in a conversation with his friend, Professor T. N. Gill.

hind foot alternates with the fore foot of the same side *lateral heterochiry* occurs. When with the fore foot of one side the hind foot of the opposite side alternates, *diagonal heterochiry* takes place.

In connection with the terms flexion and extension the following will be used: The movement of a limb against the medium in which the animal is moving constitutes the *stroke*. The movement in preparation of the stroke constitutes the *recover*. In the description of the "hand-over-hand" movements of the sloth and the ape, the word "flexion" has no place; yet the "recover" is used in as exact a sense as in the movements of any other animal.

When a limb of a terrestrial quadruped rests upon the ground it may be said to be "on," and when not on the ground, to be "off."

The term *sura* will be employed as a convenient word to include the hind limb from the knee to the ankle. *Crus* has been retained so generally as a synonyme for the entire posterior extremity as not to be available.

"Stroke" is the period of impact. It is included in flexion, and constitutes its first stage. "Recover" embraces the last stage of flexion and the whole of the period of "extension." The terms "stroke" and "recover" are by no means the same as flexion and extension. They simply express certain phases of limb-function which are seen during the acts of flexion and extension.

The support of the trunk begins in advance of the neck—viz., at or in front of the occiput (see p. 54)—and passes back to a point midway between the withers and the rump. In the camel the fore foot supports the trunk at a point as far back as the middle of the posterior dorsal hump. In the same animal the posterior extremity supports the body from the dorsal concavity backward. (See p. 52.)

In the Canadian deer (series 695, Fig. 1) and in the fallow deer (series 682 B, Figs. 2 and 3) the fore limb at one stage of the gait is directly under the trunk, and is the only support of the body. In Procyon (series 744, Fig. 3; see also p. 72) two limbs (the right fore limb and the left hind limb) are in the same position as the foregoing. In the sloth (series 750, Figs. 1, 6, 7, 8, 9, and 12; see also p. 78) the two lateral limbs are also the same.

The right hind foot of the horse (series 631, in the interval between 11 and 12) is in the same attitude. (See p. 43.)

Wherever occurring the position illustrates the tendency for one or two feet of the same, or opposed sides, to support the trunk at some point between the vertical lines of the limbs. It is proposed to call such support *central*. Central support is opposed to the support of the limbs in the extreme or forward motion of the fore limb and the backward motion of the hind limb, which may be called *terminal*.

The Movements of Limbs.

If a limb can be conceived moving in vacuo it can be at once understood that propulsion is impossible. For propulsion can follow only upon the initiation of an impetus, and this in turn only by the resistance of the limb against the medium in which the animal is moving, or, in the case of the terrestrial animal, the surface of the ground.

The resistance of the air and the water is so much less than that of the earth that the acts of flying and of swimming become radically different from those of walking, of running, or of any allied movement. In flying and swimming the resistance made by the limb against the medium in effecting an impetus does not arrest the movement of the pinion or the foot; whereas in terrestrial movements the instant that the foot strikes the earth the resistance is great and the arrest is complete.

In the swimming-turtle the first stage of the recover drives the foot in spite of the resistance of the water to the point at which the second stage begins. With some slight modifications the same is true of fossorial animals. Thus in flying, in swimming, and in burrowing the limb describes a continuous movement which unites the path of the stroke to that of the recover. In the animal moving on the surface of the ground, the foot being brought to rest, an absolute break occurs between the beginning of the act of recover and its completion,—the time which would be required to describe the interval and thus to complete the union corresponds to the period that the foot is on the ground.

The limb rests on the ground until the trunk moves beyond the point at which it can maintain itself. It is lifted at intervals which are dependent upon the momentum of the moving mass.

One, two, or three limbs may be on the ground at the same time. The rates at which the succession of the foot-falls occur, in their turn, depend not only upon the rate of speed at which the animal is moving, but on the gait as well. (See p. 59 and *infra.*)

The Positions of Limbs.

In studying the motions of the limb of a vertebrate the position which answers to that taken by the salamander, when at rest, is assumed to be the best adapted for comparison. In this position the limb is horizontal to the plane of the longitudinal axis of the body. The ventre of the body and the ventral surface of the limb are on the same plane nearly. The limb of a reptile varies scarcely at all from that just named. When a terrestrial animal is erect the limb instead of being on the same plane with that of the body is moved a quarter of a circle downward. In the bird the posterior extremity when at rest is in the same position as the terrestrial, but the anterior extremity, in marked contrast to it, is flexed. When extended the extremity is thrown upward to a position as far removed from the horizontal position of the salamander in one direction as is that of the terrestrial quadruped in the other.

In the movement of all limbs the directions in the main are forward and backward. The forward movement will be described as *forward strain*, and the backward movement as *backward strain.* Both the movements are oblique, but between them is a position which is straight. In the terrestrial animal this position may be said to answer to a line in the anterior extremity which lies immediately in advance of the withers and in the posterior extremity to the centre of the acetabulum.

THE ACTION OF THE LIMB WHEN ON THE GROUND.

Kinds of Work done by the Limbs.

The kinds of work done by the limbs are two in number,—viz., that done by the fore limbs and that done by the hind limbs. The hind limbs are more powerful than the fore limbs, and in some animals, as the kangaroo and the jumping-mouse, are the main effectives. No terrestrial animal depends for support upon the fore limbs. When all the limbs are equal, or nearly equal, in length, the preponderance is still in favor of the hind limbs,

owing to the fact that the great backward movement of these limbs on the trunk is made possible by the fixation of the bones to the pelvis, and through this structure to the vertebral column. Not only is this the case, but the hind limbs alone possess the power of propelling the body, so as to throw upon the fore limbs the labor of accommodating themselves to the rate of work of their more powerful associates. When an animal is moving at a high rate of speed, as in the gallop, the synchiral action of the hind limbs projects the body with such force as to compel the fore limbs to act simply as props, which successively carry the body forward until one of the hind limbs is again in position to give the body a second impetus. In proof of this assertion it is only necessary to observe that the greatest height attained by the trunk is that secured by the rump when both hind feet are off the ground. The statement generally made that the horse leaves the ground by one of the fore feet creates the impression that he gains the springing force from this foot, all the previous movements being in preparation for such a spring. In place of this statement another is here substituted,—viz., that the horse springs from that hind foot which last leaves the ground, and is "off" from all feet when he simply relinquishes the support afforded by the last prop,—that is to say, the last fore foot. (See pp. 53, 62.)

If the fore and hind limbs were based on the same plan, the motion of an animal would be either a series of springs—the two feet pushing against the ground at the same moment—or a series of steps, the two feet moving alternately. While closely resembling one another, the two limbs are not on the same plan. If any motion takes place in the vertebral column at the time that the fore limb is moving, it is noticed that it occurs in the region of the neck. The scapula has a slight motion downward and backward. The trunkal motion for the hind limbs occurs in the region of the lumbar vertebræ, while the pelvic bones are fixed. The limit of the forward motion of the hind limbs is dependent upon the flexibility of the lumbar vertebræ. The limit of the similar motion of the fore limb is determined by the action of the muscles alone. The forward motion of the fore limbs is essentially the same in all animals, but the forward movement of the hind limbs is variable, because the lumbar vertebræ differ in degrees of flexibility. In clawed forms there is more lumbar flexibility than

in the hoofed. In backward movements the opposite obtains, for in these positions the fore limbs can be carried back to a variable distance. In the deer and its congeners, owing to the great obliquity of the humerus, the fore foot can be brought to a point near the centre of the body, and the limb be vertical. (See p. 92.) In the horse the fore limb in backward strain is very oblique, and the foot, while well placed under the trunk, cannot reach the centre. In the baboon the fore foot cannot pass beyond a vertical line which intersects the trunk a little back of the shoulder-joint. The backward movement of the hind limb is nearly the same in all animals. The leg is always carried in a direct path, the limit of the movement being determined solely by the length of the limb. In a word, the forward movement is the less constrained in the fore limb, while the backward movement is the least constrained in the hind limb. The most variable movements are the backward for the fore limb and the forward for the hind limb.

The "stroke," or period of impact against the ground, can be divided into three stages,—first, that of forward movement, when the foot rests against the ground, chiefly on the outer border (see p. 50); second, the vertical position, when the weight is borne upon the foot as a whole, or when the marginal toes are shorter than the third and fourth upon the central portion; and, third, the backward movement, or backward strain, when the foot rests chiefly upon the inner margin. I am informed by Dr. M. H. Cryer that skaters invariably bring the skate "on" the ice by the outer edge of the runner, and take it "off" by the inner edge. Practically the same motion is seen in swimming for both hands and feet.

The fore leg may be said to be thrust forward as the hand is thrust when used for grasping. The ground may be said to be seized by the foot and the body pulled up to the point of purchase. (See p. 52.) The hind leg (usually of the opposite side) pushes the hind part of the body forward at the same moment. As the fore foot passes its vertical it also would tend to push the body, and in this way assist the hind leg.

In clawed animals the seizing power is carried to a high state, and in hoofed animals it remains at a low one. In all domesticated animals the pushing power of the hind foot is unimpaired. (See p. 92.) It is most modified in forms adapted for tree life, as the ape and the sloth.

Motions essentially the same in all Quadrupeds.

The motions of all quadruped animals are essentially the same. If a comparison is made between the dog and the raccoon, the contrast between the two forms is at first sight great. But if a careful analysis of the figures be made, it will at once be noticed that the points of variance are in the main due to the rate at which the animal is moving, the gait being the same. The flat, broad, yet exceedingly flexible foot of the raccoon is raised deliberately from the heel to the toes, and at each stage of the strain, which is coincident with the heel elevation, the graphic expression of the pictures is totally unlike the short, decisive motion of the small and almost digitigrade foot as seen in the dog. (See p. 50.) But the order of the foot-falls is similar in the two animals.

In like manner contrast may be established between the appearance of the foot as it is being carried through the air in preparation for a stroke. When an animal is going at a high rate of speed the succession of the movements of the fore and the hind feet is altered. In slow rates the fore foot remains on the ground until the hind foot is in its turn lodged. For an appreciable time both feet remain on the ground nearly at the same spot. This position is well seen in the raccoon (series 744, Figs. 3 and 4) and in the baboon, as well as in the sloth (series 750). It affords a good example of central support. (See p. 38.)

But in fast rates the fore foot has left the ground before the hind foot reaches it, so at no moment are the two feet on the ground at the same time. Flat-footed forms are capable of retaining the two feet on the ground at the same time without the sacrifice of speed noted in the small-footed types, such as the soliped and the ungulate are compelled to submit to.

In the raccoon the fore limb may be, in some positions, used as a balance to prevent the animal being toppled forward.

Division of Parts of Limbs based upon their Movements.

The limb is easily divided into two great parts,—that from the hip to the knee and that from the knee to the toes. The movements for the most part are the to-and-fro motion of that portion of the hind limb placed to the distal side of the knee, and to that part of the fore limb beyond the elbow. The muscles which move the

toes and the body of the foot arise, or tend to arise, from the lower end of the femur, while those which move the leg arise from the pelvis in great part.

In ungulates (series 682 A, Fig. 5) the entire foot may reach the ground when the animal is in rapid motion. So that the plantigrade expression is possible in an animal as far removed from that type as is the deer from the raccoon. The plantigrade foot is more flexible than the digitigrade; the distinction between the foot of the deer and that of the raccoon is great, notwithstanding the fact that the two feet may under some circumstances do the same work.

Backward Strain.

At the end of backward strain of the hind limb the fibula will act as a check to eversion. It is probably one of the uses of the fibula to thus check the eversion and enable the same bone which affords surfaces of origin to the flexors and everters to slow down the action excited by these very factors. In mammals without distinct participation of the fibula in the composition of the ankle eversion of the foot is less pronounced than in those in which it is present. Thus, in the raccoon, the fibula enters into the joint, and eversion is evident. In those instances in which the eversion is well developed yet the fibula is rudimentary, the inversion of the knee is to a corresponding degree emphasized.

In the backward strain, as seen in the raccoon, the fifth toe leaves the ground before the fourth. The leg is always rigid, but the extent to which the limb lies back of the rump varies. It is less decided in the rack than in other movements, and is not so well developed in some animals as in others. This can be seen in contrasting the movement of the horse and that of the guanaco. For the animal last named, see series 743.

When an animal retains the hind limb in backward strain and the fore limb in forward strain (the limbs being those of the same side of the body), the trunk on the same side is stretched out to the utmost and the genu-abdominal fold is made tense. (Series 680, Fig. 8.) When the backward strain of the hind limb is associated with the backward strain of the fore limb, the trunk is flexed (if such a term be permitted) and the folds just named are relaxed, and the creases of the skin on the sides of the trunk are

disposed in a number of vertical lines. These creases are especially well seen in the skin of the hog. (Series 675. See p. 93.)

It is a noteworthy fact that the number and the position of the folds on the side of the hog are the same as those of the bands seen on the side of the trunk of the nine-banded armadillo, and it becomes an interesting matter for consideration whether or not the bands may not have originated in the same manner, and for some reason remained permanently.

The position of backward strain, as already announced, is most variable for the fore limb. The strain is not, however, the same for all animals. The backward inclination of the humerus is greatest in the deer. It is pronounced in the other ungulates, excepting the giraffe. In the elephant it is scarcely discernible. (See p. 91.)

It is evident that the limb that leaves the ground the last is the one which does the most work. This function probably varies at different times in the same gait, although there is nothing in the photographs which proves that such variation occurs.

The amount of forward strain is also subject to variation. The deer possesses extraordinary power to throw the fore limb forward. The degree to which the facility to accomplish this act is carried is seen in series 690, Fig. 10. It is also marked in the raccoon (series 744, 745). The movement is much less marked in the horse and the ungulates generally. The deer exhibits a much larger anterior surface at the trochlear curve of the distal end of the humerus than does any other mammal which was examined. In the deer the proportion is one-sixth of the shaft of the humerus, in the ox and horse about one-eighth.

The sudden release of the backward strain, with eversion of the foot, must naturally tend to inversion of the knee; hence a simple torsion of the entire limb is effected. (See Torsion, p. 57.)

The Manner of a Limb going "off" in the "Spring."

The nature of the "spring" is not made clear by all the photographs. It is well seen in the horse (series 642), but in the dog the immense impetus which is gained by the "spring" would appear to be produced by a mechanism altogether inadequate to the end in view. The animal rises from the ground without the source of the necessary power to accomplish this act being evident. In

the rabbit and the kangaroo it is easily understood how by the simple extension of the tarsus from an acutely flexed position, followed by the flexion of the digits, the body is sent upward and forward; but the leg of the dog is already extended at the time that the "spring" is initiated. If, as is asserted by practical men, the horse is prepared for the "spring" by the same succession of foot-falls as in the gallop or run, it is only necessary to look upon the last limb which leaves the ground as though it were engaged in preparing the leg for a recover from an average stroke. Since the eversion of the foot presses the inner border against the ground, the inner aspect of the limb at the knee is directed inward and subjected to strain. But the force generated by this strain is unexpended at the time that the foot is raised from the ground, so that the limb might be compared to a coiled spring which has not lost its power, and the stored-up energy is engaged to propel the body forward the moment that the inner border of the foot leaves the ground. While acknowledging that this is an hypothesis, it remains the best of the surmises which occur to the observer.

