

Article XII.—STUDIES ON THE EVOLUTION OF THE PELVIS OF MAN AND OTHER PRIMATES

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PLATE XXII; TEXT FIGURES 1 TO 10

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INTRODUCTION

STATEMENT OF PROBLEM AND METHODS

Although there have been many excellent papers on the osteology of the primate pelvis¹ and upon the myology of the pelvic region in many primates² there has been little attempt to show the relation between the form of the pelvis and the function of the muscles attached to it. Weidenreich (1914), in his important paper on the form of the pelvis, deals with the subject from a different point of view. He shows some of the effects of the changed distribution of body weight in the evolution from the arboreal quadrupeds to bipedal man. His references to the effects of muscular action are limited to the suggestions that the strong development of the anterior inferior iliac spine is traceable to the action of the rectus femoris which assists the ilio-femoral ligament in the maintenance of balance in the upright position of the body; that the pull of the tensor fascia lata and ilio-tibial tract causes the especial development of the anterior superior iliac spine; and that the modification of the anterior and

¹The most recent comparative study is that of v. d. Broek (1914).

²An excellent bibliography is given in Sonntag (1924).

upper margins of the symphysis depends upon the pull of the adductors. Knauer (1914) has suggested that the development of the fossa iliaca of man is due to the action of the pelvic musculature. The abdominal muscles are stretched tightly between the iliac crests to aid in keeping the pelvic viscera in place. This strong pull and the counteraction of the viscera condition the iliac fossa. He believes also that the characteristic broadening of the ilium in anthropoids is due in part to the gluteal musculature.

Sir Arthur Keith (1923) has made the following statements: (1) that the disappearance of the tail extensors consequent upon the loss of the tail has left the sacrum free for use of the erectors of the spine; (2) that the sacralization of the seventh and sixth lumbar vertebræ extends and strengthens the area for spinal fixation; (3) that the extension of the iliac crests, particularly in the dorsal direction gives an increased base for the fixation of spinal muscles; (4) that the backward tilt of the sacrum in man has still further increased their area of origin; (5) that the shortening of the anterior border of the ilium in the primate series has resulted in a weakening of the human groin; (6) that short pelvic levers are desirable in upright walking man, whereas long pelvic levers are necessary in the climbing anthropoids; (7) that the tilting of the symphyseal part of the human pelvis in the direction of the umbilicus has brought the levator ani muscles into a more horizontal position so that in man they form a pelvic floor capable of supporting the abdominal contents.

Since these papers are of a general nature, unaccompanied by diagrams and descriptions of conditions in particular animals, it was thought that a detailed study of the pelvic region in representatives of as many of the families as were available might yield additional points of interest in regard to the evolution of the primate pelvis. This investigation was undertaken, then, with the immediate purpose of determining the relation between the locomotor habits of the animal and the external form of the pelvis in a series of primates from the lemur to man. It was expected that the study would yield results which would be of value in the attempt to separate habitus from heritage characters in these forms and that it would, therefore, throw some light upon the evolution of the pelvis within the group.

In the attempt to discover the connection between the locomotor habits and the pelvic structure, certain facts established through the work of various anatomists and physiologists were kept in mind.

(1).—The force which a muscle can exert depends upon the number of its fibers.

(2). The extent through which a muscle can contract depends upon the length of its fibers.

(3).—The amount of work done by muscle fibers is inversely proportional to their rate of contraction. The greater the contraction rate the greater is the number of fibers required to do a given amount of external work.

(4).—A muscle can pull with the most force when it is under tension.

(5).—The total pull of a muscle inserting obliquely onto a bone must be resolved into two components: one, a centripetal component, or a pull along the shaft toward the joint concerned; the other, the rotation component, or a pull across the shaft. The rotation component can be shown to vary directly with the angle of insertion.

(6).—The speed of the distal end of a long bone varies inversely with the angle of insertion of the muscle, provided the rate of contraction and length of muscle are kept constant.

(7).—The speed of the distal end of a long bone becomes greater with the approach of the insertion point toward the head of the bone, provided the angle of insertion and rate of contraction are constant.

(8).—The speed at which animals can move is dependent partly upon the strength of their bones, tendons, and joints. The strength of these structures is proportional to their cross-section.

(9).—Osteoblasts build according to the stresses to which they are subjected.

In analyzing the function of muscles whose contraction causes movement in the hip-joint, the following facts were remembered: that the hip-joint is a multiaxial joint in which movement is free in all directions; that in any multiaxial joint there are, however, three cardinal axes about which movement can take place, and three cardinal planes in which movement can take place; that the actual plane of any movement is said to be defined by three points: the point of origin of the muscles, the point of insertion, and the center of rotation of the joint. The table below gives the relationship of cardinal axes, planes, and types of motion in a quadruped and in man.

Quadruped

PLANE	AXIS	TYPE OF MOTION
Dorso-Ventral or Longitudinal	Horizontal	Flexion-Extension
Transverse	Longitudinal	Abduction-Adduction
Frontal	Dorso-Ventral	Rotation

Man

PLANE	AXIS	TYPE OF MOTION
Longitudinal	Frontal	Flexion-Extension
Transverse	Longitudinal	Rotation
Frontal	Anterior Posterior	Abduction-Adduction

The theoretical analysis of function was frequently checked upon animals in which the capsule of the hip-joint had not been broken. Holes were bored through pelvis and femur at various points on the areas

of origin and insertion of the muscle in question. Thread was drawn through the holes and knotted at one end. The other end was left free so that it could be pulled when the animal had been put into the desired position. A pull from the insertion upon the origin or vice versa gave some idea as to the function of the muscle.

The pelvic region was dissected in the following forms:

1. <i>Lemur varius</i>	adult male
2. <i>Lemur</i>	adult female
3. <i>Perodicticus</i>	adult female
4. <i>Galago gallarum</i>	adult female
5. <i>Cebus hypoleucus</i>	adult female
6. <i>Alouatta seniculus</i>	young female
7. <i>Alouatta seniculus</i>	adult female
8. <i>Macacus</i>	adult female
9. <i>Lasiopyga</i>	adult male
10. <i>Papio hamadryas</i>	adult male
11. <i>Hylobates</i>	young male
12. <i>Pan</i>	young male
13. <i>Pongo</i>	young female
14. <i>Gorilla</i>	young male
15. <i>Homo</i>	male

Excellent skeletons of the forms dissected were made available for study through the courtesy of the authorities of The American Museum of Natural History.

I am greatly indebted to Dr. William K. Gregory of Columbia University and The American Museum of Natural History for suggesting this problem and for his helpful criticism throughout the course of the work. My thanks are also due to Mr. Harry C. Raven of the Museum for his aid in securing material and for the benefit which I have derived from discussion with him in regard to the habits of the animals studied and the action of muscles in mammals. I am grateful to Mrs. Helen Ziska for her aid in preparing the plate and text figures.

CLASSIFICATION AND HABITS OF THE ANIMALS STUDIED

The following outline gives the systematic position of the forms dissected.

Suborder Lemuroidea

Family Lemuridæ—*Lemur*

Family Lorisidæ

Subfamily Galaginæ—*Galago*

Subfamily Lorisinæ—*Perodicticus*

Suborder Anthroidea

Series 1. Platyrrhini

Family Cebidæ—*Cebus*, *Alouatta*

Series 2. Catarrhini

Family Cercopithecidæ—*Macacus*, *Papio*, *Lasiopyga*Family Simiidæ—*Hylobates*, *Pongo*, *Pan*, *Gorilla*Family Hominidæ—*Homo*

The animals listed above are arboreal quadrupeds, with the exception of *Papio*, the anthropoids, and man. *Papio* is a quadruped but is secondarily terrestrial. The anthropoids are arboreal but they go upright in the trees swinging along by their arms, a method of locomotion known as brachiation.

A short description of the peculiar life habits of each animal is given below:

Lemur.—Capable of running with great speed along the branches and of leaping with marvelous agility.

Galago.—An excellent climber and leaper. The shortening of its anterior limbs makes it a poor walker or runner.

Perodicticus.—Very slow in all its movements. It never leaps or runs.

Cebus.—Very active. It walks and runs on the branches of the trees and often descends to the ground. It approaches a semi-upright position in squatting.

Alouatta.—A sluggish animal. It has a prehensile tail which it uses in swinging from tree to tree.

Macacus.—Like all Old World monkeys it is capable of sitting upright with a straight back.

Lasiopyga.—An active leaping form.

Papio.—Rarely ascends into the trees but lives in the open country. It can run swiftly over the ground.

Hylobates.—An excellent climber and bipedal walker. In the trees it holds itself erect and on the ground it can run in the erect position holding its hands above its head to aid in the maintenance of balance.

Pongo.—Extremely arboreal. Its fore and hind limbs are used more for suspension than support. On the ground it moves like a quadruped but very awkwardly. According to Pocock it is fourth among the apes in bipedal locomotion.

Pan.—An excellent climber. It runs on the ground like a quadruped. It stands upright only occasionally and then for very short periods of time.

Gorilla.—Not as good a climber as the other anthropoids. It ranks second to the gibbon in bipedal and second to the chimpanzee in quadrupedal locomotion.

FORM OF THE ILIUM IN RELATION TO ITS MUSCULATURE

It is realized that the pelvis functions as a whole, that the parts are so interrelated that a change in one part may be correlated with a change in some other part, and that such a change may have more than one

consequence; yet it is necessary for the purpose of analysis to consider the various parts separately.

In the ilium of primates (Fig. 1) there are three surfaces and four edges. Following v. d. Broek's terminology the surface turned toward the vertebral column is called the sacral plane; the ventrally directed surface, the iliac plane; the third surface, the gluteal plane. The margo pubicus separates the sacral plane from the iliac; the margo acetabuli, the iliac from the gluteal; and the margo ischiadicus, the gluteal plane from the sacral. The iliac crest is the anterior edge of the ilium which connects the margo ischiadicus with the margo acetabuli.

Taking as a type form an arboreal quadruped like the lemur we find the gluteal plane (Fig. 2F) divided into two parts: a lateral and a medial. The larger lateral part, the gluteal plane proper, reaches from the margo acetabuli to a swollen projection which extends from the posterior superior iliac spine to the great sciatic notch. The small medial surface which will be called the postgluteal plane extends from the swollen projection to the margo ischiadicus.

The sacral plane is likewise divided into two parts, an upper and a lower, the upper consisting of the auricular surface and the iliac tuberosity, the lower turned toward the small pelvis.

The margo pubicus (Fig. 1A) is divided into two parts which form an angle with each other. The part below the auricular surface is called the linea terminalis (*lt*); the part above this which separates the auricular surface and iliac tuberosity from the iliac plane, the linea limitans (*ll*). The linea limitans ends in a projection of the iliac crest called the spina limitans (*sl*).

The margo ischiadicus consists of two parts: the upper, forming the dorsal boundary of the iliac tuberosity and the auricular surface; the lower, the edge of the sciatic notch.

The changes in the above surfaces and edges that are correlated with the changed locomotor habits of the animals studied will be described after a necessary preliminary discussion of the length of the iliac blade in Primates.

THE LENGTH OF THE ILIUM

There is a rather steady increase in the length of the ilium in relation to the length of the body in the series from the lemur up to gorilla. In man the blade is short again as the following table shows.

Length of Iliac Blade in Relation to Length of Body

Animal	Length of Body ¹	Length of Blade ²	$\frac{\text{Length of Blade} \times 100}{\text{Length of Body}}$
Cat	33 cm.	4 cm.	12
<i>Lemur</i> , No. 755	27	4.2	16
<i>Lemur</i>	34	5.8	17
<i>Perodicticus</i>	26	4.9	19
<i>Galago</i>	12	2.6	22
<i>Cebus</i> , No. 583	31	6.1	19
<i>Cebus</i>	30	5.6	19
<i>Alouatta</i>	37.5	7.3	19
<i>Alouatta</i> , No. 557	32.5	6.1	19
<i>Macacus</i>	36	7.7	21
<i>Lasiopyga</i> No. 585	34	6.0	18
<i>Lasiopyga</i>	42	7.7	18
<i>Papio hamadryas</i> , No. 632	53	11.0	21
<i>Papio hamadryas</i>	54	11.1	21
<i>Hylobates</i> , No. 651	29	7.0	24
<i>Hylobates</i>	37.5	9.2	24
<i>Pan</i>	48	11.6	24
<i>Pongo</i>	63	15.5	25
<i>Gorilla</i>	54	15.5	28
<i>Homo</i>	72.5	11.9	16
<i>Homo</i>	75	12.0	16
<i>Homo</i>	77	12.5	16

The length of the blade may be taken as a rough measurement of the power arm of the lever concerned in the movement of the body from the fulcrum at the hip-joint. The weight arm of the lever would be the distance from the hip-joint to the center of gravity of the animal. In the case of eight of the above animals it was possible to determine the weight arm for one position of the animal.

The distance of the center of gravity from the acetabulum was determined in the following way. The animal was suspended in the quadrupedal position from a rod by ropes tied around the body in front of the shoulder and hip-joints and that rod was then balanced on the edge of another rod placed beneath it and at right angles to it. The point on the

¹Length of body measured from center of acetabulum to crown of head.

²Length of blade measured from center of acetabulum to most anterior point.

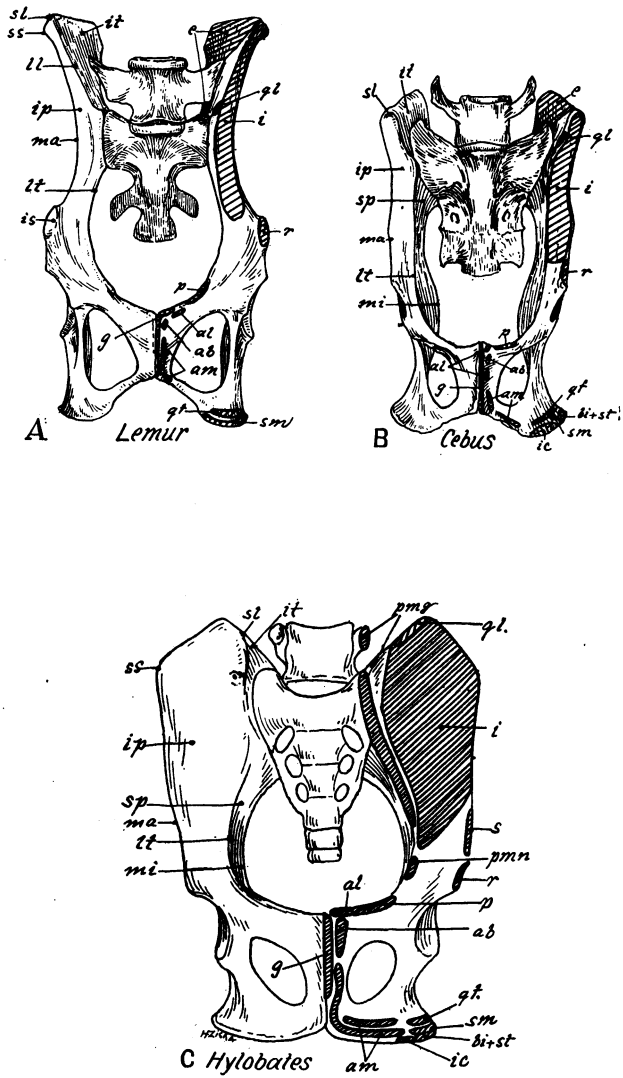


Fig. 1. Pelves in ventral view. (See page 642 for key to abbreviations.)