It has already been seen that when the limb is in the position of arrest and the momentum carries the body beyond the perpendicular line it is thrown into "backward strain." The instant that the strain begins the knee is seen to move outward and the hock to move inward. The parts of the foot below the heel remain unchanged. The impact of the structures of the limb is thus impaired in backward strain. It is well known that in the pentadactyle forms the foot can be readily rotated at the mediotarsal joint, and it is a reasonable assumption that it is at this joint that the distal part of the limb moves when the entire limb rotates outward. The femur, the bones of the leg, and the astragalus act as one factor, and the calcaneum and the remaining bones of the foot as the other factor. The socket for the proximal motion occurs at the hip, and that for the distal at the concavity of the scaphoid bone. There is also considerable motion between the calcaneum and the cuboid bone and between the calcaneum and the lower end of the fibula, if this bone is present, or with the outer end of the tibia if it is absent. Outward rotation of the main portion of the limb carries the calcaneum slightly inward by reason of the articulation between the calcaneum and the bones

of the leg. Facets are here present in most terrestrial mammals. In the wombat the articulation is evident. It is present in a rudimentary form in man.

The outer surface of the calcaneum of the bear is marked by a stout roughened ridge as it enters into articulation with the fibula. In the dog the surface is a small embossment, which probably is in contact with the fibula only at the time of the backward strain. In a single old dog examined the same ridge is present as in the bear. A similar ridge which developed under the stimulus of diseased action is seen in the skeleton of the tiger in the Museum of the Academy of Natural Sciences of Philadelphia.

As the knee is rotated outward the outer border of the foot is slightly inverted. This disposition is opposed by the peroneous longus muscle which everts the foot. Coincident with the inversion the external crucial ligament becomes tense and the tendency to torsion is checked.

The degree of outward rotation may be found to relate to the swing of the trunk. In the elephant and the camel the rotation is decided. In the goat it is apparently absent. It is less marked in the horse than in the cat.

The Act of Turning Round.

In the dog the act of turning is accomplished in the following manner:

The hind feet remaining fixed, the body moves in front. It is thrown laterally on one fore limb, so that this member becomes more and more oblique to the line of gravity. At a time when a line drawn upward through the supporting foot will lie entirely free from the trunk the opposed limb has been placed in the line of gravity and a new support assured. In the raccoon (series 745, Fig. 17) the outer border of the foot is used for turning.

Other figures which exhibit the phenomenon of the act of turning are those of the dog, the horse, the tiger, and the lion.

On the Effect of Positions of the Limbs on those of the Head, the Neck, and the Trunk.

When the forward movement of the fore limb is the most conspicuous feature of the figure the head is erect. When the position of backward strain is the most conspicuous the head is

depressed. When the head is being erected the neck becomes convex in front and concave behind. When the head is depressed the neck is concave in front and convex behind.

The movements of the head and mane can be satisfactorily studied in all rapid gaits of the horse, especially in the trot and the gallop. The mane flies backward as the head descends and clings to the neck as it ascends.

The series of figures (649 A) of the trick-horse "Hornet," rocking to and fro, is of especial value in studying correlations of head position to limb movement. (See p. 93.)

The Influence of the Body on the Shape of the Foot.

In the goat (series 677) the outer parts are larger in Figs. 10, 11, 12, and the inner are larger in Figs. 1, 2, 3, 4, and 5.

In the goat the chief weight comes on the inner toe. In the doe (series 641) the two toes separate at equal angles to the axis of the leg. In the ox and the camel no difference is perceptible. Profile views of the lioness and of the elephant are interesting in this connection. In the capybara the inner border of the foot bears the weight.

Value of the unequal Lengths of the Toes.

In a plantigrade animal like the raccoon the transition from the plantigrade to the digitigrade form will bring the short toes to the ground in the digitigrade position at times when the longer toes are yet on the ground their entire length. This position is well seen in series 744, profile, Fig. 19. As the foot passes still farther towards the tips of the larger toes the short toes leave the ground. At first they are in the axis of the metapodium, but afterwards they are thrown backward, and near the end of backward strain appear to be abducted. (See series of the raccoon, 744, Figs. 9, 12, and 13. See p. 73.)

On Obliquity of the Outer Toes.

The oblique movement will be essentially the same in all instances no matter what the number of functionally active toes may be. A straight toe on the limit of the inner border and a deflected toe on the lateral aspect are always seen. In man the first toe is straight and all the others are inclined outward. In

the goat, which has but two functionally active toes, the outer of the two is deflected.

The action of the toes must be studied in connection with the outward rotation. It is evident that the outward rotation must be at an end, or near an end, before the digits are taken from the ground. (See rotation in elephant, p. 90.)

THE ACTION OF THE LIMB WHEN GOING OFF THE GROUND AND WHEN IN THE AIR.

The first movement noticed in the limb after it is beyond the centre of gravity is the flexion of the foot. In the horse the hoof is thrown backward, and the under surface of the foot is directed backward, the heel being raised first. The sole is next directed upward. In animals possessing more than one functionally active toe the toes are quickly adducted in the air, so as to offer the least resistance to the impetus of the entire body. Associated with the above, a pronounced flexion of all parts of the limb occurs excepting at the hip, where the movement is slight. A movement of the thigh towards the trunk is faintly discernible. In animals possessing long thigh-bones, such as the elephant, the movement is more decided than in hoofed animals. The same remarks are applicable to the movements of the humerus. The degree to which flexion is carried is more marked in the young than in the adult, and in terrestrial than in arboreal creatures. In the sloth (*Cholœpus*) flexion is absent, the limbs being advanced by a swinging motion at the shoulder and the hip. (Fig. 11, p. 83.) In rapid gaits the unaided eye receives the impression of backward movement, but fails to be impressed with forward movement. It may hence be inferred that the former is a quicker movement than the latter.

In the fore limb the last state of extension of the forearm answers to the action of the extensors of the carpus and of the digits. In the less delicate movements of the hind limb the muscles which extend the tarsus and the toes move the foot with less precision, and, it is likely, with less speed. The first stage of the recover is a deliberate act. Beginning at the toes, it ends at the hip. The second stage is quicker than the preceding and is more abrupt. Beginning at the hip, it ends at the toes.

Proposition that the Foot strikes the Ground by the Outer Border.

This movement most probably takes place in a constant manner in all quadrupeds. Huxley* describes the act in the chimpanzee as though it were peculiar to that animal. In the horse the movement is well seen in series 601, Figs. 3 and 4, left hind foot. It is also seen in Fig. 4 of the right foot of the same series. The action is well seen in series 581, Figs. 10 and 11. (See pp. 42, 84, 88.)

The foot in all animals excepting the horse (and even in this single-toed form the movement of the foot is in nearly all essentials the same) is carried forward in semipronation. After the foot strikes the ground on the outer border pronation begins, and is completed by the time the perpendicular line is reached. The foot leaves the ground by the inner border (the toes being successively abducted), so that the pressure of the body is borne from without inward across the foot. (See Fig. 4, p. 73.) The foot is always everted as it leaves the ground. In a plantigrade animal, as the raccoon, the foot is carried during the last part of recover nearly parallel to the plane of support. In the rapid motion of ungulates and of the horse the foot may actually touch the ground nearly to the hock. (See p. 43.) In backward strain the hock or heel is gradually raised, and at the end of strain the animal is seen touching the ground by the tip of the inner functionally active toe. In the horse the foot leaves by the tip of the hoof. It is likely that the degree of impact of the outer border of the foot will be found to correlate with the degree of development of the calcaneo-sural joint,† since the weight must be carried along the outer border to the rest of the limb. At the end of backward strain the limb from the knee distally is in the same line.

The entire series of changes from semipronation to pronation, as studied in connection with the transfer of weight across the foot, is well seen in the tiger (series 729 and 730; see also p. 85).

The Eversion of the Foot.

The moment flexion begins eversion is established, and the limb becomes angulated outward at the ankle. The main axis of the proximal facet of the astragalus is correlative with the degree of

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* *Medical Times and Gazette*, April, 1864, 398.

† A name proposed for the joint existing between the fibular process of the calcaneum and the fibula, or the tibia.

this obliquity. The angulation is most pronounced in the horse, less so in the ox, and scarcely, if at all, in the hog. (See p. 55.)

It is evident that the more the toes are separated the better the limb is supported. It would appear to be one of the uses of the digits that they are capable of moving so as to increase the width of the under surface of the foot. Such an increase of width ensues from two causes,—first, from the pressure outward of the foot against the ground; and, second, from the traction of the digits by the action of muscles. The muscular action is most pronounced. It is well defined along the outer border of the foot. As the pressure shifts across the foot from the outer to the inner border, the digits leave the ground and are lifted and abducted as they are relieved from duty. In the capybara the movement of abduction begins before the limb reaches the ground (series 746, Fig. 6). Just as the foot is lifted the inner border is turned outward and the sole is disposed to the air in the position of eversion,—that is to say, the sole, while directed outward, is so arranged that the inner border of the foot is directed downward and the outer border upward. As the foot is everted the toes become abducted.

Eversion is well seen in the horse (series 622 and 633). It is present, but less marked, in the deer (series 681). A good study can be seen in series 619. In the slow movement of the walk the feet are not everted at the moment of the removal of the weight, but after the feet are well in the air. This is especially noted in series 581.

In series 594 the figures of foreshortening show that when, as in Figs. 3 and 6, the fore foot is lifted, the foot moves towards the median line, and when the hind limb moves it swings off from the trunk. It is likely that the greater width of the pelvis over that of the withers compels the hind limb to describe an excursus outward.

That the amount of motion inward under the body is susceptible of modification is evident from the fact that among fast pacing-horses the feet are brought inward, in order to reach the same spot on the ground. Since the fore limb is the more mobile of the two, it is likely that in the process of adaptation* the in-

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* The word "adaptation" is here used in the sense that a terrestrial animal possesses the power of modifying to a slight degree the movements of the limbs according to the character of the ground it is moving upon. (See p. 96.)

ward movement is secured by the front limbs, and that the hind limbs remain the same. (See p. 42.)

In the sloth the foot is lifted as well as swung. (See Fig. 11, p. 83.) It would be interesting to ascertain if the ape also lifts the limbs in swinging.

All elements of the swing of the hind limb appear to be lost in the "jump" if the two hind feet act synchronously.

In the camel the fore foot in backward strain answers to a vertical line which intersects a point as far back as the middle of the posterior dorsal hump, while the hind limb advances forward as far as the concavity between the humps. (See p. 38.)

The Degrees made by the Limbs at the Extremes of Forward and Backward Movement.

The fore limb when at the extreme of forward movement presents an axis which is very oblique as compared to the limb when in the perpendicular position. Again, when in the extreme of backward movement it is again oblique to the same perpendicular position. It has been thought of sufficient interest to record the exact degrees presented by these extremes of movement in the fore limb and to contrast them with similar movements of the hind limb.

By the use of the word plus, or the plus sign (+), a deviation to the right of the vertical is indicated. In like manner minus, or a minus sign (—), indicates a deviation to the left.

In the elephant (series 733, Fig. 13) the forward strain of the fore limb is 25° minus. The backward strain is 35° plus. In the hind limb (Fig. 10) the forward strain is 15° plus and the hind strain (Fig. 9) is 45° minus. In the lioness (series 728, Fig. 3) the forward strain is 50° and the backward strain 20°. In the hind leg the forward strain is 50° and the backward strain 50°.

In the dog (series 707, Fig. 1) the fore foot at the end of backward strain, but as yet on the ground, is in an axis of 10° minus; the rest of the limb being 20° plus nearly. In Fig. 2, the foot having left the ground, marks 80° minus, nearly, while the rest of the limb remains nearly the same as when on the ground,—namely, 18° plus. In the hind leg, as in Fig. 5, the foot when at the end of backward strain gives an axis of 90° minus; while that of the metatarsus gives 10° minus; and that of the thigh is

less than 5° from the vertical. In Fig. 6, the foot has left the ground, and with the metatarsus and leg to the knee, become deflected to 40° minus, while the thigh remains the same,—namely, less than 5° plus. In series 690 (*Cervus dama*, fallow deer) the anterior oblique is 140°, and the posterior 10°.

The method here accepted of determining the degrees of the deflection of the different parts of the limb is sufficiently accurate for all purposes except in the case of the thigh, where the slight movement of the entire mass forward is an imperfect index to the deflections of the femur.

It will be seen that the fore limb moves as a whole, while the hind limb varies in each of its segments. It is true the fore limb presents an angulation between the axes of the digits in hoofed animals and the rest of the limb, but on the whole the limb may be compared to a prop. (See pp. 41, 62.)

In a general way it may be said that the forward strain of the fore limb is parallel in the lioness to the forward strain of the hind limb; but the deflection of the hind limb in forward strain is two and one-half times greater, as compared with that of the fore. In the elephant the forward strain of the fore limb is greater than the forward strain of the hind limb by ten degrees; and the backward strain of the fore limb is ten degrees less than that of the hind. The general trend, therefore, of the two limbs in animals so remote as the tiger and the elephant presents contrasts which in their way are as great as the anatomical peculiarities of the animals themselves.

The correlations of these deflections with the trunk are doubtless exact, but no systematic effort has been made to define them. A vertical line drawn upward through the foot and made to intersect the vertebral column might be made available in the formation of an index of importance. It is noticed that in the photograph of the lioness this vertical line corresponds to the second of the minute dorsal elevations. As a general rule, it may be said that the line intersects the vertebral column at a point answering to a distance of twice the breadth of the withers. Again, in the lioness the forward strain of the hind foot yields a point by which the vertical line can be drawn upward which intersects the vertebral column at the last of the dorsal marks.

While the purpose of the forward strain in the claw-footed

animals is to secure a purchase on the ground by which the trunk can be pulled forward, in the hoofed animals it exhibits another, —namely, to protect the massive head. (See succeeding section.)

The following measurements have been made of the hind limb of the horse at end of backward strain in the rack, the pace, the trot, and the gallop:

Rack.	Pace.	Trot.	Trot.	Gallop.
		Time, 17.	Time, 19.	
590, Fig. 2	591, Fig. 9	607, Fig. 16	609, Fig. 2	631, Fig. 3
Foot, 2°+	Foot, 0°	Foot, 0°	Foot, 1°+	Foot, 0°
Metat., 8°+	Metat., 21°+	Metat., 21°+	Metat., 30°+	Metat., 40°+
Leg, 40°+	Leg, 50°+	Leg, 40°+	Leg, 40°+	Leg, 60°+

Extent of Forward Movement of the Anterior Extremity.

The position of the hoof of the fore foot in forward strain varies with respect to the head in different ungulates. In the heavily-built forms, as the ox, it reaches the occiput only, in the Indian buffalo (series 701) the ear, while in the deer (series 688) it appears to advance even beyond the muzzle. (See p. 38.)

This arrangement doubtless correlates with the massiveness of the head, when the fore limb comes to the rest beneath the head, as in the Indian buffalo and allied animals, and with speed, when it reaches the ground in advance of the centre of the head.

The extreme position of the hind limb after it is taken off varies greatly, as indeed it also does in the limb just prior to its being lifted from the ground.

The changes in the relative positions of the fore foot when off in the various gaits are important. In the dog and the doe the entire extremity is acutely flexed. In the adult deer it is extended, as is also the case in the cat. (See p. 92.)

The hind foot appears to retain its position for a longer time than the fore foot,—that is to say, in the fore limb the impression is given that it is preparing to leave the ground soon after it passes its vertical, while in the hind limb the propulsive power is expended through the entire period of the "stroke," and is as pronounced in the positions back of the vertical as in any other.

The toes of the fore leg are flexed quickly, even in Echidna

and Solenodon. So far as observed, all mammals flex the toes of the fore leg not only quicker than the hind, but more completely.

The adduction of the toes after the removal of the weight of the body does not appear to be the result of a mechanical necessity, for it is subject to variation. It is less prompt in the fore limb than in the hind. At times when the hind foot is raised it tends to be abducted. An example of such retention is seen in series 594, Fig. 5.

"Slowing Up."

The descent of the limb must have an appreciable effect on the momentum of the body by presenting a surface of resistance to the air. This occurs in the manner made familiar by the bird in the act of depressing the tail-feathers to arrest flight. Great breadth of limb is therefore an unfavorable condition for rapid locomotion. The figures of a cat jumping, as seen in series 719, Figs. 1, 14, and 15, serve to illustrate the action.

Position of Feet in the Last Stage of Recover.

The feet in forward motion are carried in the position of semi-pronation during the first stage of the movement. This act is the best adapted to rapid action, since it presents the smallest surface of the limb to the resisting air. (See p. 49.)

The Angulation of the Limb at the Ankle due to Direction of the Trochlear Axis of the Astragalus. (See p. 50.)

Among the more pronounced correlations which exist between the contour of the limb and the deeper structures is the shape of the ankle. This is seen in the horse, the ox, and the hog. If the astragalus of each of these animals is examined, it will be found that the deflection of a line drawn through the upper or pulley surface forms an angle with the axis of the limb of varying degrees in the horse and in the ox, but none in the hog. The production of such a line in the limb whose leg- and foot-bones are in the positions assumed in life will show that the produced line of the surface in the horse intersects the metatarsus twenty centimetres below the proximal end of the bone, in the ox at eleven centimetres, and in the hog the axis is parallel with the tarsus.

With these facts before us and the photographs examined, it will be seen that in the horse (series 576), the figure of the animal being seen foreshortened from behind at ninety degrees, the right hind foot is barely off the ground, and has not lost the position of the ankle when seen in backward strain. The produced axis of the leg will intersect the axis of the metatarsus at the position which corresponds to the production of the axis of the astragalus-pulley in the skeleton.

In the ox (series 671, Fig. 12) the rear view of the left hind leg exhibits a totally different inclination. The foot is on the ground, but is about to leave it, and the produced line is much nearer the vertical. In the hog, as shown in series 674, Fig. 4, the axis of the astragalus as far as can be ascertained is also that of the leg.

Training and Age as Factors of Disturbance.

The difficulty in studying the actions of the domesticated animals, especially of the horse, is owing in the main to the fact that the training to which the animal has been subjected modifies his movement. The draught-horse comes down on the tip of the foot instead of the heel, as is the case with other quadrupeds. In like manner the movements of the well-bred horse are influenced by the skill of the driver. In the gallop (series 624) it is evident that the rider is at fault in the management of the horse and disturbs his action.

The trot and the fast gaits, such as the run and the act of the leap as taken by the horse trained for the circus, are unnatural, and belong to the class of the acts of the acrobat and the contortionist as seen in the human movements. (See p. 66.)

The fact that the horse in racing can place each of the feet in succession in the same spot is in this relation unessential, and need not militate against any conclusion drawn from slower and more natural movements. The same remark is applicable to the fact that the fast horse, even in the walk, will place the hind foot on the ground in advance of the fore foot.

The age of an animal will modify the movements. An old horse, as already seen, will place the tip of the hoof to the ground instead of the heel. In the same class the hind foot is advanced to a less degree than the young. In the colt, on the other hand,

the forward strain is the greater. In the fawn, as already remarked, the feet are more flexed than in the adult deer. An untrained adult feral animal is, all things remaining the same, the best form which should be taken for study.

The weight of the rider being thrown forward on the fore legs may modify the gait. That the depression of the head in the forward movement of the legs is not dependent upon this circumstance is shown in the figures of the rocking horse (series 649 A). An additional reason is here presented why, when practicable, a form taken for study should be feral. (See also remarks on the trot, p. 66.)

Torsion of the Trunk.

An animal in thrusting out a limb from the body may be compared to a boxer making a thrust with his arm. With each lunge the body is turned in the direction in which the lunge is made, and the impetus of the body-movement is added to the force of the blow. The twist that the body describes is checked by the planting down of one of the disengaged feet.

In the dog (series 707), while both hind limbs are off the ground and the body is being vaulted on the single fore limb, the entire posterior part of the body is deflected from the line of the main axis of the vertebral column. This motion is certainly dependent on the bending of the column, and is probably an example of torsion. If unchecked the motion would "twirl" the body round on itself.

But since the impression of the foot on the ground remains sharply outlined, it is probable that the "twirl" is greater in the proximal than in the distal joints, and is entirely lost by the time that the parts of the limb are reached which rest upon the ground. Thus the first impetus towards deflection, while originating in the vertebral column, is gradually transferred to that limb which at the time is serving as a prop, and the force of the movement is dissipated as the animal is carried forward.

In animals possessing a rigid vertebral column the torsion which corresponds to the movement above described is not marked. But the disposition of the body to incline towards the side which perfects the forward strain—*i.e.*, delivers the blow—is the same. Such inclination if unchecked would throw the body

off the straight line. The check is secured by the hind foot of the opposed side of the trunk coming on the ground.

Series 707, Fig. 6, shows to advantage the disposition exhibited by the dog to twist the trunk during progression. This tendency is never seen in the finer varieties of the animal.

The Act of Kicking.

In series 658, which exhibits the kick of the horse, Fig. 1 shows the hind foot as not quite extended. When the kick is complete the foot is fully extended, as seen in Fig. 2 of the same series.

The Position of the Fore Limb as to the Axis of the Trunk.

An inclination exists for the foot to rest on the ground directly in the middle line of the body; but the foot is not brought to the ground in this position, but to the opposed side,—that is to say, it crosses the median line, and comes down on the right side of the line if the left foot is considered, and to the left if the right side is considered. Such disposition is seen in the photographs of the dog (series 703, Fig. 2, and series 704, Figs. 5 and 6). The motion described is best seen in the heavy type of animal. It disappears in the slender breeds, as the greyhound. The same remark is applicable to the horse, the crossing of the fore legs being seen only in the heavy breeds.

The foot which comes to the ground at the median line will gradually be drawn to the lateral portion of the trunk, as seen in series 709, Figs. 4 and 5. In this position it leaves the ground. The prop movement must from this circumstance be less efficient towards the end of the vault than it was at the beginning.

The crossing of the fore legs is admirably well seen in same series.

Depression of the Heel.

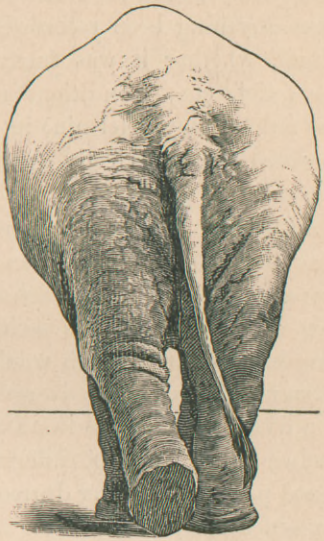
Complete forward movement of the limb tends to depress the heel, or, *per contra*, the forward movement of each extremity tends to draw the toes away from the plane on which they are to fall (series 601, trotting-horse).

Inward Rotation.

After the hind leg leaves the ground the limb is disposed to rotate inward, an act well seen in the horse and the elephant

(Fig. 1). The ilio-psoas would have an apparent effect in preventing this. It may be surmised that this muscle is a check to the excessive inward rotation, or the muscle may not contract until later, and prove to be the chief factor in the second stage of the recover. (See p. 89.)

FIG. 1.



The figure is designed to illustrate the disposition for the limb to rotate inward. The inner border of the uplifted foot is oblique, and the leg is inclined towards the median line of the body.

THE GAIT, OR THE SUCCESSIONS OF FOOT-FALLS.

The order in which the feet comes to the ground would be a simple matter for study if the animal moved constantly at a given speed and gait. It is rational to assume that the movements are in part automatic, and the alternate motions of the right and left limbs, or the motions of both the left limbs alternately with both the right limbs, would insure a succession which could be premised.

Motions are as a rule rhythmical. One expects the serpent to undulate the trunk after a regular method, no matter what the speed of the animal may be. In flying and swimming, so far as is known, the movements are synchronous and constant.

In the terrestrial movements of the quadruped, however, such is far from being the case. This is owing to a variety of causes.

So far as the photographs in the Muybridge series are concerned the order of succession of foot-falls could have been improved—that is to say, could have been more accurate—if the movements in the record of each gait had been of exactly the same character. But in point of fact, owing to the practical difficulties surrounding the subject, scarcely any two of the series begin and end in the same manner, nor has anything been recorded of the mental conditions of the animal, whether it was tractable or intractable, whether excited or quiet, etc.,—conditions so essential to the manner in which an animal may determine its motions.

If it can be conceived that a perfectly tractable and composed animal had been moving in a circle, and the cameræ instead of being arranged in a line had been grouped in a central cluster in such a manner that they could secure correct pictures of the moving form in the same way as in the method actually adopted, it is likely that out of such an endless series a uniform set of pictures might have been secured which would have given completeness of representative actions. It is reasonable to suppose, that the motion of a living creature, as in an unvital mechanism, when starting and when halting, may be different, and may present contrasts of the several parts to a greater degree than when studied at a regularly maintained rate, whether this be a high or a low one.

Each position of the foot when three feet are down embraces the laterals with one of the opposed feet in addition. Thus, in series 738, Fig. 1, in addition to the right laterals the left hind leg is on the ground. But in none of the pictures were the left laterals detected in which the right hind limb was "on." It is probable that the diagonal heterochiral grouping is a weaker form of support than the lateral, and is used as an expedient to shift the laterals from the right to left and back.

In the use of the laterals, in all gaits the feet as they approach the end of the time at which they are "on" are at the side of the trunk, while the feet in use as diagonals always remain beneath the trunk.

The facts that no variety of the deer ever paces, that the mule-deer is the only variety that bounds,—*i.e.*, that all the feet leave and strike the ground together,—that the Canadian deer soon becomes fatigued in the run, while this gait is the one longest

assumed by the Virginia deer,* point to the conclusion that natural gaits are correlative with structural peculiarities; and while quadrupedal movements are based on the same plan, they are subject to modifications in animals otherwise closely related.

Gait may be modified, if not controlled, by the proportion of the length of the limbs to the trunk. The hippopotamus walks in perfect synchrony, so far as the unaided eye can detect. The fat pig can walk, but cannot gallop. The lean pig, on the other hand, can gallop.

The fact that the giraffe is the only animal which is a pacer for both slow and fast movements cannot be easily disassociated from the great length of the limbs.

The subject of the gait can be studied by *observation* of the animal as a whole, by *numerical analysis* of each foot as it is either "on" or "off" the ground, by numerical analysis of each combination of any number of feet, and by *graphic analysis*, by which means tracings of the feet in combination are secured.

For convenience the subject is divided into the following heads:

The Synchiral Gaits.

The Heterochiral Gaits.

Synchiral Gaits.

The Synchiral gaits embrace the canter, the gallop, and the run.

In the canter the momentum of the body is not sufficient to enable both the fore limbs to act as props until the hind limbs again are in the position to urge the body forward. Hence the animal is observed to come down upon a fore limb after being in the air.

In the gallop the fore limbs act successively as props before the hind limbs come down. The run is the variety in which the limbs attain the greatest possible amount of strain, and in which the quick succession of the paired feet is absolute.

The "jump" is an incident in the run. In jumping a hurdle the horse, in series 641, appears to come down on two fore feet at the same moment. In series 637 the horse comes to the ground on the left fore foot, and is instantly followed by the hind foot of the same side.

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* J. D. Caton, The Antelope and Deer of America, p. 270.

The Gallop. (See pp. 41, 53.)

In series 632, the front legs are "on" and "off" equally, each being "on" 2 and "off" 10 in a series of 12. While the hind legs are unequal, the left leg being "on" 5 and "off" 7, the right is "on" 4 and "off" 8.

In series 631, the fore feet are equal, being 3 "on" and 9 "off;" the hind legs are again unequal, the left being "on" 3 and the right 4.

In series 633, the feet are all moving equally. Each foot is "on" 3 and "off" 9.

It will be seen that the fore feet move evenly for the front, and in two of the three series twice unevenly and once evenly.

When the horse is going at a moderate rate of speed the greatest distance between any two of the impressions made on yielding soil answers to the interval between the anterior of the impressions of the hind feet and the first of the fore feet. When the animal is going at a high rate of speed the greatest distance is between the fore foot by which he leaves the ground on the leap and the hind foot by which he alights.

In the canter the impressions made by the hind feet on the soil are in the same relative positions as in the gallop,—*i.e.*, they follow one another at wide intervals. The fore feet, however, yield impressions which lie close alongside one another,—at about the same place.

In contrasting the two gaits, it is evident that in the canter the hind feet act with such ineffective energy that the fore feet are compelled to follow each other in rapid succession to prevent the fore part of the trunk from falling. In the gallop the momentum of the body carries it easily over both fore legs, which can leisurely in succession act the part of vaulting-poles.

The gallop as well as other gaits show irregularity.

In series 680, oryx, this is reduced to a minimum. In this interesting series all the limbs excepting the right fore limb are "on" and "off" equally. Even in the right fore limb the departure from uniformity is not great, the order being "on" 4 and "off" 6.

In the fallow deer (series 682) the limb-movements are uniformly "on" 5 and "off" 11, except the left hind foot, which stands "on" 6 and "off" 19.

In the Virginian deer (series 683) the right fore limb is "on" and "off" 13. The left fore limb is "on" 9 and "off" 15. The right hind limb is "on" 8 and "off" 16, while the left hind limb is "on" 10 and "off" 14.

Intervals between the Fore and Hind Synchiries.

The interval is larger in the horse than in the ungulates. It is exceedingly small in the guanaco, series 743.

The horse may assume the lateral position in the gallop, as is seen in series 632, Fig. 11. In this figure, as well as one in series 612, the animal uses the lateral position immediately after reaching the ground. That the assumption does not depend on speed is shown in the canter. In series 616 there is lateral support in twenty-four pictures, in series 617 two in twelve pictures, and in series 619 one in twelve pictures.

HETEROCHIRAL GAITS.

The heterochiral gaits embrace the walk, the trot, the rack, and the pace.

The Walk.

This gait has been especially studied from the figures of the series of the horse, the buffalo, the ox, the cat, and the raccoon.

In the study of the walk by the numerical method it is found that in the horse (series 579), while the hind feet are synchronous, the front feet are asynchronous.

In the *horse* (series 574) the hind limbs are practically as asynchronous as the fore, while synchrony exists in the diagonal between the left hind limb and the right fore limbs.

In the same series of twenty-four pictures the following is the order of the feet that are "on" and "off:"

Rh "off" 14, "on" 10.
Rf "off" 9, "on" 15.
Lh "on" 13, "off" 11.
Lf "on" 14, "off" 10.

It will be seen that the right hind and the left fore legs are synchronous.

Series 579. Rh "on" 8, "off" 4.
Rf "on" 7, "off" 5.
Lh "on" 8, "off" 4.
Lf "on" 9, "off" 2.