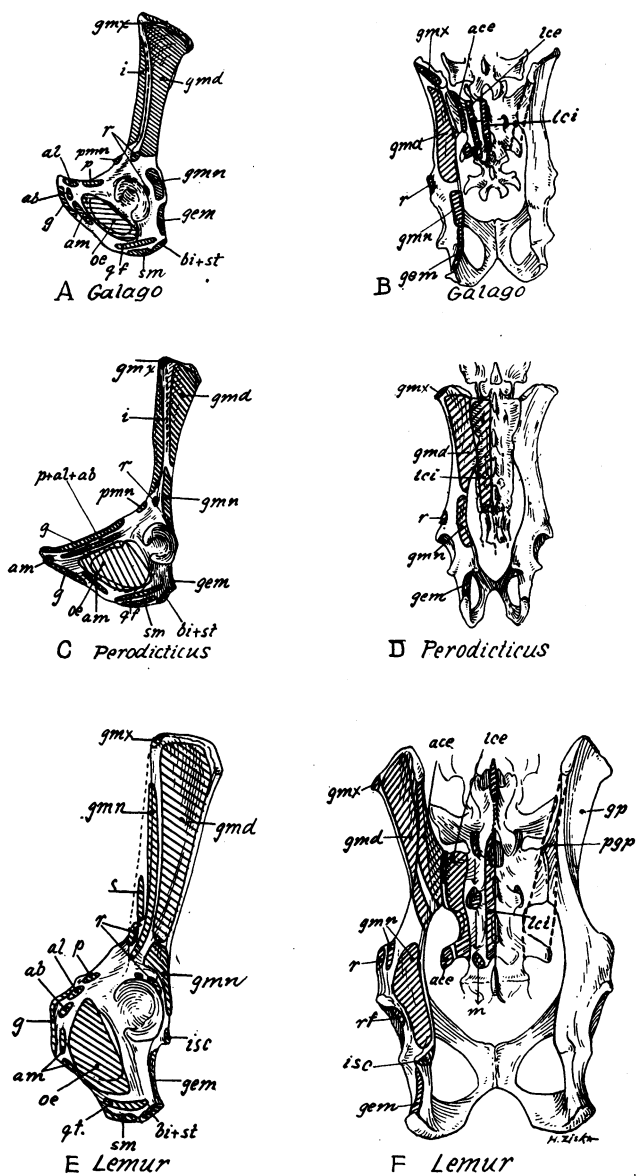


Fig. 2. Pelvises of lemurs in lateral and dorsal views.

animal beneath the balancing point on the rod was marked and the distance from that point to the acetabulum measured.

For purposes of comparison the cat, a non-arboreal quadrupedal animal, was included in the study.

Length of Iliac Blade in Relation to Position of Center of Gravity

Animal	I Length of Body	II Distance of Center of Gravity from Acetabulum	$\frac{II \times 100}{I}$	III Length of Iliac Blade	$\frac{III}{II}$
Cat	33	14	42	4	29
<i>Lemur</i> , No. 755	27	9	33	4.2	46
<i>Cebus</i> , No. 583	31	12	39	6.1	50
<i>Alouatta</i> , No. 557	32.5	12.5	38	6.1	49
<i>Macacus</i> , No. 1046	36	17	47	7.7	45
<i>Lasiopyga</i> , No. 585	34	14.5	43	7	48
<i>Papio</i> , No. 632	53	24	45	11	45
<i>Pan</i> , No. 531	48	18	37	11.6	64
<i>Pongo</i>	63	28	44	15.5	55

The table brings out the fact that the long ilium of the lemur, an arboreal leaper, provides a much more powerful lever arm than the ilium of the non-arboreal leaper, the cat. It shows that as the blade has increased in length in the series of primates the center of gravity of the body has moved forward. Therefore, the relation in percentage of power arm to weight arm has remained almost the same, except in the chimpanzee and the orang. In the chimpanzee the center of gravity is nearer the acetabulum again, but the blade is even longer so that there is an arrangement for even greater power. In the orang the center of gravity is far forward, but the blade is longer so that the lever there is powerful also.

The determination of the weight arm was not made for man, but the construction of the human body makes it evident that the center of gravity would lie closer to the acetabulum than in the anthropoids. The short blade, then, would give sufficient power and it would provide for more speedy movement than the longer blade, a desirable thing in bipedal man as Keith has pointed out.

There is a certain provision for speed of movement, however, in the blade of the arboreal primates, for the long blade in itself gives an

extensive surface for the attachment of muscle fibers and so makes possible the presence of powerful muscles capable of rapid contraction. In man the decrease in height of the blade is compensated for by an increase in width so that the muscle areas are large. The short blade is, then, simply an added factor for speed.

THE GLUTEAL PLANE

In the lemur the gluteal plane (Fig. 2 E, F) faces almost entirely laterally. There is, to be sure, an outward flare at the anterior end which conditions an antero-posterior concavity and there is a tendency toward horizontal flaring especially marked at the anterior external angle of the blade and at the anterior inferior iliac spine. The plane in its anterior part is concave dorso-ventrally.

The gluteus medius, two portions of the gluteus minimus, and a few fibers of the gluteus maximus take origin from this surface. Of these, the gluteus medius is by far the most powerful. It is a bipenniform muscle having an origin not only from the bone but from the gluteal fascia above it and from the fascia between it and the abductor caudæ externus as far down as the tip of the last sacral vertebra. On the bone it extends from the anterior edge of the ilium almost to the region of the anterior inferior iliac spine. It is inserted on the lateral surface of the great trochanter. The gluteus minimus is in two parts. One, sometimes called the scansorius, arises from a narrow strip along the ventral edge of the gluteal plane and from a ligament stretching between the anterior external angle of the ilium and the anterior inferior iliac spine. The other arises from the surface of the ilium posterior to the gluteus medius. These two parts are inserted separately into the anterior crest of the great trochanter. The gluteus maximus arises by muscle fibers from the anterior superior spine and through an aponeurosis from the anterior crest of the ilium, the margo acetabuli and the spinous processes of the sacral and caudal vertebræ, and by muscle fibers from the transverse processes of the second and third caudal vertebræ. The part arising from the anterior superior spine is inserted into the third trochanter. The rest of the muscle continues below the great trochanter to the posterior part of the femur.

One of the chief functions of the gluteus medius in the lemur is lateral rotation of the pelvis. If the point of origin of any one of the muscle fibers arising from the laterally directed portion of the plane is connected with its point of insertion and the center of rotation of the joint the three are seen to lie almost in the frontal plane. The move-

ment is, therefore, rotation: inward rotation of the thigh when the pelvis is fixed; lateral rotation of the pelvis when the thigh is fixed. Undoubtedly, the more posterior fibers of the muscle, especially those lying above the piriformis, function in abduction, but the more important action in relation to the form of the pelvis is lateral rotation, a fundamental

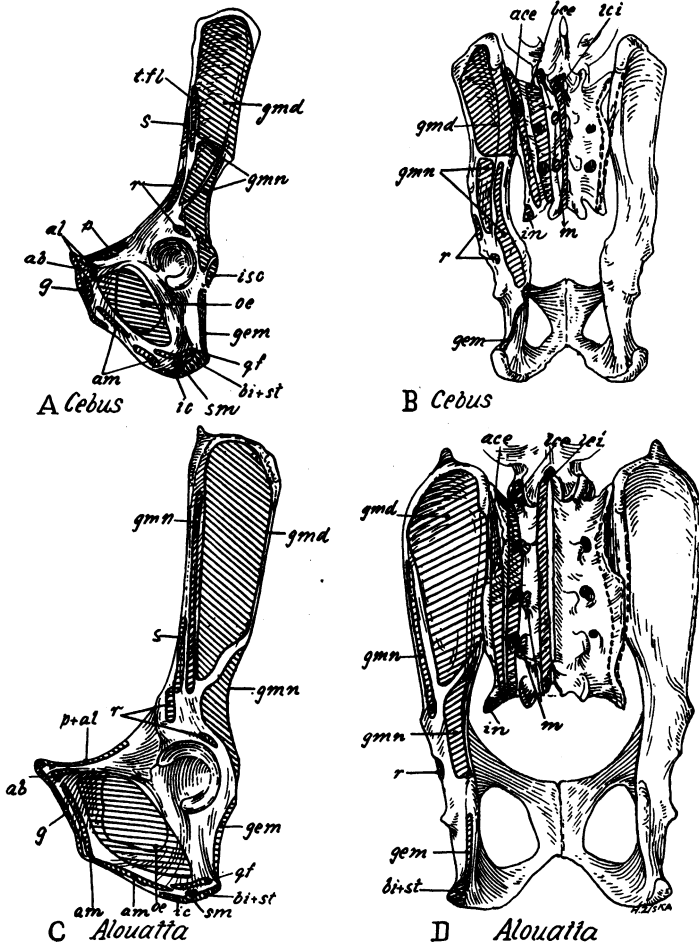


Fig. 3. Pelves of South American monkeys in lateral and dorsal views.

movement in an arboreal leaper which must be able to turn its whole body very quickly in order to maintain its footing in the trees, to insure a good "take off" from uneven branches and a safe landing on the desired spot. The long curved iliac blade provides an extensive surface for

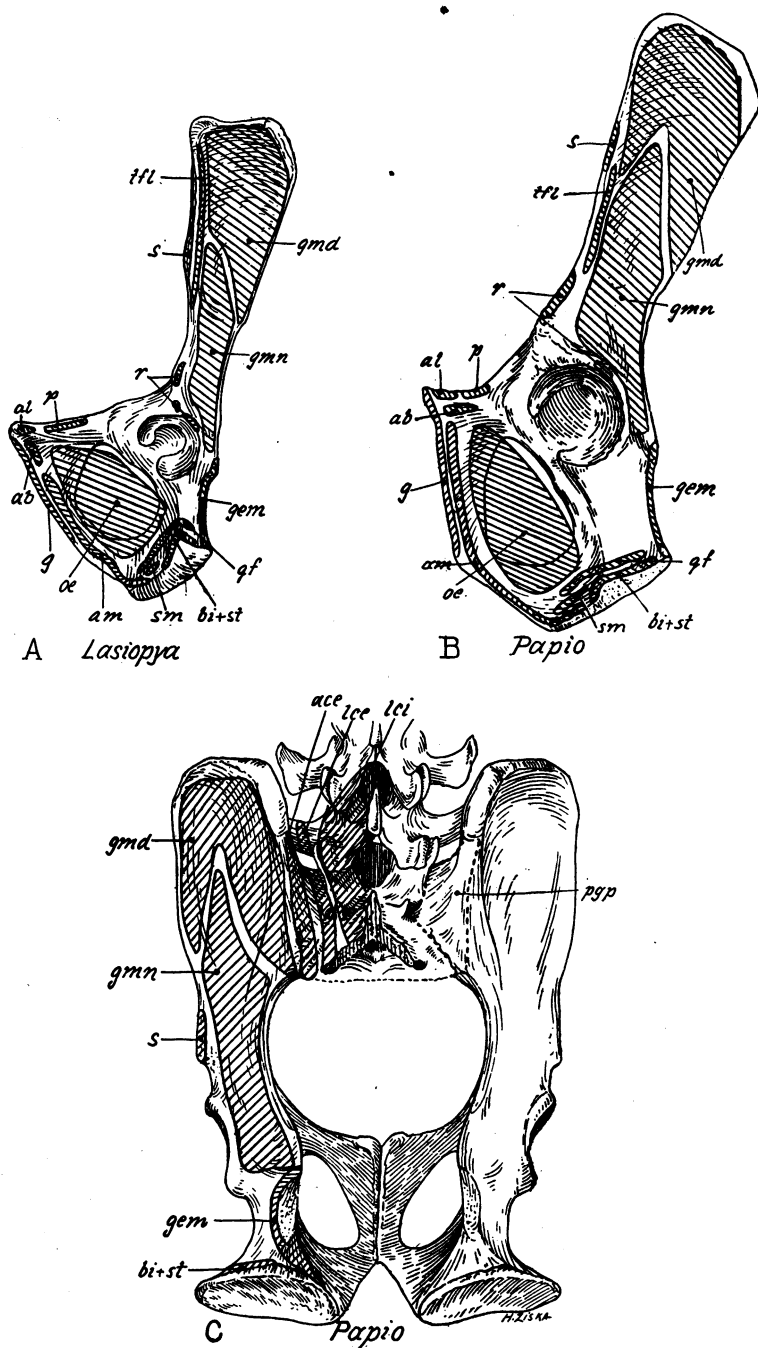


Fig. 4. Pelves of Old World monkeys in lateral and dorsal views.

this muscle and the outward flaring of the blade at the anterior end means a wider angle of insertion for the muscle fibers on the pelvis, an arrangement for power. The portion of the gluteus minimus arising along the ventral edge of the plane is in a position to assist in the lateral rotation of the pelvis as is the portion of the gluteus maximus which extends from the third trochanter to the anterior superior spine.

Another adaptation for the leaping habits is seen in the horizontal flaring which is so noticeable in the gluteal plane. This permits the gluteus medius as well as those fibers of the gluteus maximus which extend toward the anterior end of the iliac blade to act with power in holding the pelvis in the desired position just before the animal leaps and to aid in the extension of the hip joint which occurs simultaneously with extension of the knee and ankle at the moment of the "take off." It is evident that when the animal is crouched for the spring the hamstrings cannot maintain any extension of the pelvis on the thigh. The glutei, however, are under tension and by the degree of their contraction can help to determine the angle which the pelvis shall make with the thigh. Thus they help to determine the direction of the leap.

Galago (Fig. 2, A, B) and *Perodicticus* (Fig. 2, C, D) reveal their lemuroid heritage in the orientation of the gluteal plane, the presence of a third trochanter on the femur, and in certain of the muscular arrangements. The gluteus medius occupies the greater portion of the gluteal plane and there is a portion of the gluteus maximus attached to the third trochanter as in the lemur. The scansorius portion of the gluteus minimus is lacking, however, and the gluteus maximus (Fig. 7 C, D) in these two members of the family Lorisidæ is muscular over the entire surface of the gluteus medius. In *Galago* it arose by muscle fibers from the entire anterior edge of the ilium, in *Perodicticus* by muscle fibers from the anterior superior spine and by short tendinous fibers from the remainder of the anterior edge. There is no gluteal fascia and the gluteus medius is not bipenniform.

In contrast to the condition in the lemur, the margo acetabuli in both these forms is faintly marked and a portion of the iliac plane faces laterally. The outward flaring at the anterior end of the blade is less marked.