In the walk of the *buffalo* (series 699) the order is as follows: Rh "on" 18, "off" 6; Rf "on" 16, "off" 8; Lh "on" 10, "off" 14; Lf "on" 15, "off" 9.

Nothing here is synchronous; the greatest discrepancy is seen in the diagonal and the least in the lateral feet.

In the *ox* (series 670) the difference between the two fore legs alone is great: Rf "on" 11, "off" 1; Lf "on" 8, "off" 4.

In the *cat* (series 720): Rf "off" 20, "on" 4; Lf "off" 15, "on" 9; "Rh "on" 9, "off" 15; Lh "on" 9, "off" 15.

Here all feet are acting synchronously excepting Rf. Between the fore limbs there is the most marked difference. The left fore limb remains on the ground over twice as long as its fellow.

In the horse (series 576) the diagonal Rf and Lh are "on" 8, "off" 4; while the opposed diagonal is Rh "on" 11, "off" 11; and Lf "on" 6, and "off" 6.

The walk in the *raccoon* (series 744) shows that the fore leg moves slower than the hind leg. When the momentum of the animal is increased the fore leg attains the same speed of rapid change as the hind.

The rate of the "on" and "off" of the fore feet is $\frac{1}{2}$ to $\frac{1}{2}$, while in the horse (series 579) the rate is $\frac{2}{3}$ "on" to $\frac{1}{3}$ "off."

The left fore foot is "on" the ground in 1, 2, 3, 10, 11, 12, 13, 14, 20, 21, 22, 23, = 12.

The left fore foot is "off" the ground in 4, 5, 6, 7, 8, 9, 15, 16, 17, 18, 19, 24, = 12.

The left hind limb is "on" in 1, 8, 9, 10, 11, 17, 18, 19, = 8.

It is "off" in 2, 3, 4, 5, 6, 7, 12, 13, 14, 15, 16, 20, 21, 22, 23, 24, = 16.

Thus the left fore foot is in the act of supporting and propelling the body for the same length of time as it is engaged in preparing for a second stoke. In the left hind foot the time of the foot when engaged in support or propulsion is but one-half that of the time when it is engaged in the air.

Combinations in the Walk.

Out of the number of combinations which it is possible to secure from the feet when on the ground the following is the arrangement most frequently seen in the act of walking: Two hind feet alone; two fore feet alone; two hind feet and two fore

feet. The combination one hind foot and two fore feet has not been seen, though no reason can be urged for the non-occurrence. (See especially series 744.)

Support of the Vertebral Column in the Walk.

The lateral disposition of the feet in the walk supports the vertebral column at the ends, and the figure of the trunk and limbs compares with a truncated triangle whose base is on the ground. In the diagonal disposition the opposed feet meet at a point near each other under the centre of the trunk (when the other feet are "off"), and the figure compares with that of an inverted triangle whose curved base is directed upward.

The animals which assume the diagonal central support are short-legged creatures. The best examples are the raccoon and the baboon. (See p. 72 and p. 75.) The approximation to it is seen in the capybara. It is never seen in the ungulate.

The Trot.

In the trot the succession of foot-falls is inclined to synchrony from the circumstance that the motion becomes more constant as the animal increases in speed.

Thus, in the trot in a series of twenty pictures,

Rh is "off" 15.
"on" 5.
Lf is "off" 15.
"on" 5.

In 593—another series—the order is as follows in a series of twelve pictures:

Rh is "on" 5.
"off" 7.
Lh is "on" 9.
"off" 3.
Rf is "on" 4.
"off" 8.
Lf is "off" 9.
"on" 3.

The left feet have moved in synchrony. The right feet show a disposition to remain on ground longer, and, therefore, are doing more work.

In the trotting-horse the fore leg which is about to leave the ground is apt to interfere with the hind leg of the opposite side as it is advancing to come to the ground. In order to avoid this mishap the animal is trained to lift the fore legs to a degree which is not required in the walk. The motions of the animal suggest that the act of trotting as developed in the horse for fast gaits is artificial and is not especially useful for studies in locomotion. It has the same value as the study of the motions of a "trick-horse." (See p. 56.)

The Rack.

That the rack is not a uniform gait is seen from the following statements:

In 594, in a series of twelve pictures, the animal stands on one foot alone once; is in the air in six; and on laterals in five.

In 595, in a series of the same length, one foot remains "on" in three; laterals are "on" in six; and the animal is "off" in three.

The transition between laterals is well seen in the series 593. In the walk at least the transition between the laterals and the diagonals is effected by the hind limbs.

In racking the impressions made by the hoofs on the ground are in regular alternation of front and hind feet.

Pacing in the horse is a delicate motion, since any irregularity of the ground interferes. The giraffe is a natural pacer. The pace is often accepted by the dog.

Transitions and Contrasts of Gait.

The walk is the basis of the trot and the amble, which is indeed nothing but a running walk. The gallop leads to the run. The run may be called an extended gallop. The amble and the rack are trained forms of the gait. The walk often breaks directly into the amble, and this into the gallop.

The difference between the trot and the pace, as noticed in the effect the positions of the limbs make on the eye, is but slight.

In series 602, Fig. 4, the fore and hind legs on the right side are both in forward strain. The fore leg comes down first, and is instantly followed by the hind. If the two had come down together, we should have had the initial step of the pace.

The trot and the walk are closely allied in all essential particulars. The manner in which the imprints of the feet are made on

the ground is in both gaits the same. The front and hind feet of heterochiral pairs impress the ground at the same places. The intervals between the sets of heterochiral impressions are in the walk about thirty-eight inches; in a small horse they may be twenty-five inches. The contrasts between the figures in the photographs of the horse at the walk and at the trot are very pronounced in the profiles. (See series 584 and 601.) But in the foreshortenings the two gaits present appearances which are very similar. The reader may compare Figs. 4 to 8 with profit.

The trot and the walk are both heterochiral, and vary in the manner of lateral or diagonal positions of limbs.

The chief difference between the impressions made on yielding ground of the feet in the trot and the walk is seen in the relative distance between them. The impressions are much farther apart in the trot than in the walk.

Gaits are more variable in the slow than in the fast varieties. This is inevitable, since the fast gaits depend upon uniformity. Dr. Cryer, in conversation with the writer, states this as an impression.

The Laterals in the Walk and the Rack contrasted.

The lateral position as seen in the walk is essentially different from that seen in the rack. In the walk the fore foot is in forward strain, while the hind limb is in backward strain. In the rack, the fore foot being in forward strain, the hind foot is in the same position, so that the limbs are parallel to each other.

In Procyon (series 744), the diagonal heterochiry shows that the fore and the hind leg, say of the right side, are both in forward movement, while the fore and the hind leg of the left side are in backward movement.

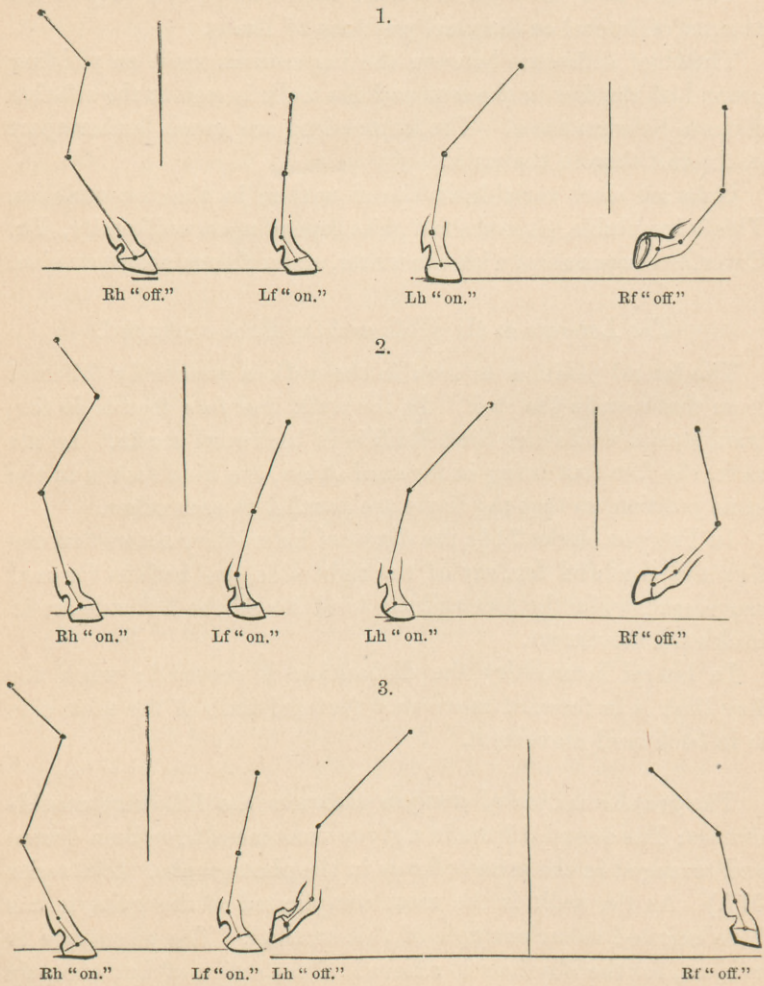
In lateral heterochiry the disposition is reversed: when the fore limb is in forward movement the hind limb of the same side is in backward movement.

The *graphic method of analysis* embraces the following consideration: The essential lines in a given movement have been drawn and arranged in the same order as in the photographs. (See series 577.) As the walk is the most complicated of the gaits, it has been selected as an example of this method. The advantage is evident, for the observer is relieved of the action of but one pair

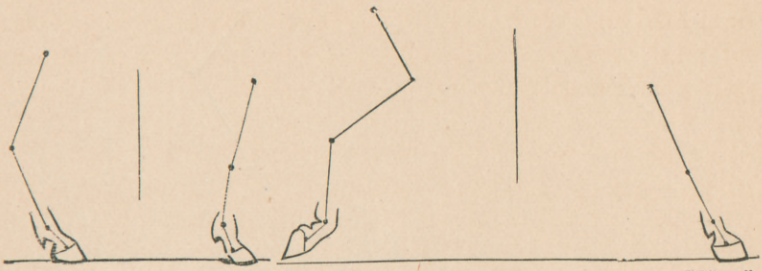
of feet. The eye can pass easily from the combination of left hind and right fore feet—as in the line to the left—to that of the right hind and left fore feet of the lower lines to the right; and the plate itself being before the observer, the study of the succession of foot-falls becomes an easy matter.

The Graphic Method of Analysis.

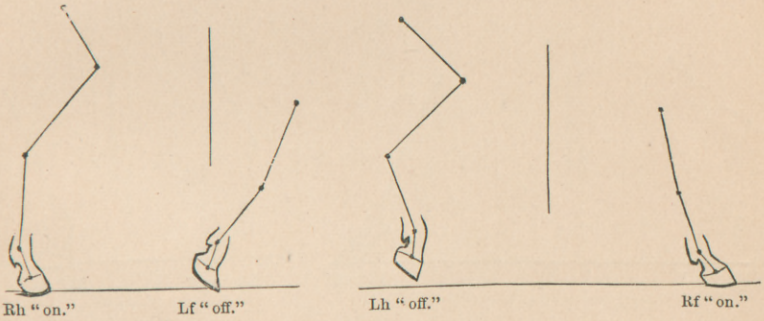
The Limbs of the Horse at a Walk in Diagonal Heterochiry.
(Series 577. See pp. 64, 67.)



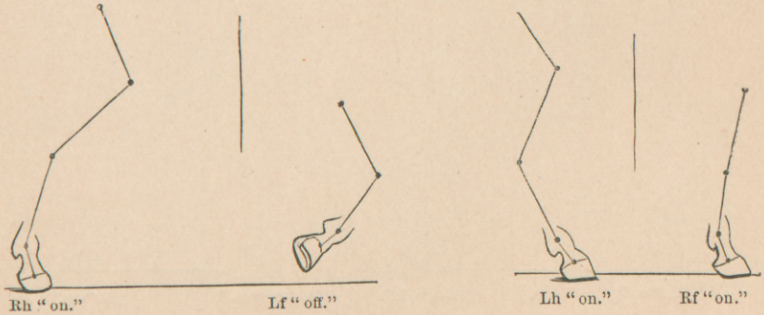
4.


Rh "on."
Lf "on."
Lh "off."
Rf "on."

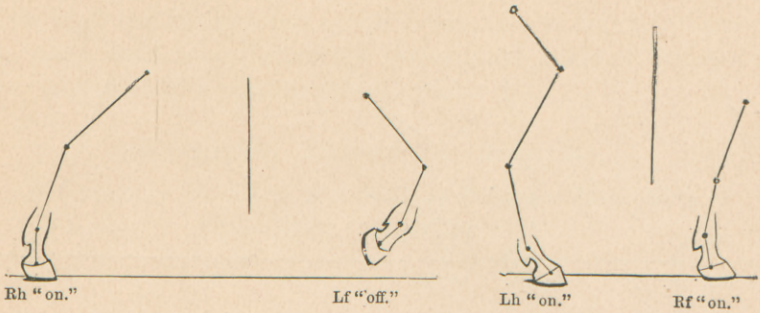
5.


Rh "on."
Lf "off."
Lh "off."
Rf "on."

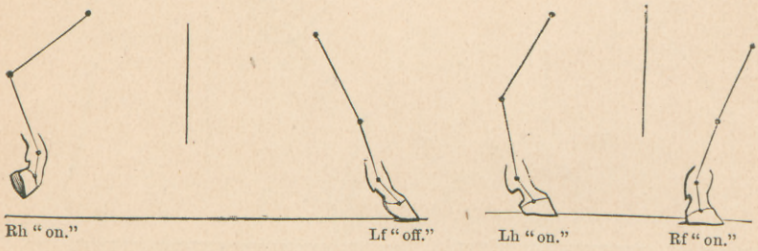
6.


Rh "on."
Lf "off."
Lh "on."
Rf "on."

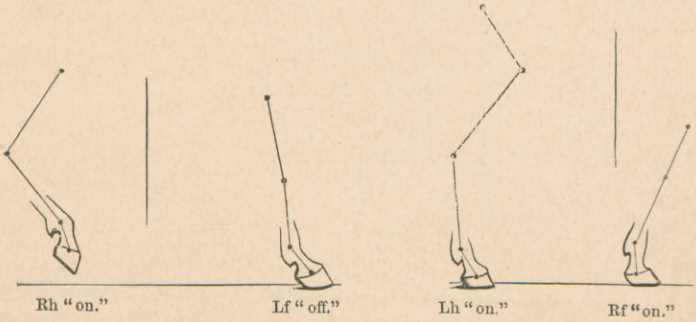
7.


Rh "on."
Lf "off."
Lh "on."
Rf "on."

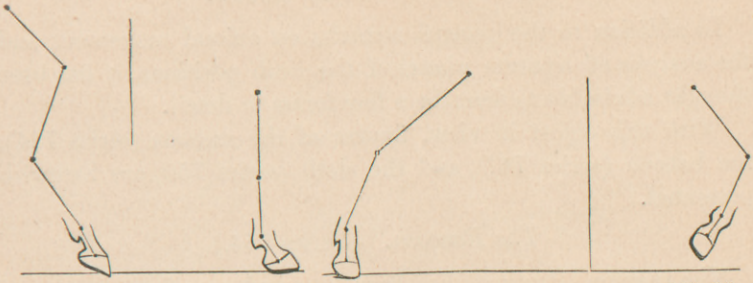
8.