The faintness of the margo acetabuli may be explained in part, perhaps, by the fact that there is no pull upon it by fibers of the gluteus medius through a gluteal fascia or by any portion of the gluteus minimus. But there is another reason for it. The dorso-ventral concavity characteristic of the gluteal plane of the lemur is lacking in *Perodicticus* and

Galago. Thus the surface for attachment of muscle fibers is not as great in these last two forms. For *Galago* this seems surprising at first because in the extreme leaping type extensive surfaces of origin for the muscles might be expected. If, however, we take into consideration the fact that in *Galago* the length of the blade makes up twenty-two per cent of the length of the body, whereas in the lemur the blade is only sixteen per cent of the body length, and that the center of gravity of the body of *Galago* is nearer the acetabulum owing to the shortening of the anterior limbs, we come to the conclusion that *Galago* does not need as powerful muscles. Nor does the sluggish *Perodicticus* need large surfaces for muscle attachment. Anthony (1914) has shown by his experiments on dogs that the formation of the sagittal crest of the skull is dependent upon the presence of two powerful temporal muscles. If the muscle on the left side of the skull were removed the muscle on the right side extended its origin to the left of the mid-dorsal line but the crest did not form normally. Thus it seems reasonable to interpret the sharp margo acetabuli of the lemur as due to the presence of a powerful gluteus medius, attempting, we may say, to extend its surface of origin while the faint margo acetabuli of *Galago* and *Perodicticus* may be due to reduction in power of that same muscle.

A comparison of dorsal views of the pelves of *Lemur*, *Galago*, and *Perodicticus* (Fig. 2, B, D, F) brings out the fact that there is less outward flaring of the iliac blade at its anterior end in *Galago* and *Perodicticus*. For the *Lemur*, as shown above, this outward flaring gives a wider angle of insertion for the fibers of the gluteus medius on the pelvis. In this connection, it should be noted that there is less contrast in *Galago* and *Perodicticus* than in *Lemur* between the distance across the small pelvis from acetabulum to acetabulum and the distance across the middle of the sacrum. Consequently, the pull backward to the great trochanter is direct in these animals, whereas it would not be direct in the *Lemur* if there were no outward flaring.

In the South American monkeys, *Cebus* and *Alouatta* (Fig. 3), the entire ventral portion of the gluteal plane is turned at an angle to the rest of the plane so that it looks dorsally. There is no ligament comparable to that in *Lemur* which stretches from the anterior superior to the anterior inferior iliac spine. It is as if the area occupied by the ligament had become filled out with bone in such a way as to make the margo acetabuli almost straight. The distance between the spina limitans and the anterior superior spine is greater than in the lemur.

From the dorsally directed portion of the plane arise fibers of the

gluteus medius, gluteus minimus, and tensor fascia lata. The gluteus maximus has no attachment through muscle fibers to any portion of the blade and in this connection we may note the disappearance of the third trochanter from the femur.

In the two specimens of *Cebus* measured, twelve per cent of the entire area occupied by the gluteus medius was found to face dorsally, whereas in the lemur, only six per cent faced directly dorsally. The habits of *Cebus* differ from those of *Lemur* in one important respect upon the basis of which the difference may be explained. *Cebus* approaches the semi-upright position in squatting. The fibers arising from the dorsally directed portion of the iliac blade are ideally placed to aid in the maintenance of this position. The primates squat with the feet close to the ischial tuberosities and the thighs parallel with and close to the abdomen. In this position the hamstring muscles are of no use in holding the pelvis upright, but the glutei, put into a state of tension by the flexion of the hip-joints, are in a position of physiological advantage for preventing a forward fall. The opposing iliacus would prevent a backward fall.

The horizontal flaring of the gluteal plane is more pronounced in *Alouatta* than in *Cebus*, more even than in some of the Old World monkeys. Forty-eight per cent of the gluteal plane faces dorsally. It is difficult to account for this since *Alouatta* is a sluggish creature. As noted by v. d. Broek, it is much like *Ateles*, however, in the skeletal characteristics of its pelvis. These likenesses may perhaps be taken as indication of relationship. It is said that *Ateles* goes upright in the trees to a greater extent than the other South American monkeys, that it is, in fact, a very primitive brachiator. The broadening of the gluteal plane would, then, have significance not only in relation to the action of the glutei but also in relation to the action of the muscles attached to the crest above it, since those muscles in brachiating forms must help to support the weight of the pelvis and lower limbs when the animal hangs by its arms. The broader crest would give a firmer origin to the suspending muscles.

The muscle maps shown in the diagrams of the pelvis reveal the fact that in *Cebus* (Fig. 3), as in all the Old World monkeys (Fig. 4), anthropoids, and man (Plate XXII), the gluteus medius is limited to the anterior portion of the gluteal plane, whereas in *Lemur* (Fig. 2 E) and *Alouatta* (Fig. 3, D), the muscle extends almost to the region of the anterior inferior iliac spine.

An examination of the relative lengths of muscle fibers in the series

revealed the interesting fact that, with the exception of *Alouatta*, the fibers of the gluteus come to approach more nearly in length those of the iliacus in the same animal as one ascends in the series.

Animal	I	II	$\frac{I}{II}$
	Length of Fibers of Gluteus Medius	Length of Fibers of Iliacus	
<i>Lemur</i>	2.6	4.3	62
<i>Cebus</i>	2.7	3.5	77
<i>Alouatta</i>	2.2	5.7	39
<i>Lasiopyga</i>	4.2	4.7	89
<i>Papio</i>	7.6	7.7	99
<i>Hylobates</i>	4.5	4.5	100
<i>Pan</i>	7.0	7.0	100

The length of fibers of a muscle may be taken as an indication of the extent through which the muscle can contract. The amount of movement in a joint produced by muscular contraction is dependent not only upon the extent of contraction of the muscle but upon the distance of the point of origin and insertion from the center of rotation of the joint. The fibers of the iliacus arising from the anterior end of the blade are inserted on the lesser trochanter which is almost equidistant with the insertion of the gluteus medius from the center of rotation of the femur. The points of origin of the two muscles on the blade would be comparable. Therefore, the difference in length of muscle fiber is taken to indicate a difference in function. In all of these animals rotation is less free than flexion and extension. In a lemur, so beautifully preserved that its limbs were very flexible, the rotation range equalled 45° ; the flexion-extension range equalled 75° . The shorter fibers of the gluteus medius in the lemur adapt that muscle for its function in rotation. The longer fibers in the higher forms make the gluteus medius a more perfect opponent of the iliacus. *Alouatta*, again, is difficult to explain.

The removal of the gluteus medius to the anterior end of the blade necessitated by the increased length of the fibers of the gluteus medius leaves the posterior portion of the gluteal plane free for the gluteus minimus. The insertion of this muscle on the anterior edge of the great trochanter makes it an important rotator. Undoubtedly, the fibers of the gluteus medius attached to the laterally directed portion of the gluteal plane can act as rotators just as they did in the lemur, but the reduced size of the area occupied by those fibers necessitates compensation through an increase in the area of the gluteus minimus. The gluteus minimus, arising as it does only from the bone is, however, a much

weaker muscle than the gluteus medius. But rapid rotation of the pelvis is not as important a movement in *Cebus* as in *Lemur*.

The lateral edge of the gluteal plane affords secure origin to the tensor fascia lata in *Cebus*, a muscle not discovered in any of the Lemuroidea. The muscle has some fibers also from the fascia over the gluteus medius. It is inserted into the fascia lata which is strongly developed (Fig. 7B). It helps to extend the knee and to keep it extended and is therefore useful to the animal in climbing and standing. The muscle was present in *Alouatta* but very reduced in size.

The adaptations for upright sitting, indicated in *Cebus*, are brought to a higher degree of perfection in the gluteal plane of the Old World monkeys (Fig. 4.). About thirty per cent of the plane is turned dorsally in *Lasiopyga*, thirty-six per cent in *Papio*, sixty per cent in *Macacus*. In a *Macacus* weighing 2265 grams this portion of the plane measured five square centimeters, whereas in a *Cebus* weighing 1698 grams the corresponding area was only .5 square centimeters. Thus there is an absolute increase in the area, not merely a relative increase dependent upon increase in the mass of the animal.

In *Lasiopyga* and *Papio* the portion of the gluteal plane which is turned at an angle to the more laterally directed portion is also much larger in proportion to the mass of the animal than the corresponding surface in *Cebus*. In both of these forms, however, this portion of the plane is not turned directly dorsally, but rather dorso-laterally owing to an increase in the size of the angle between it and the rest of the plane. This orientation may be explained as a secondary condition correlated with the peculiar life habits of these forms. *Lasiopyga*, like *Lemur*, is an excellent leaper. Again, the gluteus medius must act as a powerful rotator. The downward tilting of the lower portion of the plane favors this action since it places the origin of fibers arising from it more to one side of the axis of rotation than they would be if the surface faced directly dorsally. *Papio* has become secondarily terrestrial. In such a swift-moving ground dweller rapid turning of the body from the hip-joint as a fulcrum is one of the fundamental movements. The gluteus medius, then, is as important in lateral rotation of the pelvis as in the maintenance of balance in the squatting position.

The anthropoids (Plate XXII) show still further increase in the area of the dorsally directed portion of the gluteal planes. In *Hylobates* sixty-eight per cent of the entire area was directed dorsally, in *Pan* and *Pongo* eighty per cent and eighty-two per cent, respectively. In *Gorilla* the blade is very flat, facing almost directly backwards. A comparison

of *Hylobates* with *Macacus* reveals an absolute increase in the dorsally directed area occupied by the gluteus medius. In *Pan* and *Pongo* the increase in this area above the amount in *Macacus* was almost an exact function of increasing mass.

Animal	Weight	Area of Dorsally Directed Portion of Gluteus Medius	Area of Gluteus Minimus
<i>Cebus</i>	1698 gms.	.5 sq. cms.	2.4
<i>Alouatta</i>	1644	4.0	4.0
<i>Macacus</i>	2265	5.0	4.0
<i>Lasiopyga</i>	1585	3.0	4.3
<i>Papio</i>	7134	6.0	15.0
<i>Hylobates</i>	1812	5.0	3.9
<i>Pan</i>	8380	18.9	6.0
<i>Pongo</i>	24516	50.64	15.0

There was no gorilla available for study which had been weighed before being dissected.

That there has been a broadening of the anterior end of the iliac blade is shown by the following table in which the distance across the broadest portion of the area of the gluteus medius is shown in its relation to the length of the blade.

Animal	I Length of Blade	II Distance across Broadest Part of Area Occupied by the Gluteus Medius ¹	
			II I
<i>Lemur</i>	5.8	.35	6
<i>Cebus</i>	5.6	.5	10
<i>Alouatta</i>	7.3	1.6	22
<i>Macacus</i>	7.7	1.1	14
<i>Lasiopyga</i>	7.7	1.2	16
<i>Papio</i>	11.0	2.0	18
<i>Hylobates</i>	7.0	2.4	34
<i>Pan</i>	11.6	5.6	47
<i>Pongo</i>	15.5	8.0	51
<i>Gorilla</i>	23.0	19.0	83
<i>Homo</i>	13.0	11.6 ¹	88

¹This is a straight line measurement between the anterior superior spine and the linea limitans.

Since the increase in area occupied by the gluteus medius is proportionately greater than the increase in area occupied by the gluteus minimus, the broadening of the gluteal plane is especially marked at the anterior end. Dorsal views of the pelves of the monkeys (Figs. 3, 4) and anthropoids (Plate XXII) disclose the fact that the shape of the area occupied by this muscle is roughly rectangular in the monkeys, that in the anthropoids, on the other hand, it is broadest through the region of the anterior superior spine, and that above and below this region it decreases in lateral extent. If the shape of the area had been kept the same in these last forms as in the monkeys the broadening would not have had to be so great to give the required increase in area. The excessive broadening, then, provides for a longer iliac crest and this is in relation to the brachiating habits as will be shown in a later paragraph.

It is believed that the gluteus medius in the anthropoids, as in the Old World monkeys, helps to maintain the balance of the body in the squatting position. It is possible that the glutei acting together help in raising the body to the semi-erect position and that they may aid in maintaining the balance of the animal once that position has been assumed. They could function in this way only so long as the angle between the ilium and the femur remained great enough to keep them tense, however. From such an action of the glutei we would have a partial explanation for the fact that *Hylobates* is a better bipedal walker than the other anthropoids since the area for insertion of this muscle on its pelvis is absolutely greater than in the others.

The gluteal plane with its muscles, then, fulfills the postural requirements of upright sitting and of the semi-erect standing position. The function of rotation is not so well cared for, but in these brachiating forms rotation of the body occurs through action of the shoulder and trunk muscles. The suspending arms furnish the support about which the body turns rather than the hind legs as in the leaping and running quadrupeds.

The gluteal plane of man (Plate XXII, E) is like that of the brachiating anthropoids in respect to its great breadth through the region of the anterior superior spine. In its orientation, however, it is different. The extensive development of the iliac fossa and growth of the bone backwards from the spina limitans has caused the gluteal plane to curve so that the most anterior point of origin of the gluteus medius is much further removed from the posterior point than is the case in the anthropoids. Thus the plane as a whole faces rather more laterally than the anthropoid plane. Since the thigh is held parallel to the longitudinal

axis of the vertebral column and since the insertion of the gluteus medius remains on the lateral surface of the great trochanter the chief movement caused by this muscle is abduction. The anterior fibers may cause some lateral rotation of the pelvis, the posterior fibers some medial rotation. The gluteus minimus has a similar action. These two muscles help to keep the center of gravity over the supporting foot as man walks.

THE ILIAC PLANE

Changes in the iliac plane go hand in hand with the changes in the gluteal plane which have already been described. The plane is narrow and ventrally directed in *Lemur* (Fig. 1A), the margo acetabuli sharply marked. In *Galago* and *Perodicticus* (Fig. 2 A, C) a portion of the plane is visible from the side, the margo acetabuli faintly indicated. As the dorsally directed portion of the gluteal plane increases in breadth in the monkeys, apes, and man, the iliac plane must of necessity increase in the same manner, it being merely the ventral surface of that portion of the bone. Since the iliacus muscle which arises from this plane is never as powerful as the gluteus medius, its origin being only from bone and not from bone plus investing fascia, it is believed that changes in this portion of the ilium are adaptations not to the action of this muscle but rather to the action of the gluteus medius. To be sure, the iliacus muscles have been looked upon as opponents of the glutei in the maintenance of balance in the squatting position and they are admirably placed for that purpose, but they are not the only muscles which could help to pull the trunk forward from the hips if there were danger of a backward fall. The psoas major attached at one end to the lesser trochanter and at the other to the bodies of the lumbar and last thoracic vertebræ could help in this movement. The glutei, however, are the only muscles on the posterior surface of the joint which are favorably placed for holding the pelvis upright when the animal squats.

In *Lasiopyga* and *Papio* the plane faces more medially than in *Macacus* or *Cebus*. This change in direction is believed to be correlated with the change in function of the gluteus medius in these two forms.

The iliac fossa, so striking a feature of the pelvis of man, is not present at all in the monkeys. It is indicated in *Hylobates* and more strongly developed in the other anthropoids, particularly the gorilla. But in none of these forms is it as prominent a feature as in man. Whether or not its development is dependent upon the pull of the abdominal muscles and the counteraction of the viscera as Knauer supposed, the consequences of its development in relation to muscular action are im-

portant. The curvature of the bone causes an increase in area for the glutei and iliacus, helps to make possible a change in function for the glutei, and makes the iliac crest longer and curved so that the muscles arising from it may act as balancers of the upright trunk.