Rh "on."
Lf "off."
Lh "on."
Rf "on."

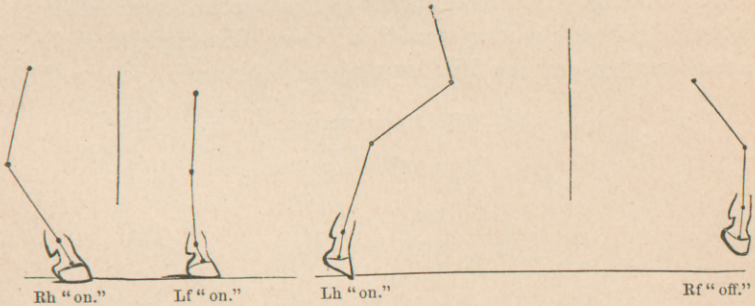
9


Rh "on."
Lf "off."
Lh "on."
Rf "on."

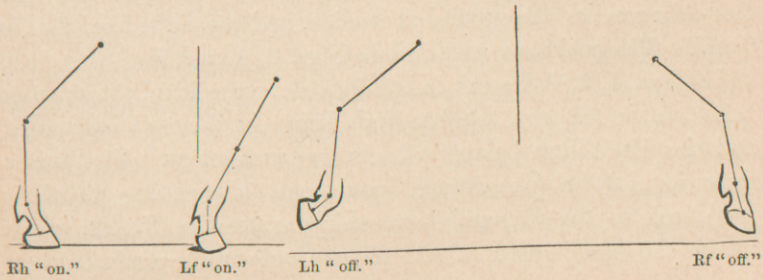
10.


Rh "off."
Lf "on."
Lh "on."
Rf "off."

11.


Rh "on."
Lf "on."
Lh "on."
Rf "off."

12.


Rh "on."
Lf "on."
Lh "off."
Rf "off."

An Analysis of the Movements of the Raccoon, the Baboon, and the Sloth.

In addition to the general remarks on animal movement and the analysis of separate phases of the limb positions, it has been thought advisable to describe a few forms in detail.

With this object in view, figures of the raccoon (series 744), the baboon (series 747), and the sloth (series 750) are herewith presented.

The Raccoon. (Series 744.)

The raccoon (Procyon) has been accepted as a form worthy of careful analysis, since the genus is one of the most ancient of the extant Carnivora, and presents in its gait opportunity for ascertaining the manner in which a primitive flesh-eater moved when of small size and of short limb. (See p. 38.)

The gait from Fig. 1 to Fig. 4 is in diagonal heterochiry. In Fig. 1 the right fore foot lingers so long on the ground that the left hind foot is about to come "on" also. The right hind foot is about leaving, and the fifth toe projects backward. (See p. 51.)

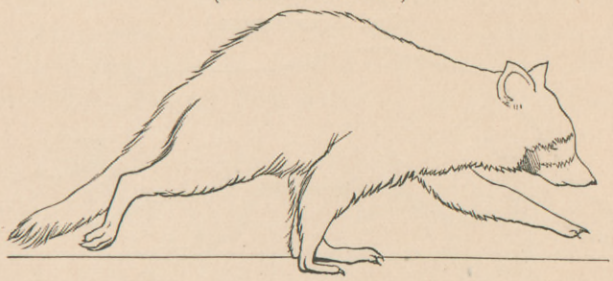
(Fig. 2 of series.)

In Fig. 2 the right fore foot remains on the ground, the left hind foot now reaches the ground at its side, and the right hind foot is "off." The position is retained in Figs. 3, 4, and 5.

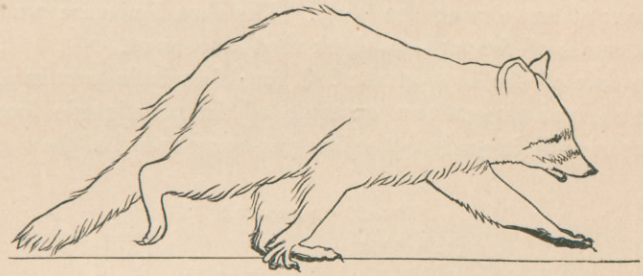
In Figs. 5, 6, 7 the gait is left lateral heterochiry, the support being on the left legs, the fore limb being in forward movement and the hind limb being in backward movement. Fig. 8 is a transitional form (the animal movement only resting on three legs) back to the diagonal heterochiry, as seen in Fig. 9, which retains the combination in one picture only, to be again in right

lateral heterochiry in Figs. 10, 11, 12. The fifth toe of the right hind foot is here seen to extend horizontally. The change to

(Fig. 3 of series.)



(Fig. 4 of series. See p. 50.)

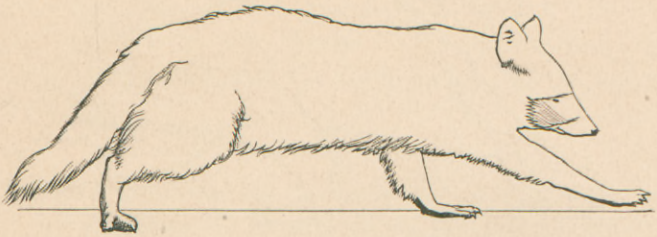


(Fig. 12 of series.)

diagonal heterochiry is made in Figs. 13, 14 (which are repetitions of Figs. 1, 2, 3), and a stride is completed. The animal now alters its gait from heterochiry to synchiry. Fig. 15 is the form of transition. In Fig. 16 the change has been completed and the animal is sustained alone by both hind feet. He maintains this position in Fig. 17, but again is in a transition form of three legs on the ground in Fig. 18.

In Fig. 19 the animal is in diagonal heterochiry, in which position the right hind leg shows the fifth toe in the axis of the leg, and greatly abducted from the fourth.

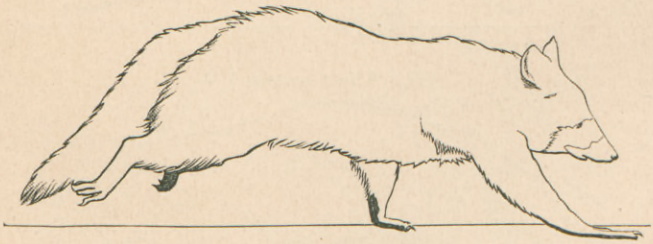
(Fig. 19 of series.)



In Fig. 20 it is again synchiral, the fore pair now assuming the work of supporting the body. The fore limbs are nearly at the extremes of forward and backward movement.

The sole of the foot in the left fore foot is in part in aid of the limb, and presents an example of the plantigrade foot becoming semi-digitigrade as the foot passes backward of the vertical line.

(Fig. 20 of series.)



It will be seen that the gait is irregular; it is first a walk or trot, afterwards assumes the position of pacing, and finally ends in a gallop, or as much of the latter gait as can be assumed to exist in an animal with short legs.

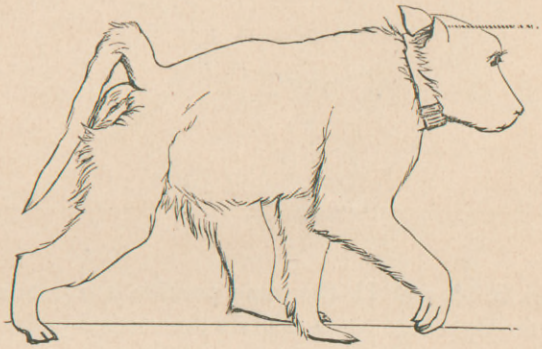
The Baboon. (Series 747.)

In the series of the baboon the animal is seen in the walk. The form was accepted for comparison with the raccoon because of the position of the animal near the other end of the scale of quadrupeds. The limbs have great length, and the intervals be-

tween the two feet of a single pair when in extremes of forward and backward movement are correspondingly great.

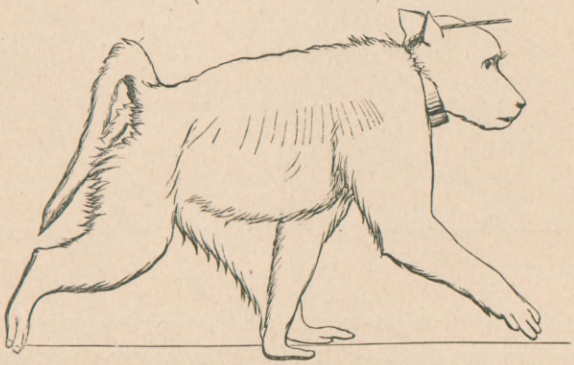
In Fig. 1 the animal has just left lateral support, in which both limbs move in the centre of the body by the left fore foot leaving the ground. In Fig. 2 the support is diagonal, and both limbs (right fore and left hind) are removed from the centre. This is retained through Figs. 3 and 4. In Fig. 5 the same dis-

(Fig. 5 of series.)



position continues, but it is noteworthy because of the shape of the left hind limb, which resembles the shape of the ungulate foot. The right fore limb is now in the extreme of backward movement.

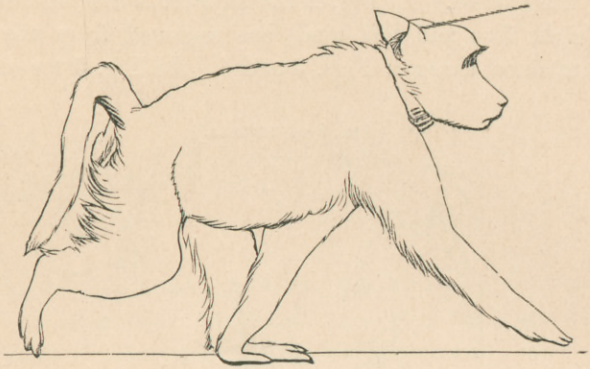
(Fig. 6 of series.)



In Figs. 6 and 7 the position is left fore and right hind (lateral heterochiry).

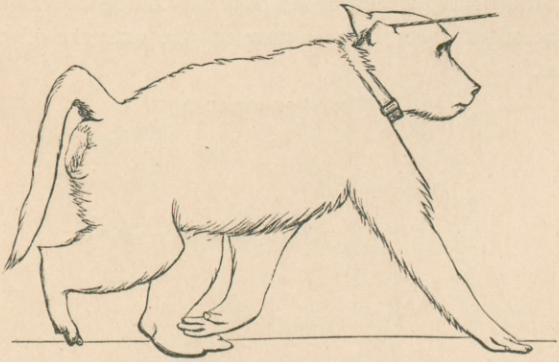
In Fig. 8 the laterals have changed to diagonals by the right fore foot coming down as the left leaves the ground.

(Fig. 7 of series.)



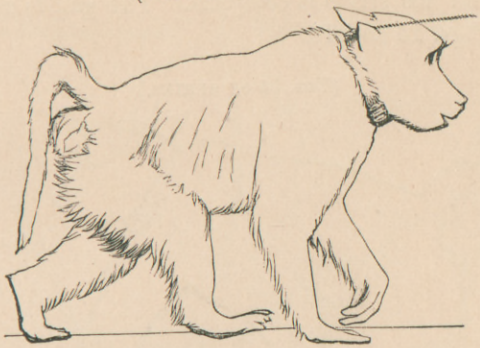
In Figs. 9, 10, and 11 the same position is maintained. The shape of the right fore leg as it nears the vertical position is noteworthy.

(Fig. 8 of series.)

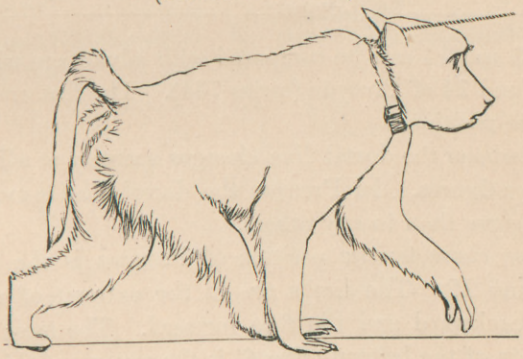


The left hind foot has overtaken the lingering right fore foot, and three feet are on the ground. This position is instantly lost by the lifting of the left hind foot from the ground, when a diagonal support ensues, which closely resembles in general effect the lateral support in Fig. 6.

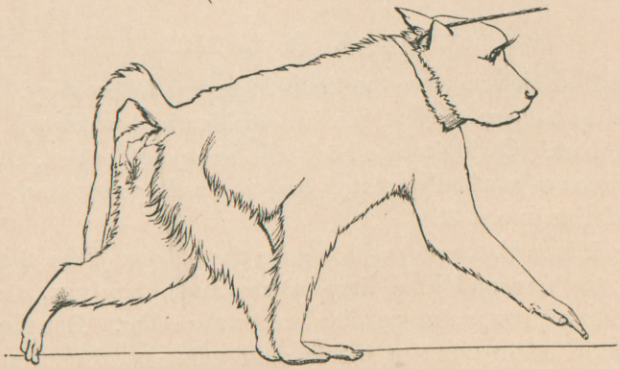
(Fig. 11 of series.)



(Fig. 12 of series.)

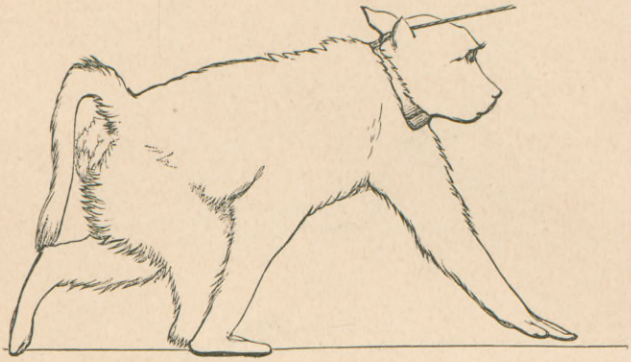


(Fig. 13 of series.)



This position is maintained in Fig. 14. Fig. 14 is a repetition of Fig. 1, and the stride is complete. The gait is shifted to left laterals in Figs. 15 and 16.

(Fig. 14 of series.)



Figs. 13 and 14 can be compared with advantage with Figs. 3 and 4, 13 and 14 of Procyon (series 744). The feet are relatively in the same position.

In the baboon the dorsal line changes scarcely at all from that in the other figures. In Procyon the dorsal line is more convex in these figures than in any others.

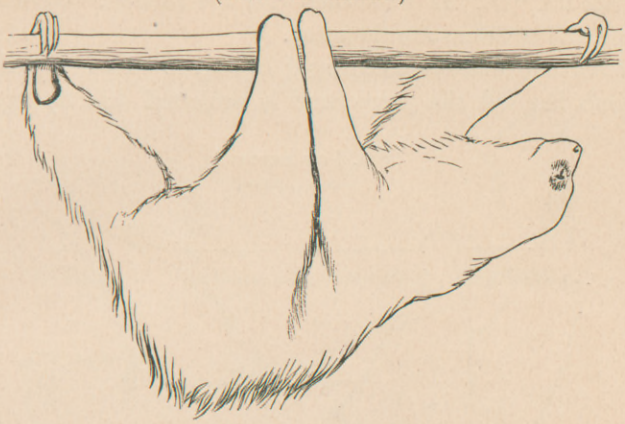
The most characteristic position of Procyon is the laterals in Figs. 11 and 12. The limbs are in the extreme of movement, the hind backward and the fore forward. The most characteristic position of the baboon (Fig. 6) is the reverse of this, the hind limb being forward and the fore backward. The relative places of the "on" and "off" feet are directly opposed.