THE SACRAL AND POSTGLUTEAL PLANES

The sacral plane (Fig. 1) of primates comprises two parts which in most cases are bent at an angle to each other. The upper part includes the iliac tuberosity and the auricular surface. The lower forms part of the lateral wall of the small pelvis. The muscles arising from the lower portion, namely, the obturator internus and the ilio-coccygeus, are small and weak. Its form is believed to be dependent upon a combination of mechanical and obstetrical conditions. The width of the sacrum is obviously dependent upon mechanical conditions. The vertebral centra must be wide enough to form a supporting column for the trunk in the various positions which the animal assumes. The distance across the small pelvis between acetabula is a function not only of the locomotor needs but also of the obstetrical. There must be a sufficiently wide base of support for the animal and there must be a sufficiently wide pelvic outlet. Since the lower sacral plane forms one surface of the bridge between the acetabulum and the auricular surface, its length and degree of curvature is determined by its relation to the size of the pelvic outlet, and by its weight transmitting function. Limitation of material did not permit an analysis of these factors.

Changes in the upper portion of the sacral plane are correlated more directly with changes in the musculature than is the case in the lower sacral plane. Since the evolution of the iliac tuberosity is connected with the history of the erectors of the spine and since these muscles involve also the postgluteal planes and the dorsal surface of the sacrum, it is thought best to review all of these bony surfaces together.

The iliac tuberosity and crest of the lemur give rise to fibers of the erector spinæ, the postgluteal plane to the abductor caudæ externus, and the dorsal surface of the sacrum to the levator caudæ internus, levator caudæ externus, and to the multifidus spinæ. The detailed origin and insertion of these muscles follows:

ERECTOR SPINÆ (Fig. 1A, e)

Origin.—From the iliac tuberosity, the crest of the ilium above it, and from the deep layer of the lumbo-dorsal fascia.

Insertion.—Anapophyses and transverse processes of the lumbar vertebrae. In the upper lumbar region the muscle separates into two

divisions: one, the longissimus, attaching to the transverse processes of the thoracic vertebræ; the other, the iliocostalis, attaching to the posterior borders of the ribs.

ABDUCTOR CAUDÆ EXTERNUS (Fig. 2F, *ace*)

Origin.—Postgluteal plane and lateral edge of posterior surface of the sacrum.

Insertion.—Transverse processes of first and second caudal vertebræ.

LEVATOR CAUDÆ EXTERNUS (Fig. 2F, *lce*)

Origin.—Dorso-medial edge of the transverse processes of the last five lumbar vertebræ, the dorsal surface of the sacrum between the ilio-sacral joint and the articular processes.

Insertion.—Caudal metapophyses.

LEVATOR CAUDÆ INTERNUS (Fig. 2F, *lci*)

Origin.—From the spines of the sacral and caudal vertebræ.

Insertion.—Caudal metapophyses.

MULTIFIDUS (Fig. 2F, *m*)

Origin.—All along the precaudal spine from the metapophyses of the vertebræ.

Insertion.—Each fasciculus is inserted into the spinous process of a vertebra anterior to the vertebra of origin.

The sacro-iliac joint of the lemur occupies approximately the middle region of the space between the acetabulum and the anterior edge of the iliac blade so that the iliac tuberosity is almost as long as the postsacral portion of the blade. The anterior edge of the ilium lies opposite the transverse process of the next to the last lumbar vertebra. The outward flaring of the ilium at its anterior end, already noted under the discussion of the gluteal plane, causes the iliac tuberosities to diverge from the mid-line. The muscle fibers arising from the tuberosity are inserted chiefly on the transverse processes of the last three lumbar vertebræ. They are so placed, then, that those of one side acting alone can aid the gluteus medius in the quick turning of the body so necessary in an arboreal leaper. Those of the two sides acting together can help to lift the trunk.

The margo ischiadicus is well marked, it being the edge between the powerful erector spinæ and the well-developed abductor caudæ externus.

In *Galago* the iliac tuberosity is relatively shorter than in *Lemur*, the area for the insertion of the erector spinæ, relatively smaller. This reduction in area is due to the more forward placement of the sacro-iliac joint in *Galago* (Fig. 2B), not to an increase in the antero-posterior

extent of that joint. The possibility for decrease in size of the erector spinæ in *Galago* as compared with *Lemur* may be explained on the same basis as the relative decrease in the gluteus medius, namely, the more posterior location of the center of gravity of the body and the greater length of the pelvic lever. The margo ischiadicus is not as sharply marked in *Galago* as in *Lemur*, not only because of the reduction of the erector spinæ, but also because of the fact that the abductor caudæ externus is somewhat reduced, the tail being relatively much more slender in *Galago*.

The iliac tuberosity of the sluggish *Perodicticus* is even more reduced, the sacro-iliac joint having so increased its antero-posterior extent that it almost reaches the cranial end of the blade (Fig. 2D). The transverse processes of the lumbar vertebræ lie entirely in front of the anterior end of the blade. The small erector spinæ is sufficiently powerful for an animal which never leaps, sits, or stands upright. The tail is very short and slender. In connection with this fact, we note the disappearance of the abductor caudæ externus, the levator caudæ externus, the consequent disappearance of the postgluteal plane, and the narrowing of the sacrum. The levator caudæ internus spreads over the dorsal surface of the narrow sacrum.

An increase both in the antero-posterior and transverse extent of the sacro-iliac joint of *Cebus* (Fig. 1B) strengthens it against the stresses to which it is subjected when the animal sits upright or hangs by its tail. The erector spinæ is relatively smaller than in the lemur but it is more advantageously placed for extension of the spine. Measurement of the angle between the horizontal line connecting the posterior superior spine and a dorso-ventral line across the surface of origin of the erector spinæ proved that the area in *Cebus* faces rather more ventrally than the similar area in *Lemur*. This, in connection with the fact that the tuberosities diverge less and that the transverse processes of the lumbar vertebræ in *Cebus* are wider than in *Lemur*, enables the muscle fibers to run from the ilium directly forward and downward upon the transverse processes. Thus, they are in a position to exert a direct backward and upward pull. This again would be of advantage in the maintenance of the semi-upright position in sitting.

Ventral views of the pelves of *Lemur* and *Cebus* (Fig. 1A, B) show that in *Cebus* the wings of the sacrum have extended anteriorly on the iliac tuberosity. The insertion of the quadratus lumborum has been shifted anteriorly.

The iliac tuberosity in *Alouatta* is extremely reduced owing to the encroachment of the sacro-iliac joint. The lumbar vertebræ are entirely

in front of the blade. The erector spinæ is small as might be expected in this sluggish creature. There is no sharp edge between the iliac tuberosity and the postgluteal plane. The latter is small but the broadening of the sacrum and increase in its bony surface due to the fusion of the transverse processes of the sacral vertebræ has given a large area for the abductor caudæ externus as well as for the tail muscles. The spines of the sacral vertebræ are fused into a crest which gives firm origin to the levator caudæ internus. All these modifications in the sacrum are correlated with the importance of the prehensile tail in the locomotion of the animal. Similar but not as extreme modifications in the sacrum are indicated in *Cebus*.

In the Old World monkeys studied, the iliac tuberosities have the orientation that one might expect in quadrupeds adapted for upright sitting. That is, they face ventro-medially, as in *Cebus*. One erector spinæ acting alone could aid in the rotation of the body from the hips, a necessary movement in a quadruped, and the two together could help to lift the trunk and to keep it upright. It is interesting that in *Lasiopyga* and *Papio* we find again evidences of their peculiar life habits. In both of these forms the antero-posterior extent of the iliac tuberosity is relatively greater than in *Macacus* and the iliac tuberosities diverge more so that the surface of origin of the erector spinæ is brought more to one side of the transverse processes. These modifications favor the lateral rotation of the spine which must characterize an arboreal leaper and a swift-moving ground runner.

All of these Old World forms possess a well-defined postgluteal plane (Fig. 4C) which gives rise to the abductor caudæ externus and in all the dorsal surface of the sacrum gives rise to the tail muscles. The quadratus lumborum occupies the portion of the linea limitans anterior to the sacrum.

The iliac tuberosity of the anthropoids is very small. It does not give rise to muscle fibers as is the case in the monkeys but is roughened for the attachment of the heavy ligaments of the sacro-iliac joint. The crest above it, however, is greatly broadened in comparison with the crest of the monkeys and it gives rise to the erector spinæ. This portion of the crest is relatively very much shorter than the similar region in the lower primates but increased surface for the erectors of the spine is gained through an extension of their origin laterally onto the region of the crest beyond the spina limitans (Fig. 5) and through the disappearance of the tail muscles from the postgluteal plane and the dorsal surface of the sacrum. The multifidus extends its area of origin over the whole

dorsal surface of the sacrum and the postgluteal plane (Plate XXII, A, B, C, D), the region occupied in the lemurs and monkeys (Figs. 2, 3, 4) by the levator caudæ externus and the abductor caudæ externus. The absolute increase in the area of origin of this muscle gives it added power as an erector of the spine.

The history of the muscles on the iliac crest will be reviewed in the next section.

The small tuberosities of the gibbon and the chimpanzee face ventromedially, that of the chimpanzee rather more ventrally than that of the gibbon. The distance between the posterior superior spine and the spina limitans is very short.

The very small tuberosity of the orang faces almost directly ventrally so that there is no sharp bend between it and the iliac plane. As a result the line of the iliac crest (Fig. 5C) from posterior superior spine to anterior superior spine is almost straight.

The tuberosity of the gorilla is a very small surface opposite the transverse processes of the last lumbar vertebræ. The angle at the spina limitans has been obliterated. The crest (Fig. 5D), then, would be straight if it were not for the development of the iliac fossa.

In man the iliac tuberosity is large, again, owing to a growth backward of the iliac blade from the spina limitans along the lateral surface of the sacrum. This backward growth of the tuberosity is necessitated by the characteristic tilting of the human sacrum.

The greatest extent of the auricular surface is along its antero-posterior axis (dorso-ventral axis of the quadrupeds) rather than along the superior-inferior axis as in the brachiators. Extension of the joint surface in the new direction is a provision for strength against the downwardly directed forces of the upright trunk. The wedge-like shape of the sacrum, another provision for strength, makes the posterior parts of the tuberosities and crests converge. The backward growth of the bone causes the deepening of the greater sciatic notch. The postgluteal plane loses its identity in the portion of the bone which is new in man. With its disappearance the multifidus is almost entirely removed from the ilium, a mere portion of it arising from the inner surface of the posterior superior spine.

THE ILIAC CREST

The iliac crest of man is the broad superior margin which extends from the posterior superior spine to the anterior superior spine connecting the margo ischiadicus with the margo acetabuli. In the lower primates there is an homologous crest, the dorsal and ventral limits of which may

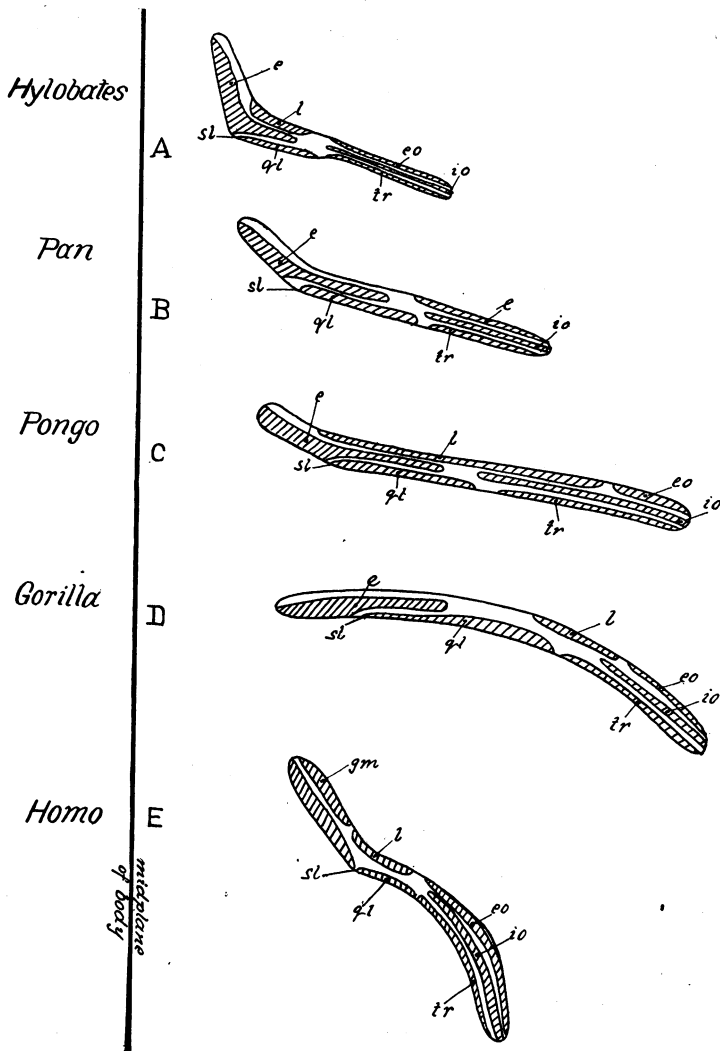


Fig. 5. Diagrams of the iliac crest in the anthropoids and man.

A, *Hylobates* (adult); B, *Pan* (juv.); C, *Pongo* (juv.); D, *Gorilla* (juv.); E, *Homo* (after Cunningham).

be called, respectively, the posterior and anterior superior spines. As far as osteological relationships are concerned, these two spines are homologous throughout the series; the posterior always marking the turning point between the margo ischiadicus and the iliac crest; the anterior, the turning point between the margo acetabuli and the iliac crest. In respect to their relationships to muscles, however, the spines are not homologous.

There are two main portions to the iliac crest, one which lies above the iliac tuberosity and separates it from the gluteal plane and another which forms the upper edge between the gluteal and iliac planes. The following table shows the relation in percentage of the length of each of these parts to the total length of the crest.

Animal	I Length from Posterior Superior Spine to Spina Limitans	II Length from Spina Limitans to An- terior Superior Spine	III Total Length	<u>II+III</u> III
<i>Lemur</i>	2.6	.3	2.9	10
<i>Cebus</i>	2.5	.5	3.0	17
<i>Alouatta</i>	1.8	2.2	4.0	55
<i>Macacus</i>	3.1	2.1	5.2	40
<i>Papio</i>	5.7	2.7	8.4	32
<i>Hylobates</i>	2.5	5.0	7.5	66
<i>Pongo</i>	3.2	11.6	14.8	71
<i>Pan</i>	2.8	13.5	16.3	82
<i>Gorilla</i>	2.0	18.0	20.0	90
<i>Homo</i>	9.0	17.0	26.0	65

Changes in the iliac crest are correlated with changes in the margo acetabuli and margo ischiadicus. The margo ischiadicus has been reviewed in connection with the postgluteal plane and the iliac tuberosity. The crest and the margo acetabuli of the lemur give rise either directly through fibers or indirectly through fascia to the following muscles:

ERECTOR SPINÆ.—Origin and insertion given above.

INTERNAL OBLIQUE ABDOMINIS

Origin.—From the transverse processes of the lumbar vertebrae through the lumbo-dorsal fascia, from the posterior borders of the cartilages of the last three or four ribs, from the iliac crest beyond the iliac tuberosity, from the ligament between the anterior superior spine and anterior inferior spine as far down as the posterior half of the origin of the sartorius muscle and from the crural arches.

The crural arches are delicate ligamentous arches giving exit to the ilio-psoas muscle, the femoral vessels, and the spermatic cord. The

lateral arch really represents the line of union of the fascia iliaca with the fascial lining of the abdominal cavity.

Insertion.—Linea alba and anterior margin of pubis.

SARTORIUS (Fig. 2E, s)

Origin.—From the anterior inferior iliac spine and from the posterior half of the ligament which unites the anterior inferior to the anterior superior spine.

Insertion.—Anterior crest of the tibia above the insertion of the gracilis.

RECTUS FEMORIS (Fig. 2E, r)

Origin.—Anterior inferior spine.

Insertion.—Anterior margin of the patella.

GLUTEUS MAXIMUS, GLUTEUS MEDIUS, GLUTEUS MINIMUS.

Origin and insertion given under discussion of the gluteal plane.

LATISSIMUS DORSI

Origin.—Through the lumbo-dorsal fascia from the portion of the crest above the iliac tuberosity.

Insertion.—Anterior surface of humerus.

The same muscles are attached to the iliac crest and margo acetabuli in *Perodicticus* and *Galago*. The crest, however, has only one part since the spina limitans and spina anterior superior fall together. The prominence of the inferior spines of *Galago* and *Lemur* is due to the strong pull of the rectus femoris, a powerful leaping muscle; the prominence of the anterior superior spines to the action of those fibers of the gluteus maximus which extend from it to the third trochanter.

Because of the broadening of the gluteal plane in the South American monkeys the portion of the crest beyond the spina limitans is relatively greater than in *Lemur*, and the margo acetabuli has become straight. Neither the anterior superior nor inferior spines are emphasized in these forms, both having become incorporated, as it were, into the straight line of the margo acetabuli. In connection with their lack of prominence it should be noted also that the muscular pulls upon them are relatively weaker, the gluteus maximus having lost its fibrous attachment to the anterior superior spine and the rectus femoris being relatively reduced in these non-leaping forms. With a few exceptions the muscle connections are the same as in the lemur. The internal oblique arises directly by muscle fibers from the margo acetabuli from the anterior superior spine to the upper limit of the origin of the sartorius muscle. Beyond that the origin is through an aponeurosis to the point at the posterior

end of the sartorius origin where the crural arches begin. The transversus abdominis of *Cebus* has gained an attachment to the crest beyond the iliac tuberosity. The sartorius has shifted anteriorly so that there is an interval between its origin and that of the rectus femoris.

The crest and margo acetabuli of the Old World monkeys present no striking changes. The larger proportion of the crest is that above the iliac tuberosity as in the other arboreal quadrupeds. Neither the superior spine nor the inferior are much emphasized. The relation of muscles to crest and margo acetabuli is almost exactly like that in *Cebus*. The fibrous attachment of the internal oblique extends to the upper limit of the sartorius. To that region of the blade the lateral crural arch finds attachment and from the arch arise some fibers of the internal oblique. In none of these forms does the external oblique have attachment to the margo acetabuli. The fascia with which it is continuous laterally, however, is inserted along the blade as far as the region of the crural arches. Then it arches over the iliopsoas and femoral muscles to a medial insertion on the pubis. Where it spans the iliacus it becomes continuous with the fascia of the thigh.

Evidence of adaptation to brachiating habits is revealed in the crest (Fig. 5) and margo acetabuli (Plate XXII) of the anthropoids. In these forms it is the portion of the crest beyond the spina limitans which has the greatest length. The work on the gluteal plane, already referred to, has shown that the broadening of the iliac blade as measured through the region of the anterior superior spine is in excess of simple mass requirements. It will be shown that the long crest between the anterior superior spine and the spina limitans gives rise to muscles which help to support the weight of the pelvis and lower limbs as the animals swing through the trees supported by their arms.

The crest of *Hylobates* (Fig. 5A) is divided into a short thick part above the iliac tuberosity, a broad part extending from the spina limitans to the highest point of the iliac blade and a thin edge curving abruptly from the highest point to the anterior superior spine. The erector spinæ extends along the thickened part from the posterior superior spine almost to the highest point. The extension of the area beyond the spina limitans is correlated with the widening of the thoracic basket and the brachiating habits of the animal. It places the erector spinæ in a favorable position for lifting the wide trunk and enables it to help in supporting the weight of the pelvis when the animal is hanging from its arms.

The latissimus dorsi has a fibrous attachment to the crest from the region of the spina limitans to the highest point. This is external to the

erector spinæ. Internal to it is the insertion of the quadratus lumborum which extends from the spina limitans to the highest point. The crest beyond the highest point gives rise to the abdominal muscles, the external oblique abdominis along the outer edge, the transversus along the inner edge and the internal oblique in the interval between them. Two new muscles, then, have gained a fibrous attachment to the crest; the latissimus dorsi and the quadratus lumborum, and the abdominal muscles have a much longer attachment to the crest than in the arboreal quadrupeds. Both the latissimus and the quadratus are so placed that they can aid the erector spinæ in supporting the pelvis whenever the animal is suspended by its arms. The fibers of the external and internal oblique can assist in this task since they ascend almost vertically from the crest to the ribs above. It is believed that the prominence of the anterior superior spine of *Hylobates* is due in part to the fact that the fibers of the abdominal muscles inserted above it frequently exert a pull in a vertical direction, while the fibers of the abdominal muscles below it exert a pull in a horizontal direction from the margo acetabuli to the linea alba or from the margo acetabuli to the pubis.

The margo acetabuli, while not so long in proportion to the total length of the blade as in the monkeys, has still practically the same relationship to muscles. The transversus, however, as well as the internal oblique, has now a fibrous attachment to the margo acetabuli, its lower portion being more strongly developed than in the monkeys. It arises directly by fibers from the anterior superior spine almost to the region of the sartorius, then by tendinous fibers to the upper limit of the sartorius. It then arches over the iliopsoas in common with the internal oblique.

The crest of *Pan* (Fig. 5B) is relatively broader than that of *Hylobates*. It is thick along its whole extent. From the posterior superior spine it runs to a highest point in the middle of its extent and then descends in a gentle curve to the anterior superior spine. The portion lateral to the highest point is more nearly horizontal than the same region in *Hylobates*. As a result of the proportionately greater broadening of the upper part of the iliac blade the margo acetabuli is concave (Plate XXII, B), and the anterior superior spine more conspicuous than in *Hylobates*. The erector spinæ extends from the posterior superior spine to the highest point. The latissimus dorsi has a broader area of origin than in *Hylobates* since it extends from the highest point to the anterior superior spine, taking up one-half of the entire crest. The quadratus lumborum is relatively broader also since it extends from the spina limitans halfway to the anterior superior spine.

The external oblique abdominis has been crowded from the blade by the latissimus dorsi. It is attached by a few fibers only to the anterior superior spine. The internal oblique extends as in *Hylobates* from the highest point of the blade to the anterior superior spine and the transversalis from the lateral limits of the quadratus lumborum to the anterior superior spine. The extension of the crest laterally gives, then, greater surface for the suspending muscles in the heavier brachiating form.

The relationship of muscles to the margo acetabuli has not changed, except that they are attached through a ligament extending from the anterior superior spine to the anterior inferior spine.

In the orang the crest (Fig. 5C) is almost straight, owing to the large angle between the sacral and iliac planes, and the portion beyond the spina limitans is very great. The erector spinæ extends from the posterior superior spine to the highest point of the blade. The latissimus dorsi is the thick heavy muscle that one might expect in this heavy-bodied creature which is second only to the gibbon in its brachiating ability. It extends along the lateral lip of the iliac crest taking up about three-fourths of its length through the central region. It is separated by a short interval from both the posterior and anterior spines. The external oblique extends along the lateral lip of the crest from the lateral limit of the latissimus dorsi to the anterior superior spine, the internal oblique along the medial lip lateral to the erector spinæ. The muscular relationships at the anterior superior spine are more manlike than in the monkeys or apes previously discussed. The sartorius muscle, which, in the monkeys, *Hylobates* and *Pan*, was to be found either in the middle region of the margo acetabuli or just anterior to the rectus femoris now arises from the spine and the notch immediately below it (Plate XXII). A true Poupart's ligament was not discovered in the form dissected but there was no attachment of the abdominal muscles to the margo acetabuli. From the distal end of the attachment of the internal oblique to the crest there was a ligamentous arch over the iliopsoas muscle, an arch which attached to the pubis medially. This arch was formed by the union of the fascia iliaca with the fascia transversalis. Fibers of the internal oblique arose from it.

The crest of the gorilla is relatively longer than that of the orang. The increase in length is gained partly as a result of the broadening of the anterior end of the iliac blade, partly as a result of an increase in the antero-posterior distance between the highest point of the blade and the anterior superior spine. The downward growth of the anterior superior

spine has of necessity shortened the straight line distance along the margo acetabuli (Plate XXII, D). The anterior superior spine is truly homologous to that of man both in its osteological relationships and in its relations to muscles. There is a true Poupert's ligament attached at one end to the anterior superior spine and at the other to the anterior edge of the pubis. The fibers of the internal oblique are attached to the outer two-thirds of this ligament as are the fibers of the transversalis. The sartorius has an attachment to the anterior superior spine. The arrangement of muscle fibers on the crest (Fig. 5D) is essentially like that in the orang, except that the latissimus dorsi does not have as broad a fibrous attachment.

The iliac crest of man, although modified to serve the requirements of a bipedal walker, yet bears unmistakable traces of its derivation from anthropoid ancestors. The great breadth between the spina limitans and the anterior superior spine may be looked upon as a heritage from a brachiating ancestry, and from whom should man derive the arrangement of the muscles on his iliac crest (Fig. 5E) but from brachiators? To be sure, the crest of man is specialized. It has a distinct S-shape owing to the great development of the iliac fossa and to the distinct growth backwards from the region of the spina limitans, already noted under the discussion of the sacral plane.

The widening of the sacrum has brought the spina limitans under the angles of the lower ribs. The erector spinæ, then, finds a favorable and sufficient surface of origin between the posterior superior spine and the spina limitans and does not extend beyond it. The extension of the crest posterior to the sacro-lumbar articulation permits the fibers of the erector spinæ to act with greater power in the extension of the spine upon the pelvic base than is possible in the anthropoids where the origin and insertion of these fibers lies more nearly in the same vertical plane.

To the outer lip of the posterior part of the crest, a part which is non-existent in the lower primates, the gluteus maximus has a fibrous attachment. The new and firm attachment to the ilium, taken in connection with an origin from the side of the sacrum, enables this muscle to act with power in lifting the trunk from the stooping position. In the monkeys and anthropoids it is an abductor and relatively much weaker. The quadratus lumborum and latissimus dorsi take up a small portion of the crest beyond the spina limitans, but their extent is relatively less than in the brachiating anthropoids. Beyond them are the abdominal muscles, the three being practically equal in extent along the crest. The

curve of the crest, due to the formation of the iliac fossa, brings the fibers of the external and internal oblique into such a relation to the ribs above them that they can act as lateral flexors of the trunk, and so these two muscles can help to balance the trunk of man as he walks.

The crest of bipedal man, then, gives extensive surface to the balancing muscles of the trunk, the erector spinæ and the abdominal muscles. The crest of the heavy brachiating anthropoids gives more surface to the powerful latissimus dorsi, and the quadratus lumborum. Yet, in spite of these differences, there is a fundamental similarity of plan in the arrangement of the muscles on the crest.

The arrangement of the muscles on the crest of man, as may be seen from the diagram (Fig. 5E), is very like that in *Hylobates* (Fig. 5A), but the arrangement around the anterior superior spine and the margo acetabuli is more like that in the orang and gorilla, particularly like that in the gorilla. This last fact, taken in connection with the length of the crest, suggests the presence of heavy brachiating forms among the ancestors of man. The reduction in extent of the latissimus in man would then be looked upon as a secondary change. It seems reasonable to regard it in this light, since in the gorilla, the poorest climber, the fibrous extent of the latissimus is not so great as in the other heavy-bodied brachiators, the orang and the chimpanzee.

The anterior inferior spine of man is much more strongly developed than that of the anthropoids. As Weidenreich has suggested, this is correlated with the importance of the rectus femoris and ilio-femoral ligament in the maintenance of balance in the upright position of the body.

THE ISCHIUM

THE LENGTH OF THE ISCHIUM

The length of the ischium, as measured from the center of the acetabulum to the most posterior point, may be taken as a rough estimate of the lever arm of the hamstring muscles. It was thought desirable to determine for the ischium, as for the ilium, the relation in percentage of this length to the length of the body as a whole and to the distance of the center of gravity from the center of the acetabulum. The first two tables following give these figures. The third gives ilio-innominate and ischio-innominate indices.

Length of Ischium in Relation to Length of Body

Animal	I Length of Body	II Length of Ischium	$\frac{II \times 100}{I}$
Cat	33	2.5	7.6
<i>Lemur</i> , No. 755	27	1.8	7.0
<i>Lemur</i>	34	2.2	6.5
<i>Perodicticus</i>	26	1.8	7.0
<i>Galago</i>	12	.9	8.0
<i>Cebus</i> , No. 533	31	2.5	8.0
<i>Cebus</i>	30	2.1	7.0
<i>Alouatta</i> , No. 557	37.5	2.5	6.4
<i>Macacus</i> , No. 1046	36.0	4.1	11.3
<i>Lasiopyga</i> , No. 585	34.0	3.4	10.0
<i>Lasiopyga</i>	42.0	4.3	10.0
<i>Papio hamadryas</i> , No. 632	53.0	6.0	11.0
<i>Papio hamadryas</i>	54.0	6.2	11.0
<i>Hylobates</i> , No. 651	29.0	2.2	8.0
<i>Hylobates</i>	37.5	2.7	7.0
<i>Pan</i> , No. 531	48.0	5.4	11.0
<i>Pongo</i>	63.0	7.0	11.0
<i>Gorilla</i>	54.0	6.5	12.0
<i>Homo</i>	72.5	6.0	8.0

Length of Ischium in Relation to Position of Center of Gravity

Animal	I Length of Body	II Distance of Center of Gravity from Acetabulum	$\frac{II \times 100}{I}$	III Length of Ischium	$\frac{III}{II}$
Cat	33	14	42	2.5	18
<i>Lemur</i> , No. 755	27	9	33	1.8	20
<i>Cebus</i> , No. 583	31	12.0	38	2.5	21
<i>Alouatta</i> , No. 557	32.5	12.5	38	2.5	20
<i>Macacus</i> , No. 1046	36	17	47	4.1	24
<i>Lasiopyga</i> , No. 585	34	14.5	43	3.4	23
<i>Papio</i> , No. 632	53	24	45	6.0	25
<i>Pan</i> , No. 531	48	18	37	5.4	30
<i>Pongo</i>	63	28	44	7.0	25

Ilio-innominate and Ischio-innominate Indices

Animal	Greatest Length of Innominate Bone	Length of Ilium	Length of Ischium	Ilio- innom- inate Index	Ischio- innom- inate Index
Cat	6.5	4.0	2.5	61	38
<i>Lemur</i> , No. 755	6.0	4.2	1.8	70	30
<i>Lemur</i>	8.0	5.8	2.2	72	28
<i>Perodicticus</i>	6.7	4.9	1.8	73	27
<i>Galago</i>	3.5	2.6	.9	74	26
<i>Cebus</i> , No. 583	8.6	6.1	2.5	71	29
<i>Cebus</i>	7.7	5.6	2.1	72	28
<i>Alouatta</i>	9.6	7.1	2.5	73	24
<i>Macacus</i>	11.8	7.7	4.1	65	35
<i>Lasiopyga</i>	9.4	6.0	3.4	64	36
<i>Lasiopyga</i>	12.0	7.7	4.3	64	36
<i>Papio</i>	17.0	11.0	7.0	65	35
<i>Papio</i>	17.3	11.1	6.2	64	36
<i>Hylobates</i>	9.2	7.0	2.2	76	24
<i>Hylobates</i>	11.9	9.2	2.7	77	23
<i>Pan</i>	17.0	11.6	5.4	68	32
<i>Pongo</i>	22.5	15.5	7.0	69	31
<i>Gorilla</i>	22.0	15.5	6.5	70	30
<i>Homo</i>	17.9	11.9	6.0	66	34

•The tables show that the mechanical advantage of the lever concerned in the lifting of the trunk through the power of the hamstrings is slightly greater in the Primates than in the non-arboreal cat and that it is greater in the Old World monkeys and the heavy anthropoids than in *Lemur* and the South American monkeys.