The Sloth. (Series 750.)

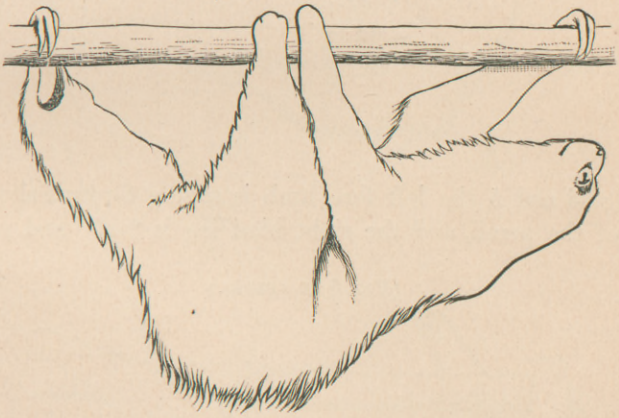
The sloth does not use the limbs in lateral heterochiry. He is compelled to keep the feet "on" in combinations which will insure his support. Owing to the hook-like grasp of the feet, the hind limb becomes markedly rotated outward as it passes back of the vertical line (see p. 38).

Fig. 1 is in the same position as in the baboon (Figs. 6 and 7), —*i.e.*, the fore and hind limb of the same size (viz., the left) are at the nearest point possible one to the other. But the other two limbs, while lying at the farthest point possible from each

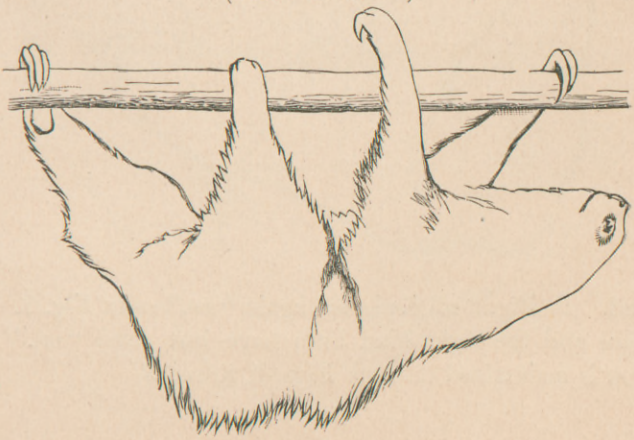
(Fig. 1 of series.)



(Fig. 2 of series.)



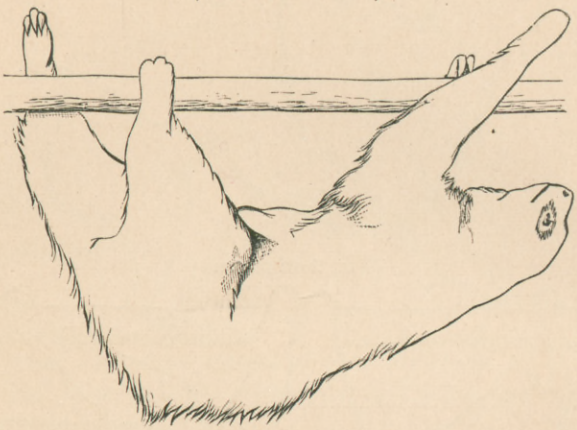
(Fig. 3 of series.)



other, are not "off," as is the case with the baboon. Save in this instance, the positions are the same.

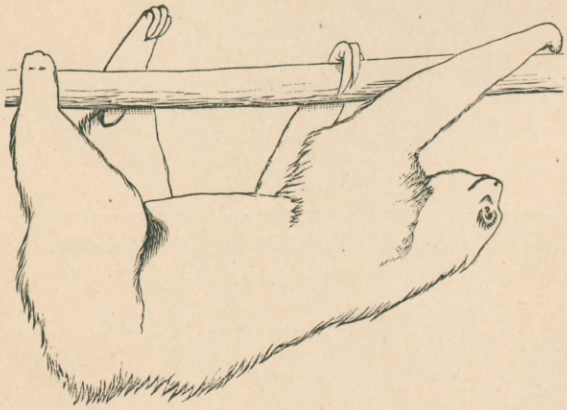
The attitude remains unchanged in Fig. 2. In Fig. 3 the left fore limb has left the perch, and is projected directly upward.

(Fig. 4 of series.)



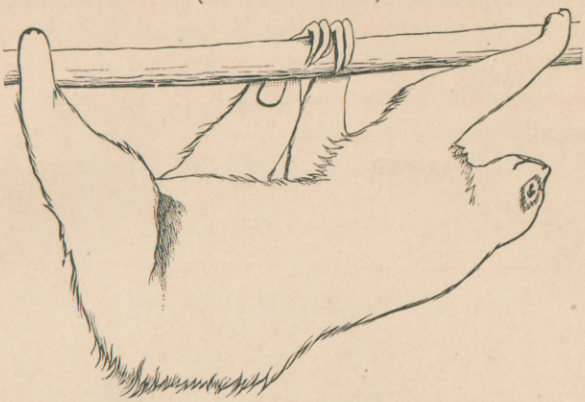
In Figs. 4 and 5 the left fore limb is swung forward above the level of the perch, and the right hind leg is "off" and projects

(Fig. 5 of series.)

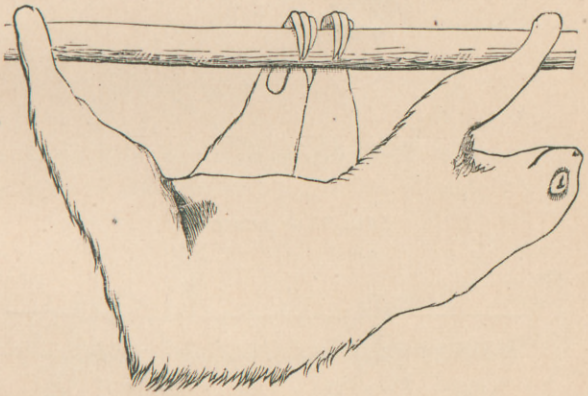


upward. In Fig. 6 all limbs are again "on," as in Fig. 1. The left fore and the right hind limb have just come "on." The position is maintained through Figs. 7, 8, and 9.

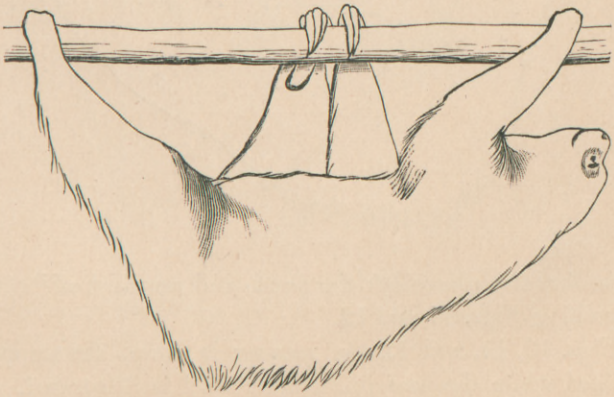
(FIG. 6 OF SERIES.)



(FIG. 7 OF SERIES.)



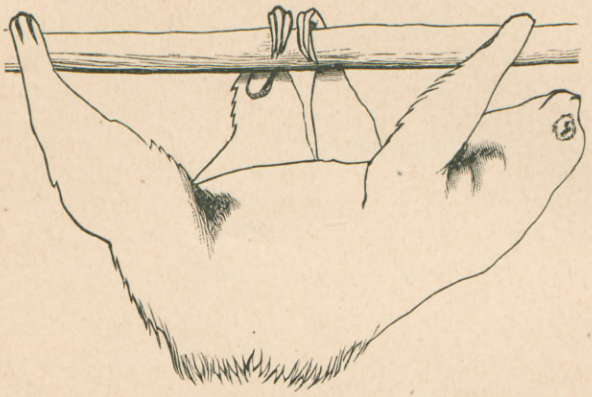
(FIG. 8 OF SERIES.)



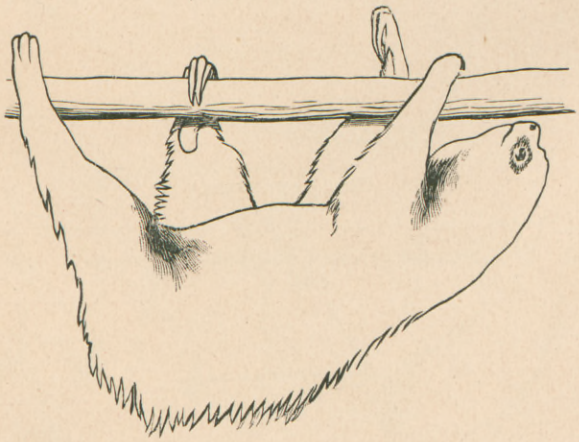
Figs. 7 and 8 closely resemble each other. They differ in the degree of outward rotation of the left hind leg. It is wider in Fig. 8 than Fig. 7, and is rotated farther outward. The head in Fig. 8 is nearer the beam than in Fig. 7. For consideration of the outward rotation, see p. 89.

In the interval between Figs. 9 and 10 both the left hind and

(Fig. 9 of series.)



(Fig. 10 of series.)

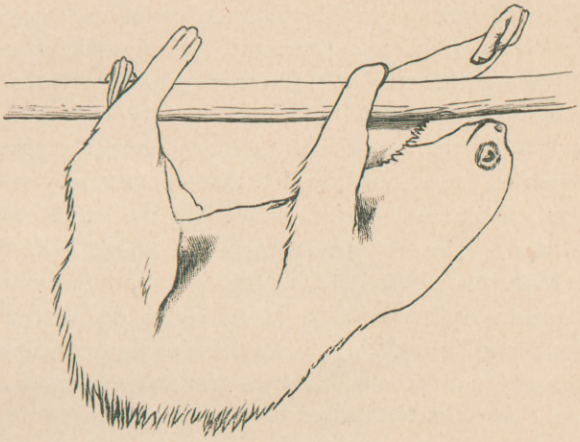


the right fore limb have left the perch and remain "off" through the remaining Figs. 11 and 12.

In Figs. 10, 11, and 12 the manner in which the support is maintained while the two limbs are "off" is illustrated. It is

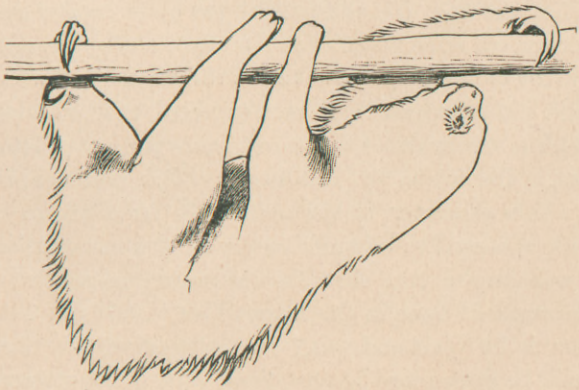
strictly diagonal heterochiry. Yet in Fig. 12 the same positions as in Figs. 1, 6, 7, 8, and 9 are about to be assumed, showing that,

(Fig. 11 of series.)



while support may be diagonal, the limbs which relatively are farthest apart or the nearest together are laterals. Thus the gait

(Fig. 12 of series.)



of the sloth is peculiar in having all four feet "on" at one stage of movement, while the gait is the usual disposition of alternate feet by diagonal.

ZOOLOGICAL CONSIDERATIONS.

The object which the writer has had constantly in view in studying the photographs is to endeavor to determine the value of attitude and gait to classification. Many of the notes bear to a greater or less extent upon zoology, but a few which appear to apply in an especial way to taxonomy are conveniently brought together at this place.

As is well known, the manus and pes present a plan in the arrangement of the elements which may conveniently receive the name of the lateral and median series. In the manus, the cuneiform and the unciform bones constitute the lateral, and all the remaining bones the median, series. In the pes, the calcaneum and cuboid bone are embraced in the lateral series, and all the remaining bones form the median. With this necessary understanding, the writer will now proceed to state the premise upon which he undertook a special examination of the manus and pes in connection with the phenomena of limb-movement. The episode may be accepted as an instance in which the photographs suggest various lines of research, even though nothing of especial value be claimed for the results here secured.

When it was determined, chiefly by the study of the stroke (see p. 50), that the foot comes down by the outer border and leaves by the inner, an attempt was made to ascertain by examination of the structure of the carpus and tarsus the mechanism which correlated with the movement. It was expected that an oblique line by which the strain could be traced across the small bones would be found. The views of Leboucq,* which embrace a path of precisely this character in the embryonic form of the tarsus of mammals, appeared to be confirmatory of this expectation.

The well-known fact that the calcaneum occasionally ossifies with the scaphoid bone in the human foot,† and is at times found united to it by synchondrosis,‡ was suggestive that the oblique axis could be determined in that form with whose structure anat-

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* Arch. Biol. (Brussels), iv. 35.

† Gruber, Mém. de l'Acad. de St. Petersbourg, ser. vii., p. 9, Taf. xvii.; Holl, Arch. für Klin. Chirurg., 1880; Zuckerkandl, Wiener Med. Jahrbuch, 1880.

‡ Weber M., Verslag. der kon. Ak. Amsterdam, 1883, xviii. 121.

omists are most familiar. Aeby* describes a similar arrangement in the foot of the gorilla.

It was reasonable to infer from these data that the disposition of the calcaneum to transfer the strain transmitted to it across the foot to the scaphoid would characterize the mammalian foot.

A careful examination of the *tarsus* has not warranted the inference. As shown by Leboucq, the arrangement exists in the embryo, but it is not maintained as a rule in the adult, nor is it seen in the phylogeny of the group.

FIG. 2. FIG. 3. FIG. 4.

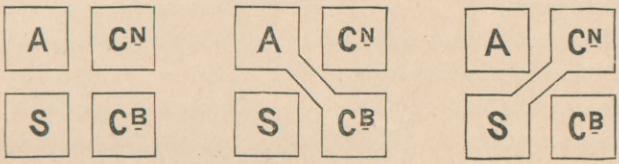


FIG. 2.—Diagram of the relation of the astragalus (A), the calcaneum (CN), the scaphoid bone (S), and the cuboid bone (CB) in the foot of mammals.

FIG. 3.—Diagram to exhibit the disposition for the astragalus to form a junction with the cuboid bone. (Letters as in Fig. 2.)

FIG. 4.—Diagram to exhibit a disposition for the calcaneum to form a junction with the scaphoid bone. (Letters as in Fig. 2.)

The statement of Kowalevnsky is accepted, that the earlier forms of mammals exhibit lines of support which correspond to the arrangement of the bones of the leg. (See Fig. 2.) But in the animals now living, the lines of the bones of the carpus and tarsus do not as a rule show such independence. The bones of the tarsus are almost invariably more or less displaced. In the tapir and the rhinoceros, which are the best living examples of related forms to the earlier forms, the acquired support from adjusting rows is as exact as in any of the numerous recent specialized forms which at present inhabit the earth.

So far as examined, the calcaneum articulates with the scaphoid bone in the following genera only:

Homo,
Troglodytes,
Equus (variable; sometimes astragalo-cuboid),
Dipus,
Cœlogenys,
Erethizon (variable).

* Morph. Jahrbuch, iv., 1878.