The increased mechanical advantage of the lever in the lemur over that in the cat is due to the closer proximity of the center of gravity of the body to the center of the acetabulum. The increased advantage in the Old World monkeys and heavy anthropoids is due to the greater length of the ischium. The ischium is relatively short in *Hylobates* and in man. It was impossible to determine the position of the center of gravity for these last two forms. For man, however, as pointed out under the discussion of the ilium, it is evident that the center of gravity would be relatively closer to the acetabulum than in the anthropoids,

owing to the greater length and weight of the legs. The decreased hamstring lever arm may not, then, mean decreased mechanical advantage and it does make possible speed of movement. It is interesting that in the best bipedal walker among the anthropoids, the gibbon, the lever arm of the hamstrings should be correspondingly short.

The increase in the ilio-innominate index of the lemur as compared with that of the cat is due to the greater length of the ilium. In *Perodicticus* and *Galago* the still greater increase in the length of the ilium accounts for the higher ilio-innominate index. The decrease in the index of the Old World monkeys is due, not to a shortening of the ilium, since that has been shown to increase in relation to the body length, but to an increase in the length of the ischium. *Hyllobates* has a very high index owing to the proportionately greater lengthening of the ilium. The heavy anthropoids show indices much like those of the lemur and South American monkeys, although neither the ilium nor ischium is similarly related to the length of the body. The ischium is like that of the Old World monkeys in its relation to body length, while the ilium is longer. In man, the ilio-innominate and ischio-innominate indices are much like those in the Old World monkeys, although both ilium and ischium are proportionately shorter.

THE ISCHIUM IN RELATION TO ITS MUSCULATURE

The ischium of the lemur, like that of all primates, is divisible into a thick portion, the body, the cranial end of which forms part of the acetabulum, a rough thickening, the tuberosity, and a thin part, the ramus, which passes inward and upward from the body and tuberosity to its articulation with the pubis.

The following muscles have an attachment (Fig. 2E) to the ischium of the lemur.

ADDUCTOR MAGNUS (has two portions) (*am*)

Origin of superficial portion.—From posterior part of symphysis pubis.

Origin of deep portion.—Anterior margin of pubic arch.

Insertion.—Linea aspera internal to the gluteus maximus.

BICEPS FEMORIS (*bi*)

Origin.—In common with the semitendinosus from the anterior part of the tuberosity of the ischium.

Insertion.—Through an aponeurosis into the lateral margin of the patella, the external tuberosity of the tibia, and the external border of the anterior crest of the tibia through its proximal two-thirds.

SEMITENDINOSUS (*st*)

Origin.—From the tuberosity of the ischium in common with the biceps.

Insertion.—In common with the gracilis into the anterior tibial crest.

SEMIMEMBRANOSUS (*sm*)

Origin.—From the tuberosity of the ischium posterior to the origin of the biceps and semitendinosus.

Insertion.—Medial surface of medial condyle of tibia.

QUADRATUS FEMORIS (*qf*)

Origin.—From the surface of the ischium cranial to the origin of the biceps and semitendinosus.

Insertion.—Posterior surface of the femur between attachment of gluteus maximus and adductors, from the region of the third trochanter to the upper limit of the adductor magnus.

OBTURATOR EXTERNUS (*oe*)

Origin.—From the obturator membrane and the portions of the rami of the pubis and the ramus of the ischium which are adjacent to it.

Insertion.—Trochanteric fossa.

ISCHIOCOCYGEUS (*isc*)

Origin.—Ischial spine and internal surface of the ischium immediately anterior and posterior to it.

Insertion.—Transverse processes of the first four caudal vertebræ.

GEMELLI (not differentiated) (*gem*)

Origin.—From external surface of the body of the ischium between the ischial spine and ischial tuberosity.

Insertion.—In common with the obturator internus into the trochanteric fossa above the insertion of the obturator externus.

The shape of the body of the ischium is determined not so much by the muscles attached to it as by its function in support. In the Lemuroidea it is relatively smaller than in upright sitting forms in which it must resist the weight of the trunk.

The ischial tuberosity in the Lemuroidea is unexpanded as in quadrupeds which do not sit upright.

The build of the ischial ramus is more directly related to the muscular action. It is more slender in Lemur in which the adductor magnus does not extend along its whole length than in the monkeys in which it does.

An examination of the pelvis (Fig. 2A) and femur of *Galago* reveals an arrangement of muscles and a bony construction very similar to that

in *Lemur*. There are, to be sure, minor differences, a slightly wider ischial ramus and a less extensive insertion on the femur for the quadratus femoris. *Perodicticus* (Fig. 2C) is very specialized in the length of the ischial ramus. It is difficult to find anything in the locomotor habits of the animal to account for its great elongation. It is possible that the increased depth of the pelvic cavity gained thereby, taken in connection with the extreme shortness of the symphysis, may be of importance in relation to the size of the pelvic outlet required for the birth of the young.

There is no great change in the body or the tuberosity of the South American monkeys, but the ischial ramus, as mentioned above, is relatively broader. In correlation with this fact it should be noted that the deep portion of the adductor magnus (Fig. 3A, *am*) now arises from the entire ischial ramus and that a new portion of the adductor mass, a portion innervated by the sciatic nerve, arises from the lower end of the ramus and ischial tuberosity. This last portion is called the ischio-condyleus (Fig. 3A, *ic*) by many writers, since it extends from the ischium to the medial condyle of the femur. It is present in all the higher primates. In all it takes a position on the pelvis corresponding to that of the semimembranosus in the Lemuroidea, posterior to and below that of the biceps, the semimembranosus being crowded from the posterior edge of the tuberosity to a position internal to the biceps. It is believed that these portions of the adductor mass function not only in adduction of the thigh which is a more important movement in the climbing monkeys than in the lemurs, but also in extension of the hip-joint. The ischio-condyleus is surely as good an extensor as any one of the hamstrings.

As may be seen from the muscle plates (Figs. 7, 8), the extensors of the knee are the largest in *Lemur* and in *Galago*, whereas in the monkeys the extensors of the hip-joint are as powerful as those of the knee-joint. Sudden and violent extension of the knee is important in the forward propulsion of the bodies of the leaping forms. In the monkeys which are frequently arising either from the squatting or from the quadrupedal to the semi-erect position in order to grasp the near-by branches, the extensors of the hip must act with power to keep the trunk and tibia parallel.

The broadening of the ischial ramus provides also a slightly greater surface for the obturator externus in these forms and gives to it increased importance as a rotator.

The ischium of the Old World monkeys (Fig. 4) is greatly modified in relation to the habit of upright sitting. Strength to resist the down-

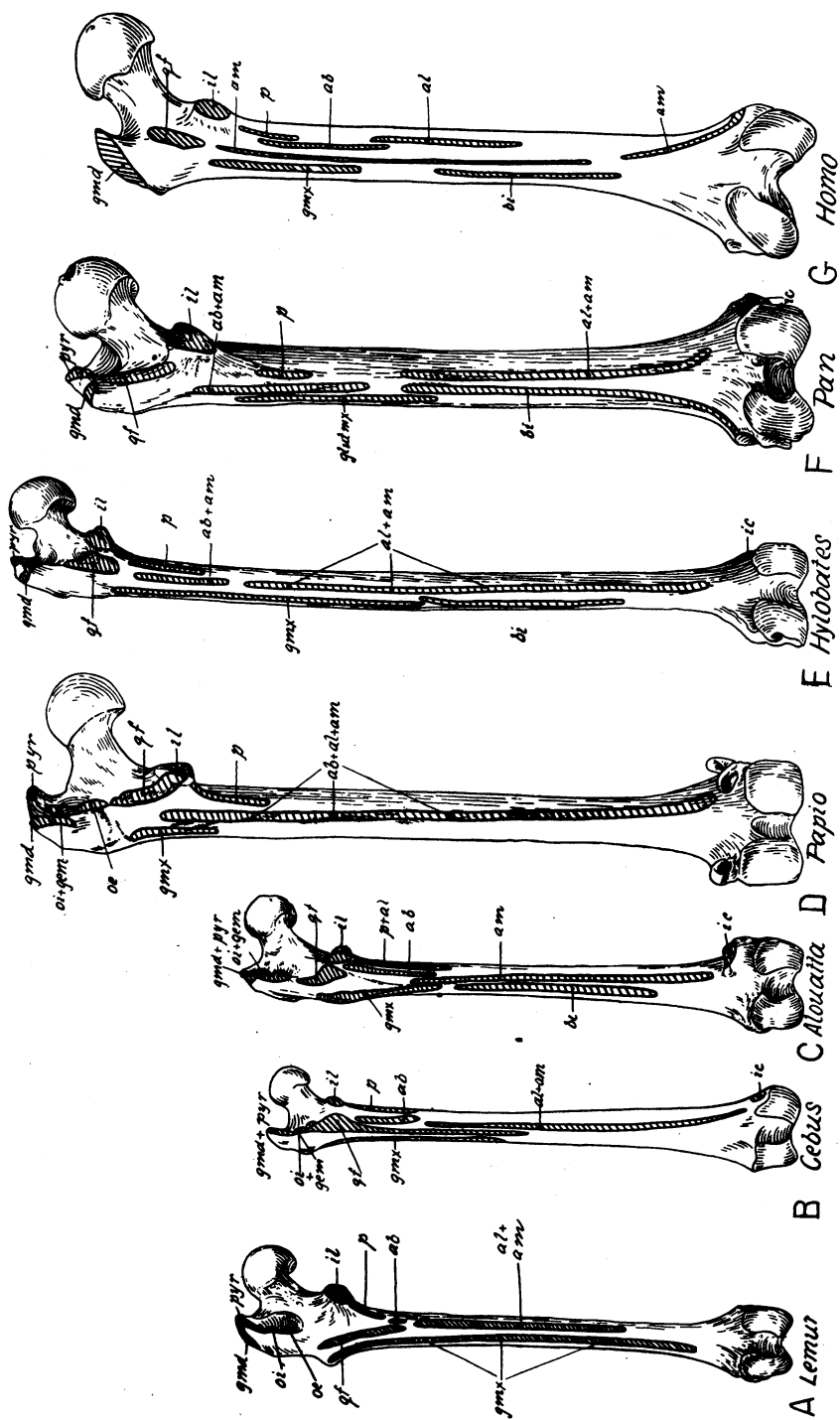


Fig. 6. Femurs in posterior view.
The width of the muscle areas has been slightly increased for the sake of distinctness.

wardly directed forces of the trunk is gained by a thickening and broadening of the body. The tuberosities are broadened and flattened to give extensive attachment to the ischial callosities on which the animal rests in sitting. They are widest along their antero-dorsal margin, narrowing to a point postero-ventrally.

There are a few changes in the muscles which are significant. There is an additional portion of the adductor magnus which runs between the ischium and the upper portion of the femur. This was called the adductor accessorius by Michaelis who found it in *Cynocephalus*. It was not readily separated in *Macacus* and *Lasiopyga* but its presence was indicated by the direction of the muscle fibers. It is responsible for the twisted appearance of the adductor magnus, in which the deep fibers arising from the ischium pass to the upper end of the femur, while those from the symphysis go to the lower part of the femur. In the lemurs and South American monkeys, as is shown by the diagrams of the femurs (Fig. 6A, B, C), the upper limit of the insertion of the adductor magnus lies some distance below the lesser trochanter. In the Old World monkeys (Fig. 6D), however, the upper limit of the adductor magnus lies opposite the lesser trochanter. It is thought that the fibers of the adductor accessorius can act as rotators. Moreover, in these forms, as in *Alouatta*, the quadratus femoris, which in the Lemuroidea and in *Cebus* has its insertion chiefly below the lesser trochanter, is now inserted on the trochanter and above it. Thus, it, too, is favorably placed for rotation. Emphasis upon the rotators posterior to the acetabulum is perhaps a necessary consequence of the change in function of the glutei. It is evident that rotation of the pelvis toward one side is accomplished by the glutei of that side assisted by the rotators posterior to the acetabulum on the other side. In the Lemuroidea the rotators anterior to the acetabulum are very powerful. As the gluteus medius of the monkeys becomes specialized for extension of the pelvis in squatting there is more provision for rotation through the action of the muscles posterior to the acetabulum.