Herewith are given examples of the common cuboido-astragaloid articulation:

Hyrax (not marked),
Rhinoceros,
Amynodon,
Ungulata,
Procyon,
Ursus,
Erignathus,
Menodus,
Palæosyops,
Creodonta,
Macropus,
Phascalarctos,
Dicotyles,
Hippopotamus,
Erethizon (variable),
Arctomys,
Myrmecophaga,
Elephas,
Equus (variable; sometimes calcaneo-scaphoid).

Neither the calcaneo-scaphoid nor cuboido-astragaloid articulation is found in the following:

Dasyprocta,
Capromys,
Fiber,
Hystrix,
Hyena crocuta,
Orycteropus (variable; tends to calcaneo-scaphoid),
Homo (variable; sometimes calcaneo-scaphoid).

While a fixed arrangement of the parts in an assumed oblique axis is thus undetected, the examination was fruitful of one result, —namely, that when in addition to the axial disposition of the tarsal bones one to another and the lateral adaptation of parts in transverse rows was departed from, the departure took place in one of two ways,—either by the calcaneum reaching the scaphoid (*i.e.*, by a direction downward and inward) or by the cuboid bone reaching the astragalus (*i.e.*, by a direction upward and inward). It is thus demonstrable that the elements in the tarsus which first distribute the weight of the outer border of the foot as it comes to the ground transmit the impact *inward* in an *oblique* manner, and, it may be assumed, tend to throw the weight of the limb towards its axial line, which sustains the weight of the body when the limb is in the vertical position.

In the study of the phylogeny it will be seen that the more distal of the two bones is first pressed inward, and that this arrangement obtained not only in the first (with the exception of Coryphodon), but in most of the extant forms. Why it should ever have departed from this arrangement and reversed the inward impact to the calcaneum is not an easy question to answer.

It is worthy of remark that in Equus and Dipus we have highly specialized forms of foot-structures; and in Primates, while the foot on the whole is generalized, the astragalus sends a remarkably inward directed and obliquely placed neck in a direction which would render it difficult for the cuboid bone to reach it.

It must be acknowledged as a great difficulty how an intermediate group arose in which a simple form of tarsal disposition is retained. While from facts presented by Professor Flower it would be natural to assume that Orycteropus might move the foot in a manner different from Myrmecophaga, nothing can be urged why Hyena should differ from Canis, or Dasyprocta and Capromys from Arctomys.

An examination of the *carpus* showed less disposition for the outer elements of the series to be placed inward than is the case in the tarsus. The cuneiform bone, which corresponds in position to the calcaneum, and the unciform, which corresponds to the cuboid bone, remain in all forms of the manus in constant relation to the rest of the carpus. But the entire lateral division of the carpus exerts a disposition to displace the os magnus inward and upward in a manner which is strikingly exhibited in the following scheme.

The os magnum articulates with the scaphoid bone in

Cœlogenys,	Tapirus,
Rhinoceros,	Sus,
Dicotyles,	Chrysochloris.
Hippopotamus,	

That is to say, the os magnum, in addition to articulating with its own axially disposed element, the lunare, secures an articulation with the scaphoid bone.

The os magnum articulates with the lunare only in

Dasyprocta,	Elephas (variable with trapezoidal-lunare),
Capromys,	Tapirus,
Erethizon,	Manatus,
Hyrax,	Orycteropus,
Hystrix,	Myrmecophaga,
Arctomys,	Myogale.
Uintatherium,	

In summarizing these results, it may be said that the fact of the outer border of the pes coming to the ground in the first stage of

the stroke is in correlation with a disposition for one or more of the tarsal elements of the outer series to secure junctures—*i.e.*, junctures not accounted for in the plan of the parts—with one or more elements of the median series. Relatively few genera resist this disposition.

In the manus, the lateral series remains intact, but in a few extant genera and in some extinct genera the outermost of the median series is seen to articulate with a carpal element which lies to its inner side.

Deviations of the Trunk with Respect to a Hypothetical Longitudinal Axis.

An interesting series of comparisons can be instituted between the anterior and the posterior parts of the trunk in the various positions of the limbs. In illustration of this subject attention is directed to the deviations of the trunk in advance of the rump with respect to a line drawn horizontally forward from the base of the tail. Assuming that the beginning of such a line corresponds to the part which shows the least motion and passes to that which shows the most, it will follow that the fore part of the trunk, together with the whole of the regions of the head and the neck, will shift positions with respect to this line. In series 675 the figures of the hog demonstrate that the body in advance of the rump are highest when the animal is resting on both hind feet. It is next highest when the animal has come down one fore foot. In the deer, when propped on the fore limbs, the animal sinks so low anteriorly as to permit the horizontal line to intersect the muzzle. The fact that the baboon exhibits no contrast of the kind named would lead to the conclusion that the clavicle prevents the fore part of the trunk from sinking,—a conclusion which is invalidated by the fact that the elephant shows a similar exemption.

Relation between the Oblique Movement across the Foot and the Number of Toes.

From the fact that the outer border of the foot first strikes the ground and that the inner border last leaves it, one can create a proposition to which the following facts are corollary. (See pp. 42, 50.)

When the outer border is longer and stouter than the inner, the first-named parts of support are of more importance than the last. The difference in this regard between the foot of man and that of the bear should be the difference between the respective lengths of the first and the fifth toes.

When the inner toe is rudimental, or lost, the foot has left the ground before the inner border is reached. But it is not so evident why the fifth toe should be lost. One would suppose that this toe would be the most persistent. The sequence of the limbs of the horse from the five- to the single-toed forms would be of interest to study in this connection.

Rotation of the Limb.

In another relation than that included in the foregoing the study of the photographs has been of interest. Allusion is particularly made to the forward swing of the fore limb and the outward rotation of both limbs (for inward rotation see p. 59).

The extent of the forward swing is found to correspond to the extent of the trochlear surface of the humerus as it enters into the composition of the elbow-joint. In addition to this fact attention may be called to the difference in the length of the olecranon in different animals. The olecranon is greatly longer relatively to the shaft of the ulna in primitive types of Mammalia than in the more specialized, as the writer has been informed by Professor W. B. Scott. The same difference is found to obtain between Dicotyles and Sus. May it not be claimed that the difference correlates with the facilities possessed of maintaining the fore limb in backward strain? The enormous leverage secured by a long olecranon must enable the limb to maintain a strong position for the limb when it is held in backward strain as compared to one in which the olecranon is short. This must be especially marked when the humerus is long, as is always the case in these types.

The mechanism which accompanies the rotation of the limb outward at the knee after it has passed the vertical line is associated, as has been seen, with inward rotation of the hock. This form of torsion is described (see p. 45), and the springing power of the limb is a resultant. The amount of springing power should correlate with the torsion, and the facets by which twists are effected be indices of the act. The conversion of the calcaneo-

cuboidal articulation into a convexo-concave joint, in forms in which the oblique impact is cuboido-astragaloid, would look as though such impact favored torsion.

The study of the rotation of the limb is conveniently undertaken in the elephant, since the fur is here absent. A number of the positions assumed by the limbs is illustrated in series 733, Figs. 1 to 12. (See the figures of the fore limb of the elephant.)

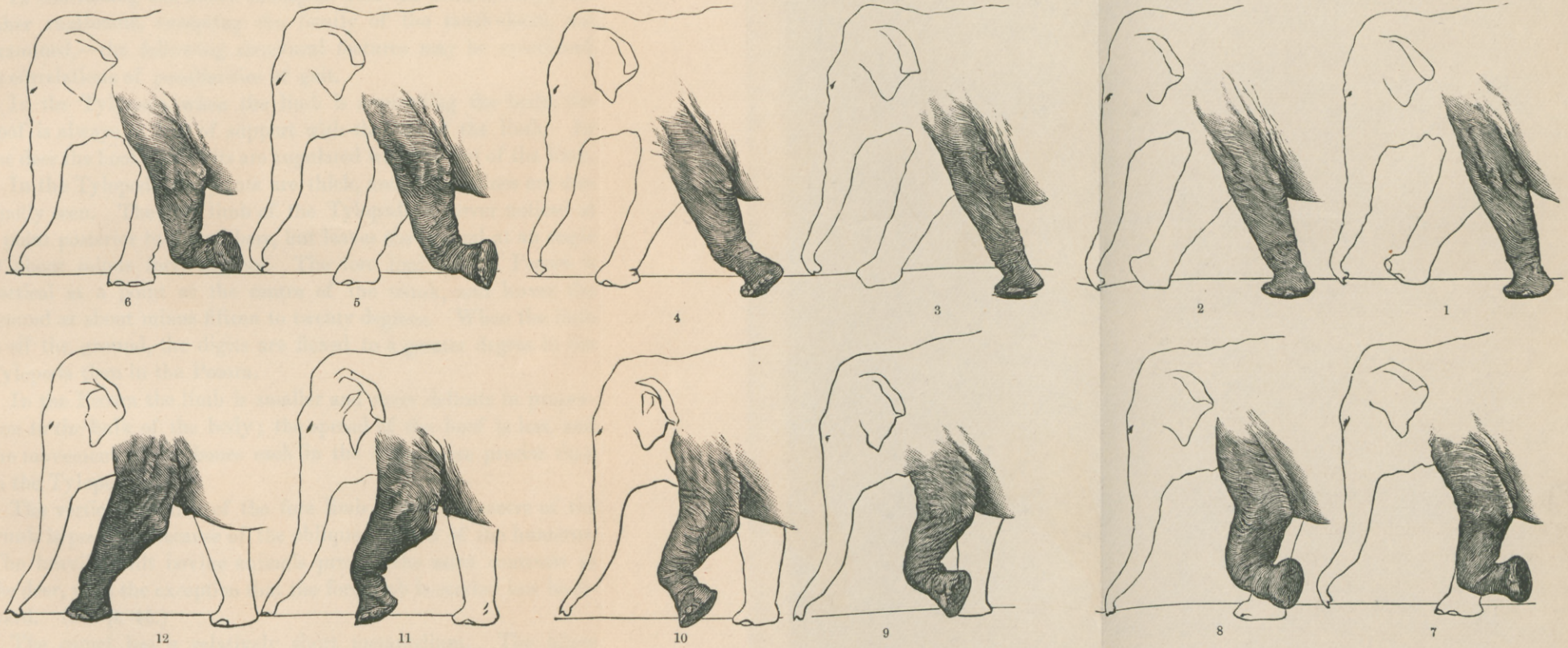
The width of the limb at the elbow is observed to be less in backward strain than in the recover.

In Figs. 1, 2, 3, and 4 the olecranon is in line with the posterior border of the arm above the elbow.

In Fig. 4 the foot is leaving by its inner border. In Fig. 5 the olecranon is more in view, since it is turned out, at the same time the foot is now everted (*i.e.*, rotation outward has taken place as the limb passes from impact of backward strain to that of recover). Extreme position of eversion (Fig. 8) is coincident with the distance between the olecranon and the humerus, and the greatest reduction of distance between humerus and anterior border of the arm. The posterior border of the arm is here beginning to leave the side of the trunk, and a white light is reflected from over the triceps muscle.

During the forward movements of Figs. 9 to 12 the limb is slowly passing back to the position where the olecranon is again in line with the posterior border of the limb (*i.e.*, strictly speaking, in profile of the limb), and the foot is preparing for a second period of impact against the ground.

The lighter shade of the prominence at the back of the elbow answers to the position of the olecranon; the elongated mass of light shade which extends parallel to the arm between the elbow and the shoulder answers to the position of the outer border of the humerus. It is evident by the pictures that the distance between the light over the humerus and over the olecranon is variable. But it is known that the actual distance is invariable, and therefore the apparent variance is due to the motion of the limb in rotation at the shoulder, by which the region of the back of the elbow is moved somewhat outward. At the same time the distance from the outer border of the humerus and the anterior contour is lessened as rotation takes place. These facts being



Series 733, Figs. 1 to 12, illustrating the rotation of the fore limb of the elephant during the act of recover. To be studied from right to left, beginning at the top row.

borne in mind the following additional observations can be made:

The torsion of the limb is pronounced in the Tylopoda examined,—viz., the camel, the dromedary, and the guanaco. This fact should not be disassociated with the absence of anchylosis between the cuboid bone and scaphoid bone with these animals.

In contrasting the above examples with the Pecora,—*e.g.*, the other ruminants, excepting the family of the musk-deers, not examined,—the following structural features may be mentioned as correlations of peculiarities of gait.

In the Tylopoda, when the limb is supporting the body, the hoof is always in line of support with the rest of the limb. In the deer the hoof and digits are angulated with the rest of the limb.

In the Tylopoda the joints are thick, and the outlines are distinctly seen. The fore limb of the Tylopoda is never noticed at a point posterior to the withers, but leaves the ground at an angle of about minus forty degrees. The fore limb of the Pecora is vertical at a point at the centre of the trunk, and leaves the ground at about minus fifteen to twenty degrees. When the limb is off the ground, the digits are flexed to a greater degree in the Tylopoda than in the Pecora.

In the Pecora the limb is smaller and more delicate in proportion to the bulk of the body; the spread of the hoof is less, and the movement of the bones each in the other more precise than in the Tylopoda.

The vertical position of the fore limb under the centre of the trunk is possible, because of the oblique position of the humerus. The heavily-built bovine animals present the same contrasts as the deer, with the exception that the fore limb is carried less backward. (See p. 45.)

The camel has a relatively short metapodium. The joints present curved contours in place of angular ones,—excepting the angle formed by the hock,—and even this is less pronounced than in other ruminants.

Minor Peculiarities.

While the general features of the quadrupedal motion are in all animals the same, minor peculiarities of the carriage have doubtless taxonomic significance. A number of these will be indicated.

The dog when off the ground flexes the fore legs, the cat extends them. This probably correlates with the size of the supraspinous fossæ of the scapulæ in the two animals. (See p. 84.)

The extended fore leg in the cat is parallel to the long axis of the trunk, while in all the ungulates it forms an angle to this axis. The angulation of the parts in ungulates is subject to variation, being more open in the deer tribe than in the ox; in a word, in the lighter-bodied as contrasted with the heavy-bodied forms. The humerus in backward movement is nearly horizontal in the Pecora. (See pp. 42, 45.)

The enormous size of the anterior dorsal spines in the hoofed animals, their smaller size in the claw-footed, their entire absence in Dipus and the bat (in which animals the fore legs are not used for support), the trend of the great extrinsic muscles of the fore limb towards the head, all prepare the observer for some taxonomic values in the relations existing between the strength of the cephalo-humeral muscles, the obliquity of the fore leg in forward movement, and the size of the anterior dorsal spines, and possibly in the shapes of the atlas and axis.

The camel protrudes and withdraws the under lip each time the fore and hind limbs are shifted.

In the North American buffalo the prepuce is drawn backward when the hind limbs are in backward strain.

Characters pertaining to the Superficies emphasized in the Photographs.

It is a well-known circumstance that the photograph will bring out details of structure which are not seen by the unaided eye. Thus, an inscription on a tombstone which was covered by lichen and was quite illegible was found by Professor J. T. Rothrock to be read with the greatest ease when seen photographed after the ordinary manner. The photographs of the series of animals studied reveal similar interesting features. The spots on the lion and the lioness are much more distinct than they are in the living models. In the lioness, in addition, five minute points are detected on the back of the trunk. They probably correspond to the eminences of the skin over the spines of the dorsal vertebræ.