Hylobates is the only one of the anthropoids that possesses ischial callosities. In this form they extend transversely rather than antero-posteriorly and dorso-ventrally as in the Old World monkeys studied. Their orientation is dependent upon two factors: the shortness of the lever arm of the hamstrings and the shallowness of the pelvic cavity in the dorso-ventral direction. In the short lever arm power is sacrificed to speed of movement but there may be compensation for that loss through the addition of a new and powerful extensor muscle. Fibers of

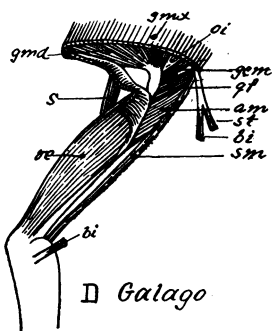
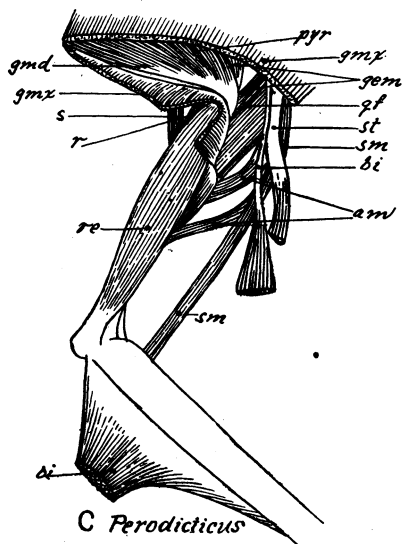
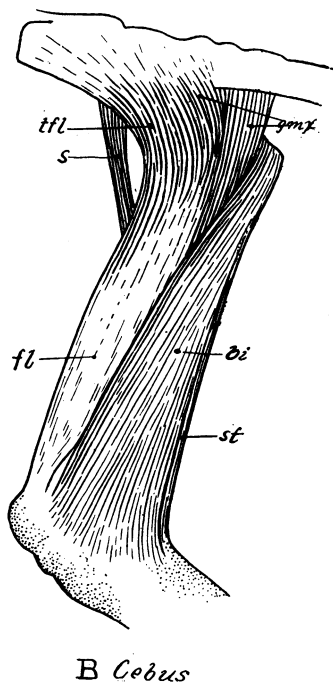
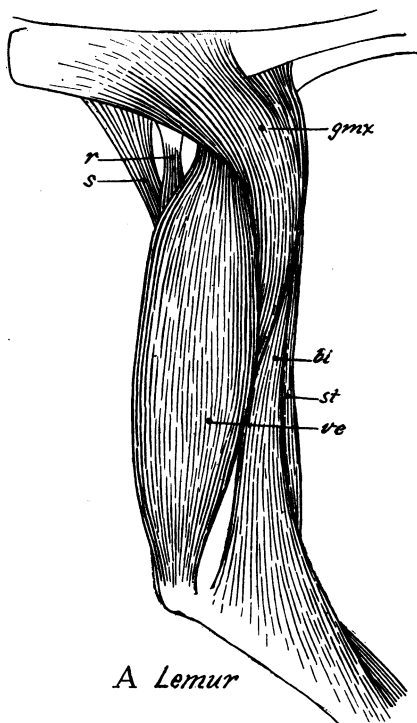


Fig. 7. Musculature of the hip and thigh, lateral view.

the gluteus maximus, which, in the tailed forms are attached to the caudal vertebræ, are inserted on the ischial tuberosity in *Hylobates* and the other anthropoids. The shallowness of the pelvic cavity goes with the brachiating habits. In the quadrupedal forms the rami of the pubis and ischium must have a relatively greater dorso-ventral extent in order to provide a favorable leverage for the adductor muscles. In the brachiating forms in which the thigh hangs parallel to the vertebral column the adductors pull at a better angle if the pelvis is shallow since

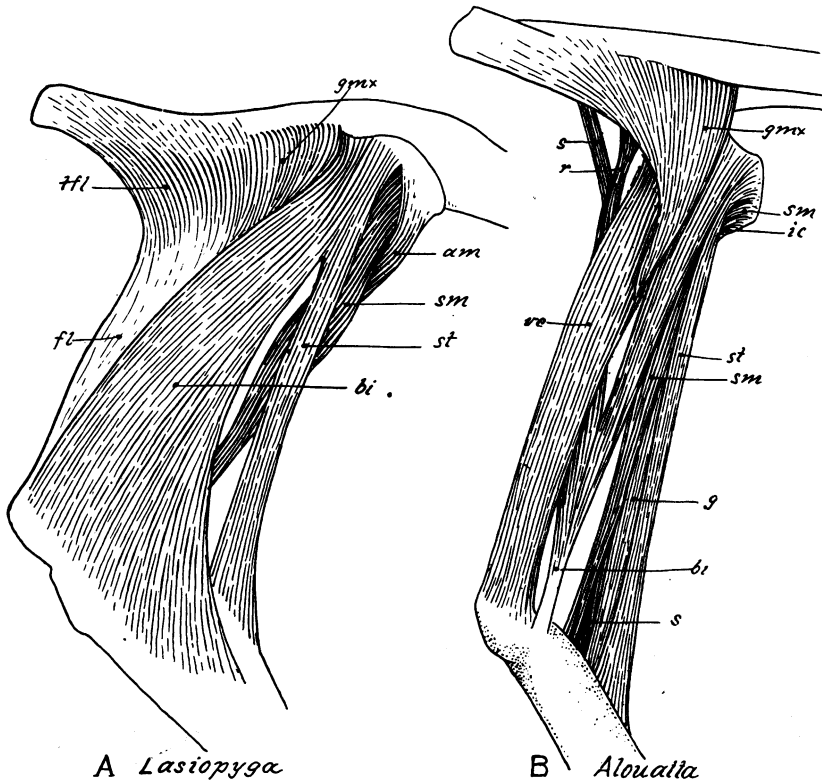


Fig. 8. Musculature of the hip and thigh, lateral view (continued).

their surface of origin is then more nearly in the same frontal plane with the line of insertion.

The tuberosities of the remaining anthropoids are curved, not flat like those of *Hylobates*. They have a greater antero-posterior and dorso-ventral extent owing to the increased length of the lever arm of the ham-

strings and the increased depth of the pelvic cavity, and they are everted. Going with this eversion is a twisting outwards of the body of the ischium in its posterior part. The eversion of the tuberosities and torsion of the ischial body are believed to be due to the action of the hip-joint extensors which exert a powerful pull on the tuberosities of these heavy forms. Certainly the angle of pull of those muscles on the everted tuberosities is more favorable for power than it would be on non-everted tuberosities.

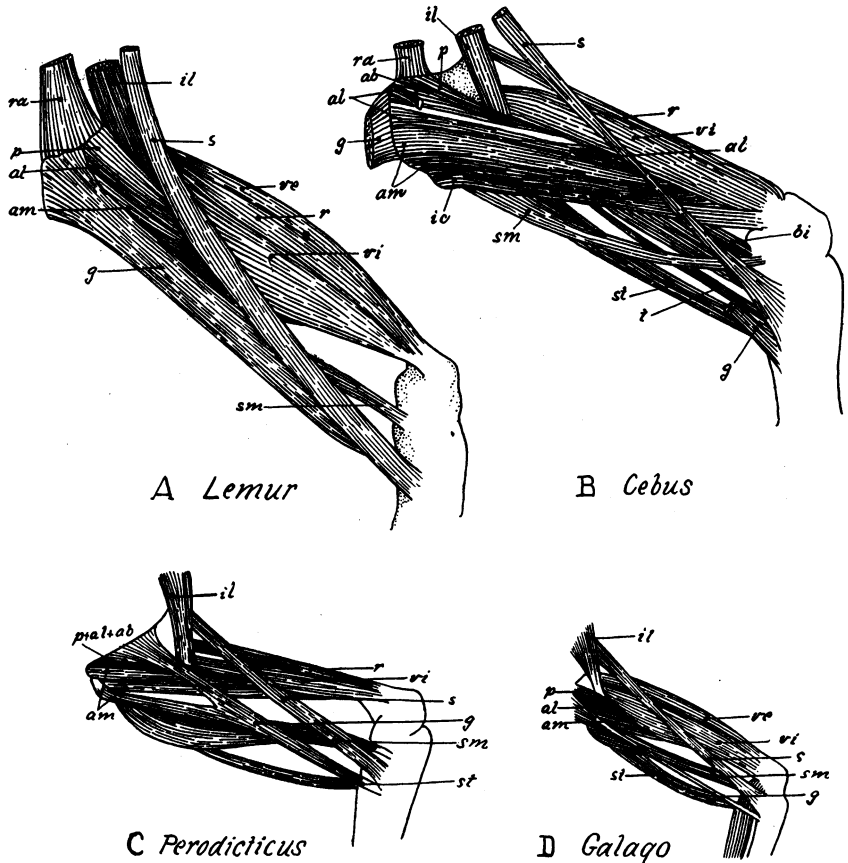


Fig. 9. Musculature of the hip and thigh, medial view.

As Weidenreich has pointed out the torsion of the ischium conditions a groove, the sulcus tubero-glenoidalis, between the ischial tuberosity and the portion of the ischium embracing the acetabulum. In the heavy anthropoids this groove runs obliquely downward. In man the sulcus

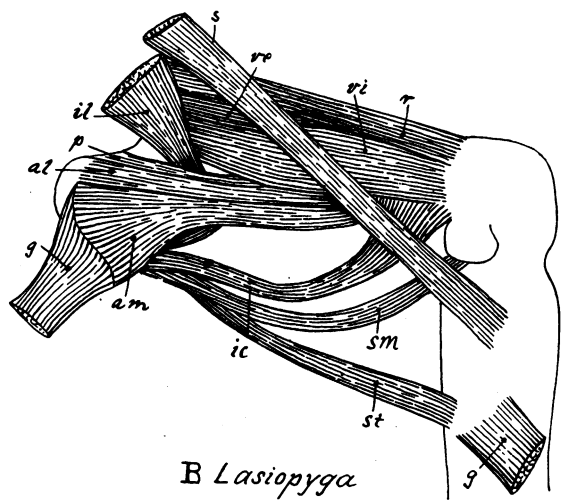
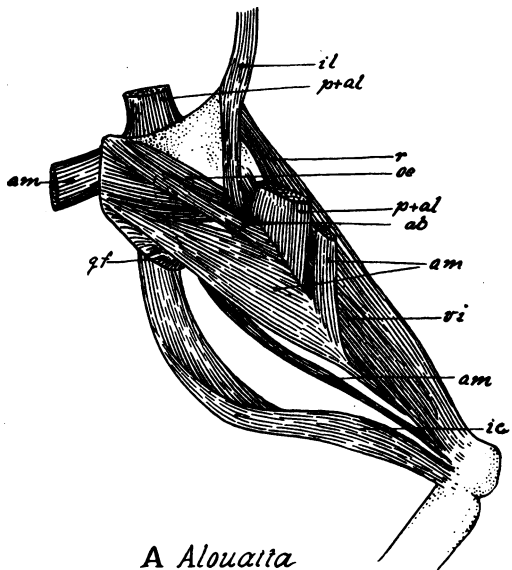


Fig. 10. Musculature of the hip and thigh, medial view (continued)

tubero-glenoidalis is present but it is narrower and directed transversely owing to the fact that the tuberosity stretches far up toward the acetabulum, covering part of the body of the ischium.

Weidenreich attributes this position of the tuberosity and the consequent alteration in the sulcus to the strong pull exerted upon the tuberosity through the action of the sacro-tuberous ligament which in man must keep the caudal end of the sacrum from rising as a result of the pressure exerted upon the base of the sacrum by the upright vertebral column and trunk. So, too, the prominent ischial spine of man is attributed to the action of a ligament, the sacro spinous, which is derived from the ischio coccygeus muscle, as Keith has pointed out.

The arrangement of muscles on the posterior surface of the femur (Fig. 6E, F) is very much the same in the different anthropoids. In all, there are portions of the adductor magnus extending from the lesser trochanter to the medial condyle. In all, the gluteus maximus has a much greater extent than in any of the Old World forms and, in all, there is present the origin of the short head of the biceps femoris.

A short head to the biceps femoris is possessed only by *Ateles*, *Alouatta*, *Lagothrix*, the anthropoids and man. The first three are prehensile-tailed South American forms. It is easily understood that a one-joint flexor of the knee is of great importance in both the prehensile-tailed monkeys and in the brachiators in which independent action of the segments of the limbs is desirable. In the other primates, with the exception of man, the knee can be flexed only through the action of the hamstrings. As Bowen (1923) has pointed out, the rectus femoris and the hamstrings when in contraction exert a belt-like action on the hip and knee such that "the two joints tend to take the same position and to move in the same direction and to the same extent." There are one-joint flexors and extensors of the hip and one-joint extensors of the knee in all of the Primates, but a one-joint flexor of the knee only in the prehensile-tailed forms, the brachiating forms, and man.

This view of the functional importance of the short head of the biceps femoris differs from that of Klaatsch (1900) who thought that the muscle could have no functional significance in climbing mammals since it was not present in lemurs or Old World monkeys. Klaatsch, like Windle and Parsons, believed that the muscle was homologous with the tenuissimus or, as he preferred to call it, the gluteo-cruralis, a muscle present in certain marsupials, some South American monkeys, some edentates, some insectivores, all carnivores, some rodents, and completely lacking in ungulates, lemurs and Old World monkeys. Its wide distribu-

tion led him to believe that in the *tenuissimus* we were dealing with a rudiment that is preserved in some mammals and secondarily lost in others. He believed that the *tenuissimus* and the short head of the biceps could be traced back to a muscle plate extending from the caudal region to the distal part of the shank in pro-mammals. He thought that since the preservation of the muscle could not be explained from the point of view of function, one must regard its presence as a primitive feature. He considered the short head of the biceps femoris to be one of the primitive structures which should place man and the higher primates at the root of the tree of mammalian life.

It is the belief of the writer that the occurrence of this muscle in man suggests the presence of brachiating ancestors. Both locomotion through the use of a prehensile tail and brachiation favor its development. In view of the many points of likeness between the brachiators and man and the points of difference between man and the prehensile-tailed monkeys, it seems reasonable to regard the short head of the biceps in man as a heritage from the brachiators and to attribute its development in the prehensile-tailed monkeys to parallelism.

SUMMARY

The results of this investigation can best be summarized through two lists: the first, a list of the habitus and heritage characters in the ilium and ischium of the animals studied; the second, a list of the habitus and heritage characters in the musculature of the main groups.

HABITUS AND HERITAGE CHARACTERS IN THE ILIUM AND ISCHIUM

GROUP	HERITAGE	ANIMAL	HABITUS
Lemuroidea	Ilium, ischium, and pubis meet in acetabulum	<i>Lemur</i>	Gluteal plane divided into gluteal plane proper and post gluteal plane
	Ilium has three surfaces and four edges		Sacral plane has two parts which meet at an angle
	Gluteal plane faces laterally		Iliac plane faces entirely ventrally
	Sacral plane faces medially		Iliac blade long and large
	Body of ischium unexpanded		Iliac blade flares anteriorly
	Tuberosity of ischium unexpanded		

GROUP	HERITAGE	ANIMAL	HABITUS
Lemuroidea	Sacro-iliac joint small	<i>Lemur</i>	Gluteal fossa present Tuberosity of ilium long Anterior superior spine present Anterior inferior spine prominent Margo acetabuli curved and prominent Ramus of ischium slender
		<i>Galago</i>	Gluteal plane as a whole faces dorso-laterally Postgluteal plane not conspicuous Iliac tuberosity short Iliac blade longer than in <i>Lemur</i> Anterior inferior spine prominent Anterior superior spine present Margo acetabuli faintly marked Margo ischiadicus not conspicuous
		<i>Perodicticus</i>	Gluteal plane as a whole faces dorso-laterally Postgluteal plane absent Iliac tuberosity very reduced Iliac blade longer than in <i>Lemur</i> and very narrow Margo acetabuli faintly marked Ischial ramus greatly elongated
Anthropoidea Cebidæ	Gluteal plane has two distinct parts—gluteal plane proper and post gluteal plane Greater part of gluteal plane proper faces laterally (average for the two forms was 70 per cent)	<i>Cebus</i>	Approximately 12 per cent of the gluteal plane faces dorsally Iliac plane wider than in <i>Lemur</i> Iliac tuberosity small—faces ventro-medially Margo acetabuli straight Neither anterior superior nor anterior inferior

GROUP	HERITAGE	ANIMAL	HABITUS
Anthropoidea Cebidæ	Two parts of the sacral plane meet at an angle Long iliac blade Body of ischium unex- panded Tuberosity of ischium unexpanded	<i>Cebus</i>	spine prominent Ischial ramus broad Antero-posterior and transverse extent of sacro-iliac joint larger than in Lemuroidea
		<i>Alouatta</i>	Almost one-half of the gluteal plane faces dorsally Length of iliac crest above iliac plane almost equal to that above iliac tuberosity Iliac tuberosity very small Postgluteal plane small Sacro-iliac joint long
Cercopithecidæ	A large part of the glu- teal plane faces laterally (average in forms studied, 58 per cent) Large part of the iliac crest is above the iliac tuberosity Margo acetabuli straight Anterior superior and anterior inferior spines not prominent Postgluteal plane prominent Iliac blade long	<i>Macacus</i>	60 per cent of the gluteal plane faces dorsally Iliac tuberosity reduced Iliac blade longer than in Lemuroidea or Cebidæ Ischium long Body of ischium ex- panded Tuberosity of ischium expanded Ischial callosities present
		<i>Lasiopyga</i>	30 per cent of gluteal plane faces dorso- laterally Iliac plane faces ventro- medially Iliac tuberosity long Iliac tuberosities diverge Iliac blade long Body of ischium ex- panded

GROUP	HERITAGE	ANIMAL	HABITUS
Cercopithecidæ		<i>Lasiopyga</i>	Tuberosity of ischium expanded Ischial callosities Ischium long
		<i>Papio</i>	36 per cent of gluteal plane faces dorso-laterally Iliac plane faces ventro-medially Iliac tuberosities long Iliac tuberosities diverge Ischium long Tuberosity of ischium expanded Body of ischium expanded
Anthropoidea Simiidæ	A very small part of the gluteal plane faces laterally Iliac tuberosity faces ventro-medially Postgluteal plane present Iliac blade long Anterior inferior spine not prominent Body of ischium large Ischial tuberosity expanded Ischial callosities in <i>Hylobates</i>	<i>Hylobates</i>	Dorsally facing portion of gluteal plane widened, especially through region of anterior superior spine Greatest portion of iliac crest is lateral to spina limitans Iliac tuberosity small Medial portion of iliac crest greatly thickened Iliac fossa indicated Lever arm of hamstrings short Ischial tuberosities extend transversely
		<i>Pan</i>	Dorsally facing portion of gluteal plane wider in proportion to length of blade than in <i>Hylobates</i> Iliac crest thick throughout its extent Portion of iliac crest beyond spina limitans relatively greater than in <i>Hylobates</i> Margo acetabuli concave Anterior superior spine prominent

GROUP	HERITAGE	ANIMAL	HABITUS
Anthropoidea Simiidae		<i>Pan</i>	Iliac tuberosity small— faces ventro-medially Ischial tuberosity curved and everted Ischium long Sulcus tubero-glenoidalis present
		<i>Pongo</i>	Dorsally facing portion of gluteal plane relatively wider than in <i>Pan</i> Iliac tuberosity small, facing almost ventrally Angle between iliac tuberosity and iliac plane large so that iliac crest is almost straight Margo acetabuli concave Anterior superior spine prominent Postgluteal plane re- duced Sulcus tubero-glenoidalis present Ischium long
		<i>Gorilla</i>	Broadest gluteal plane of all anthropoids Iliac tuberosity very small Angle at spina limitans obliterated Margo acetabuli short and concave Anterior superior spine prominent Iliac fossa prominent Ischium long Sulcus tubero-glenoidalis present
Anthropoidea Hominidae	Broad gluteal plane broadest through an- terior superior spine Greatest portion of iliac crest lateral to spina limitans	<i>Homo</i>	Orientation of gluteal plane Growth of bone from back from spina limitans Formation of great sciatic notch

GROUP	HERITAGE	ANIMAL	HABITUS
Anthropoidea	Thick iliac crest	<i>Homo</i>	Extension of crest posterior and medial to spina limitans
Hominidæ	Prominent anterior superior spine		Length of iliac tuberosity
	Thickened body of ischium		Increase in extent of auricular surface along antero-posterior axis (dorso-ventral of quadrupeds)
	Sulcus tubero-glenoidalis		S-shaped iliac crest
	Expanded ischial tuberosity		Extensive iliac fossa
			Disappearance of post-gluteal plane
			Development of anterior inferior spine
			Short iliac blade
			Short ischium (hamstring lever arm)
			Development of ischial spine

HABITUS AND HERITAGE CHARACTERS IN THE MUSCULATURE OF THE MAIN GROUPS

GROUP	HERITAGE	GROUP	HABITUS
Lemuroidea	Muscles attaching to the ilium and ischium have their homologues in the pelvic musculature of all mammals	Lemuridæ	The two joint muscles of the hip and knee are emphasized
Lemuridæ			Gluteus maximus has fibrous attachment to anterior superior spine
			Gluteus maximus has extensive attachment on back of femur
			Gluteus medius extends from anterior end of blade to region of anterior inferior spine
			Quadratus femoris extends below lesser trochanter on femur
			Scansorius portion of gluteus minimus distinct
Lorisidæ	As in Lemuridæ	Lorisidæ	Two joint muscles of hip and knee are emphasized
	Gluteus maximus attached by fibers to		

GROUP	HERITAGE	GROUP	HABITUS
Lorisidæ	entire anterior edge of blade Gluteus medius not bipenniform	Lorisidæ	Quadratus femoris ex- tends below lesser trochanter on femur Gluteus maximus at- tached to anterior end of ilium Gluteus medius extends almost to region of anterior superior spine
Anthropoidea Cebidæ	Ischio-condyleus present Representative of an- cient muscle-mass present in tenuis- simus or short head of biceps Scansorius portion of gluteus minimus present Quadratus femoris ex- tends below lesser trochanter in <i>Cebus</i>	Cebidæ	Ischio-condyleus well de- veloped and separate. It takes place of semi- membranosus posterior to biceps on outer edge of tuberosity. Semi- membranous located between biceps and ischio-condyleus on the outside and quad- ratus femoris on the inside Gluteus medius limited to anterior end of blade in <i>Cebus</i> Short head of biceps well-developed in pre- hensile-tailed monkeys Attachment of gluteus maximus on femur re- duced in extent Quadratus lumborum at- tached to iliac crest in <i>Alouatta</i> Quadratus femoris does not extend below lesser trochanter in <i>Alouatta</i>
Anthropoidea Cercopithecidæ	Ischio-condyleus present Neither tenuissimus nor short head of biceps present Gluteus medius limited to anterior end of blade	Cercopithecidæ	Adductor accessorius present Ischio-condyleus well de- veloped and fused with rest of adductor mag- nus Extent of adductor mass on posterior surface of

GROUP	HERITAGE	GROUP	HABITUS
Anthropoidea Cercopithecida	Attachment of gluteus maximus to femur very reduced	Cercopithecida	femur is from lesser trochanter to medial condyle Quadratus femoris does not extend below lesser trochanter
Simiida	Short head of biceps Ischio-condyleus present Ischio-condyleus separate in <i>Pan</i> , and some species of <i>Hylobates</i> Adductor accessorius present Extent of adductor mass on posterior surface of femur is from lesser trochanter to medial condyle Quadratus femoris does not extend below lesser trochanter Gluteus medius limited to anterior end of blade Scansorius portion of gluteus minimus separate in orang	Simiida	Short head of biceps well developed Gluteus maximus has an attachment to the ischial tuberosity and a long attachment on femur Quadratus lumborum and latissimus dorsi attached to iliac crest Sartorius attached to anterior superior spine in <i>Pongo</i> and <i>Gorilla</i> True Poupart's ligament in <i>Gorilla</i> Dorsal surface of sacrum and postgluteal plane taken up by multifidus Gluteus maximus in gorilla has a fibrous attachment to the sacrum
Hominida	Ischio-condyleus present Arrangement of hamstrings and ischio condyleus on tuberosity similar to that in monkeys and apes Extent of adductors on posterior surface of femur is from lesser trochanter to medial condyle Quadratus femoris does not extend below lesser trochanter	Hominida	Gluteus maximus has attachment by fibers to iliac crest and side of sacrum; has no attachment to iliac tuberosity

GROUP	HERITAGE	GROUP	HABITUS
Hominidæ	Gluteus medius anterior to gluteus minimus Sartorius attached to anterior superior spine Poupart's ligament Quadratus lumborum and latissimus dorsi attached to iliac crest Short head of biceps A portion of the mul- tifidus in the region of the posterior su- perior spine	Hominidæ	

CONCLUSIONS

This study of the pelvic muscles of the primates in relation to the bony surfaces to which they are attached lends support to Gregory's views (1920) as to the main stages in the evolution of the pelvis from the primitive arboreal quadrupeds to man.

These stages are as follows:

1. Primitive lemuroid stage.
2. Stage of primitive monkey in which there are incipient adaptations for upright sitting;
3. Stage of quadrupedal monkey in which adaptations for upright sitting are perfected;
4. Brachiating stage;
5. Stage of bipedal man.

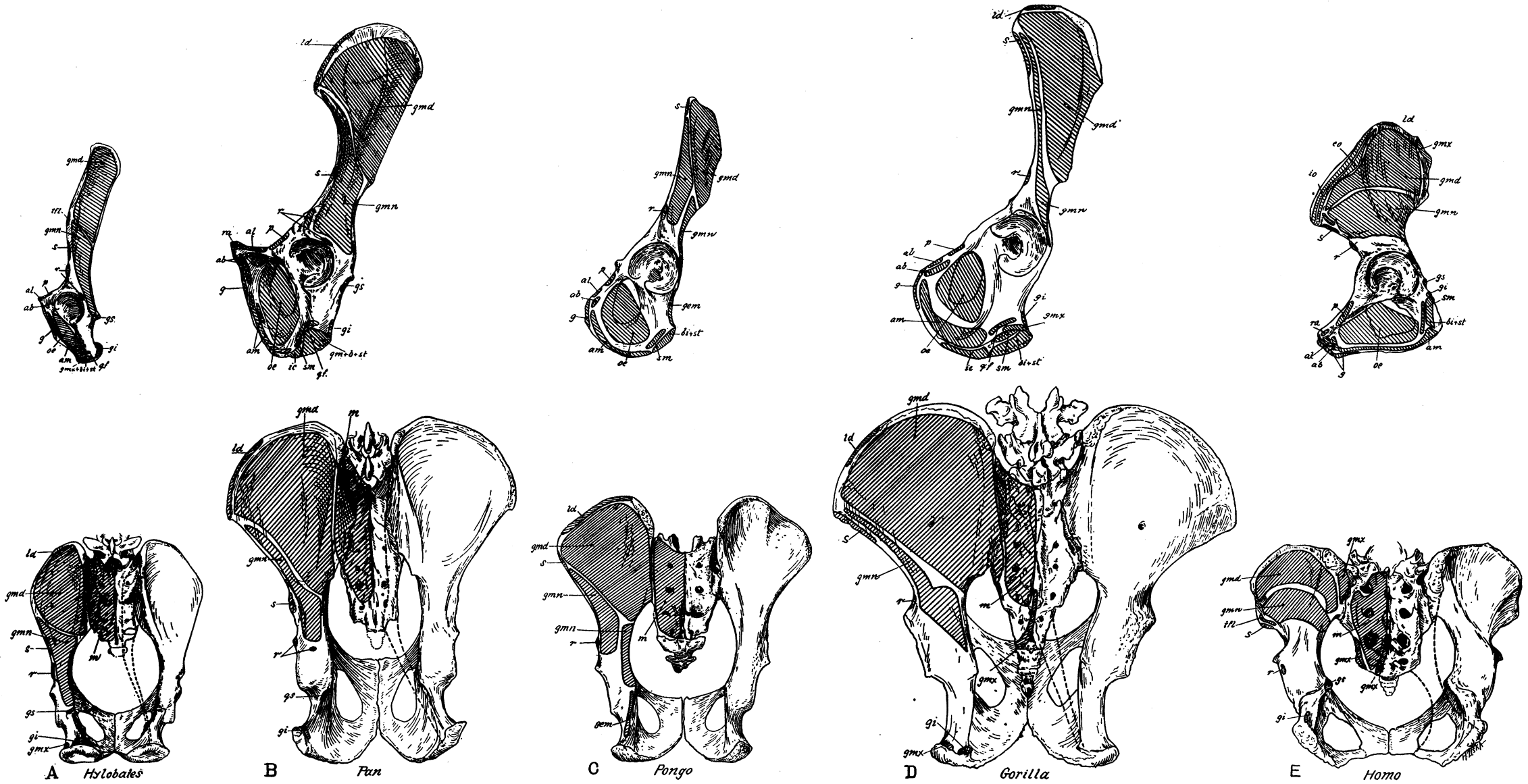
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KEY TO ABBREVIATIONS USED IN FIGURES AND PLATE

<i>ab</i>	—adductor brevis	<i>lci</i>	—levator caudæ internus
<i>ace</i>	—abductor caudæ externus	<i>ll</i>	—linea limitans
<i>al</i>	—adductor longus	<i>lt</i>	—linea terminalis
<i>am</i>	—adductor magnus	<i>m</i>	—multifidus
<i>bi</i>	—biceps femoris	<i>ma</i>	—margo acetabuli
<i>e</i>	—erector spinæ	<i>mi</i>	—margo ischiadicus
<i>eo</i>	—obliquus externus abdominis	<i>oe</i>	—obturator externus
<i>fl</i>	—fascia lata	<i>oi</i>	—obturator internus
<i>g</i>	—gracilis	<i>p</i>	—pectineus
<i>gem</i>	—gemelli (when undifferentiated)	<i>pqp</i>	—postgluteal plane
<i>gi</i>	—gemellus inferior	<i>pmg</i>	—psoas major
<i>gs</i>	—gemellus superior	<i>pmn</i>	—psoas minor
<i>gmd</i>	—gluteus medius	<i>pyr</i>	—pyriformis
<i>gmh</i>	—gluteus minimus	<i>qf</i>	—quadratus femoris
<i>gmz</i>	—gluteus maximus	<i>ql</i>	—quadratus lumborum
<i>gp</i>	—gluteal plane	<i>r</i>	—rectus femoris
<i>i</i>	—iliacus	<i>ra</i>	—rectus abdominis
<i>ic</i>	—ischio-condyleus	<i>s</i>	—sartorius
<i>il</i>	—iliopsoas	<i>sl</i>	—spina limitans
<i>ilc</i>	—ilio-coccygeus	<i>sm</i>	—semimembranosus
<i>in</i>	—intertransversarii	<i>sp</i>	—sacral plane
<i>io</i>	—obliquus internus abdominis	<i>ss</i>	—anterior superior spine
<i>ip</i>	—iliac plane	<i>st</i>	—semitendinosus
<i>is</i>	—anterior inferior spine	<i>t</i>	—tenuissimus
<i>isc</i>	—ischiococcygeus	<i>tfl</i>	—tensor fascia lata
<i>it</i>	—iliac tuberosity	<i>tr</i>	—transversalis
<i>l</i>	—latissimus dorsi	<i>ve</i>	—vastus externus
<i>lce</i>	—levator caudæ externus	<i>vi</i>	—vastus internus



Pelves of the anthropoids and man in lateral and dorsal views.

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