A fairly recognizable description could be drawn up of the superficial muscles of the limbs, especially of those fleshy masses

which pass from the trunk to the limbs. The reflections of light from the hair of the figures of the horse may be ascribed to the changes in degrees of convexity or concavity of the superficial muscle-masses, while some of the stripes of the tiger, especially those of the fore limb and the neck, will be found to answer to the depressions existing between well-defined positions of muscles which can be named with accuracy. In the figures of the roan horse (series 582) the black patch on the rump corresponds to the great biceps muscle.

In the horse (series 579) the depressions between the muscles of the posterior aspect of the thigh are most marked when the limb is in the first stage of the recover, but are obliterated when the limb is in backward strain. The masses at the inner border of the thigh, as seen in the horse (series 582), are nearly flat when the limb is off the ground, but conspicuously convex when the animal is using the limb for support.

In the dog, when both fore feet are off the ground, the muscles which pass from the trunk to the fore limbs are exceedingly tense.

On the Significance of the Skin-Folds on the Trunk of the Hog.

A number of minute changes in the contour of the animals are worth noting. In the figures of the hog (series 673 to 675), at the time when the limbs of a single side are the nearest one to the other the skin is observed to be thrown into a series of vertical folds. It is suggestive of the mechanical origin of the bands in the armadillo that the lines in the hog are in the same position as the bands. They appear to differ only in the circumstance that the folds are transient, while the bands are permanent. (See p. 45.)

The Mane.

Each time the horse, in the series 590, leaves the ground by one of the hind feet the mane streams backward. In series 638, as the animal descends the mane streams upward. This change in position is caused by the motions of the head and neck upward and downward. (See especially figures of the horse rocking, series 649 A. See p. 48.)

The Significance of the Keel on the Metapodium.

The presence of a ridge on the distal ends of the bones of the tarsus and carpus, as well as on the first and second rows of phalanges, is indicative of a precision of motion in the joints of which it constitutes a part. Such ridges are known as keels, and are found in the feet of the ruminants, excepting the group of the camels, and in the horse. The primitive types of mammalian life, as has been pointed out by Professor E. D. Cope,* were without the keel. It first appeared on the posterior surface of the articular surface, and subsequently upon its anterior surface as well. These facts suggest the conclusion that the ridge was developed for some exigencies of the foot while in backward strain, and in the action of the transition from "on" to "off," since the keel first appears on the flexor side of the foot, and that, since in extant animals the camel and its kin are without the keel, a careful comparison of the motions in these creatures with those of the other ruminants would be suggestive of the use of the keel, and lead to some interesting differences between the gaits of primitive and specialized types.

After having made careful studies of the series of the Egyptian camel (736), the Bactrian camel (737 to 742), and the guanaco (743), I have been unable to find any features which correlate with these anatomical peculiarities.

Evolution of the Gait.

The gait in its various expressions is based upon the correlations between the fore and the hind limbs. Assuming that the simplest movement is an alternate action of a single pair (synchiry), the simplest gait is that in which this alternation occurs in each pair independently. The gallop is thus the simplest gait, since the fore pair and the hind pair are independent. But the gallop depends upon a high momentum, and we must assume that the primitive animals were slow walkers. When in a slow rate the same independence is observed,—*i.e.*, when the right fore foot is moved forward at the same time as the right hind foot (lateral heterochiry),—the two pair act rhythmically, and the feet "keep step." This is seen in the rack, which thus becomes a

* The Origin of the Fittest.

practicable gait for a primitive creature. The only objection to this conclusion is the fact that in the giraffe, which is a specialized and aberrant form,—and the legs are remarkable for their length, —we have the best example of a natural pace.

The simplest forms of moving appendages are seen in the Nerita, one of the fresh-water worms, in which the bristle-like rods are moved in all directions without concert. In other forms, as in the sea-hare (Aphrodite), the bristles move in numerous lines extending alongside of the body, but each line in turn being independent of those adjacent to it. The next arrangement obtains in myriapods, whose feet, while in pairs, are seen to move as the horse's in pacing,—*i.e.*, each row acting as a whole, and the two rows alternating. In the lower crustaceans the same method obtains. In the higher crustaceans, as in the crab, the two parts of a single pair may act together.

It stands to reason that when to one side of the body a reinforcement is received from a limb of the opposed side and of a different pair advancing to the median line, a relatively high degree of development has been attained. In a phrase, in animals with highly developed central nervous systems the bilateral coordinations become as practicable as the unilateral.

The question of the manner of using the feet in progression is also likely to be a subordinate one to the question of the size and the bulk of the body. In short-legged, heavy animals of slow movement, the support of the centre of the heavy trunk by the diagonal use of a fore and a hind limb was probably early obtained. Nevertheless the Echidna, a good example of an animal possessing a large, heavy body and short limbs, walked by diagonal heterochiry.* The feet, however, did not approach each other towards the centre of the trunk, as is the case in the walk and the trot of the horse, but kept to the side of the body.

In long, slender natatorial forms, which would occasionally slide among the ooze of a river-bed,—such an animal, for example, as the Potomogale,—doubtless specialization can be attained in the line of development of many of the gaits.† We have

* This was observed in the specimen at the Zoological Garden, Philadelphia.

† The crocodile of the Jumna, according to Hornaday ("Three Years in the Jungle," 1885, p. 55), can stand upon the legs in the same manner as a terrestrial quadruped.

seen that the giraffe uses the pace for all rates of movement; also that the horse modifies his paces by the character of the ground he traverses. It is probable in like manner that an animal will by natural selection determine his methods of progression. Marsh-dwellers are uniformly of the heavy-bodied, short-legged type. In an animal emerging from the marsh to the plains the limbs would become more compact and longer and the gait more various.* Caton† states that the Virginia deer bounds up once or twice at the beginning of his gait, to observe the surrounding country before he settles down to a steady run. This habit would be of no use in an animal living on a prairie, and is absent in the mule-deer. Mere speed is not a necessity of a change of gait. A trot can be based on the walk; the fast pace on the slow pace. In the opinion of Dr. M. H. Cryer, a horse in going over a hurdle employs the same division of his stride as in the run.

Variability of gait in a single animal may be accepted as an evidence of high development. Diversity of function in the study of the gait is of the same value as in other subjects of biology. Thus, an animal starting a movement on the laterals by bringing into use a member of the opposite side, so that three feet may be on the ground at the same time, can develop a walk from the primitive pace, and can either maintain it at will or, shifting from the right to the left lateral support, show a high degree of division of functional labor in the use of the limb. In like manner, when an animal wishing to increase his rate of speed can by election leave the walk to amble, gallop, trot, or pace, an advantage is secured over another animal in which the choice is either withheld or limited.

Of the two pairs of limbs, the front one is the more adaptive for the reason that it is capable of so many secondary modifications, as grasping, flying, etc. We may assume by analogy that the fore limbs are active in changing gaits, the hind limbs acting in a more rigid and uncompromising manner. (See p. 51.)

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* According to F. C. Selous, Proc. Zool. Soc. London, 1881, p. 726, *Rhinoceros simus* can gallop.

† Antelope and Deer of North America, p. 270.

THE MOVEMENTS OF THE HUMAN SUBJECT.

The motions of the hands and feet are essentially those of the quadruped. In the series 258, the man rising from a recumbent position on the ground first uses the left arm for support, subsequently transfers the weight to the right, and after gaining the upright position retains the hand last named as though it were in the first stage of the recover, as seen in the foot of the quadruped. The dictum made in connection with the flexor muscles aiding the foot of the quadruped to maintain itself on the ground is here exemplified (p. 42). It is interesting to note that the moment the hand leaves the ground it becomes markedly flexed.

Gait.

In series 69 the position of the arms (being thrown back at the time that the hind leg of the opposed side is also thrown back) sustains the assertion that the motion of the limbs of man is heterochiral. The chief distinction between the gait of man and that of the quadruped is the degree of torsion of the vertebral column.

For a good illustration of this torsion the figure of the boxer (series 333) may be consulted.

The Action of the Disengaged Limb.

In series 311 and 312, while the right hand is engaged in throwing a weight the left is in a state of great tension. The limb is extended and the fingers are abducted. The fingers remain extended save at the terminal phalanges, and show activity of the interossei muscles. The position just named is suggestive and presents a *raison d'être* for the following reflections:

First, that the unemployed arm is thrown into a state of excitement because of the intentive strain on groups of muscles in close co-ordination with them,—viz., the muscles of the limb of the opposed side. The limb cannot repeat the exact attitude of the one in use, and naturally tends to take on the form of the primal limb. This form is that of a motion as though it were on the ground and serving the purposes of progression. As is known from the study of the quadruped, the limb after extension passes gradually into flexion. It is evident that the interossei muscles would not flex the terminal phalanges if the foot were on the

ground, but would simply hold the ends of the toes firmly to the plane on which the animal is moving. The toes are also markedly abducted in the same position. The attitude taken by the human fore limb is precisely that of the fore limb of the quadruped engaged in terrestrial progression, and is modified in its action solely by the circumstance that it "claws the air." The function of the interossei would appear to be the retention of the phalanges of the terminal row against the ground as the last act of the behavior of the foot in the first stage of the recover.

Second, that the occurrence of convulsive seizures, in which the limb assumes the position just described, may not necessarily be the result of an irritation of the centres which control the co-ordination, but an evidence of a profound irritation elsewhere in the economy. This phenomenon properly belongs to the group of influences described by Drs. Mitchell and Lewis.*

To a still greater extent than in the quadruped the superficial muscles are conspicuous. It is of interest to note that the sartorius muscle may be tense even when the foot is on the ground, as is observed in the figure of a man lifting a weight (series 322, Fig. 12). In various attitudes the several portions of the trapezius muscle are contracted. In series 323, Fig. 9, in the figure of a man engaged in lifting a dumb-bell, the upper portion of the dorsal division of the muscle is enormously enlarged.

Oscillation.

The single series designed to illustrate the movements of the pelvis in walking is not in all respects satisfactory.

Since the index at first inclines to the right side, which corresponds to the limb which is off the ground, the idea is at once suggested that the inclination is greatest towards the side not bearing weight, especially when it is noted that the index is vertical and parallel to the vertebral column when the legs are both on the ground. But when the left foot is lifted the lever remains in the vertical position, and no definite conclusion as to the effect of the movements of the limbs on the oscillation of the level is determined.

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* Philadelphia Medical News, 1885, vol. xlviii. p. 169.

FLIGHT.

The flight of the bird is illustrated in series 755, 756, 757, pigeon; 758 to 762, cockatoo; 763, 764, hawk; 769, 770, eagle. The following conclusions have been drawn from the photographs:

The wing is extended upward from the horizontal position by the deltoid and latissimus dorsi muscles to a line which is perpendicular to the body, and is quickly again depressed to the horizontal position by the pectorals. (See p. 40.) This constitutes the first stage of the "stroke."

"Recover" is initiated by an inward rotation of the humerus, semiflexion of the wing at the elbow (the pinion remaining extended and directed obliquely downward and outward), and is carried well forward to a degree sufficient, when seen in profile, to conceal the head. In this position the primaries are semi-rotated so as to present the least amount of surface to the air in the direction in which the bird is moving. The impetus excited by the "stroke" carries the bird upward and forward. In the second stage of "recover" the humerus is rotated outward, the arm is quickly raised, the primaries restored to the position seen in the bird at rest, and the wing is a second time ready for the "stroke." (See p. 38.)

In the eagle and the hawk the legs are in the position of the "stroke" when the wings are similarly placed. During the "stroke" the legs move backward. This position continues during the "recover" of the wing, so that the time of the "recover" is also that of the "recover" of the leg.

Biological Department
University of Pennsylvania,
July 1, 1887.

APPENDIX.

A LIST OF THE QUADRUPEDS AND BIRDS REPRESENTED IN THE PHOTOGRAPHS.

BY EDWIN A. KELLEY.

Series 563–657. Horse—Equus caballus, Linn.
" 658–664. Mule, hybrid—♂ E. asinus and ♀ E. caballus.
" 665–668. Ass—Equus asinus, Linn.
" 669–672. Ox—Bos taurus, Linn.
" 673–675. Sow—Sus scrofa, Linn.
" 676–679. Goat—Capra hircus, Linn.
" 680. Oryx—Oryx leucoryx, Pall.
" 681. Virginia Deer—Cariacus virginianus, Gm.
" 682. Fallow Deer—Dama vulgaris, Gray.
" 683. Virginia Deer—Cariacus virginianus, Gm.
" 684–691. Fallow Deer—Dama vulgaris, Gray.
" 692–695. Elk—Cervus canadensis, Schreb.
" 696. Eland—Oreas canna, H. Smith.
" 697–698. Dorcas Gazelle—Gazella dorcas, Linn.
" 699–700. American Bison—Bison americanus, Gm.
" 701–702. White-tailed Gnu—Connochætes gnu, Zimm.
" 703–715. Dog—Canis familiaris, Linn.
" 716–720. Cat—Felis domestica, Bris.
" 721–726. Lion ♂—Felis leo, Linn.
" 727–728. Lion ♀— " " "
" 729–730. Tiger ♀—Felis tigris, Linn.
" 731. Jaguar—Felis onca, Linn.
" 732–735. Elephant—Elephas indicus, Cuv.
" 736. Dromedary—Camelus dromedarius, Linn.
" 737–742. Bactrian Camel—Camelus bactrianus, Linn.
" 743. Guanaco—Lama huanacos, Mol.

Series 744–745. Raccoon—Procyon lotor, Linn.
" 746. Capybara—Hydrochœrus capybara, Erxl.
" 747–749. Chacma Baboon—Cynocephalus porcarius, Bodd.
" 750. Sloth—Cholœpus hoffmani, Peters.
" 751–754. Kangaroo—Macropus giganteus, Shaw.
" 755–757. Common Pigeon—Columba livia, Bris., var. domestica.
" 758–762. Cockatoo—Cacatua galerita, Lath.
" 763. Red-tailed Hawk—Buteo borealis, Gm.
" 764. Fish-Hawk—Pandion haliaëtus, Linn, var. carolinensis, Gm.
" 765–768. Turkey-Vulture—Cathartes aura, Linn.
" 769–771. American Eagle—Haliaëtus leucocephalus, Linn.
" 772–773. Ostrich—Struthio camelus, Linn.
" 774–775. Adjutant—Leptoptilus argala, Lath.
" 776–780. Groups of birds, as follows:

Muscovy Duck—Cairina moschata, Linn.
Canada Goose—Branta canadensis, Linn.
Blue Goose—Anser cœrulescens, Linn.
Bar-headed Goose—Anser indicus, Lath.
Chinese Goose—Anser cygnoides, Linn.
European (Mute) Swan—Cygnus olor, Gm.
American Swan—Cygnus americanus, Sharpl.
Black Swan—Cygnus atratus, Lath.
Sand-hill Crane—Grus canadensis, Linn.
Australian Crane—Grus australasiana, Gould.
Demoiselle Crane—Anthropoides virgo, Linn.
Crowned Crane—Balearica pavonina, Linn.
White Stork—Ciconia alba, Bechst.
Black Stork—Ciconia nigra, Linn.
Adjutant—Leptoptilus argala, Lath.
etc.

" 781. Chicken—Gallus bankiva, Temm., var. domesticus.

The following list embraces the series that are mentioned by number in the text of the report:

258	576	612	633	675	695	729	747	760
311	579	616	637	677	703	730	750	761
312	581	617	641	680	704	733	755	762
322	594	619	642	681	707	743	756	763
323	595	622	649A	682	709	744	757	764
333	601	631	658	682A	720	745	758	769
574	602	632	670	683	728	746	759	770

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