59.14,71,81:9.2

# Article V.—FUNCTIONAL ADAPTATIONS OF THE PELVIS IN MARSUPIALS

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Plates IX to XIV; Text Figures 1 to 12

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## INTRODUCTION

The purpose of the present study is to investigate the relation between the shape of the pelvis and the habitus of the animal. In the light of our present knowledge of genetics, we may assume that evolution is made possible by the occurrence of mutations, some of which provide a more perfect adjustment between the organism and its environment. In the competition for existence, the individuals which are better equipped for life in the particular environment which they occupy are more likely to live through the reproductive period. By this process of natural selection of parents, the succeeding generations come to have an increasing proportion of individuals exhibiting the favorable variation. Through the ceaseless repetition of this process with regard to the multitude of characters possessed by an animal, it is constantly being adjusted to its environment. As the available environment changes, in the course of climatic and physiographic flux, the animal is modified so as to be in harmony with its new conditions of existence. With the change of habits of life, there is associated a change in the function of the parts of the organism, which, in turn, makes a change in morphology desirable. The relation of the morphological differences in the pelvis and pelvic musculature of marsupials to the functional adaptation of the animals to their particular types of life constitutes the subject of this paper.

The most generalized form studied is the American opossum, *Didelphys* (Pl. X). The opossum is at home in the trees but spends much time on the ground. In this it differs from *Pseudochirus*, the ring-tailed phalanger, which is entirely arboreal. *Pseudochirus* moves much more slowly than *Didelphys*, a fact which correlates well with the character of the musculature. *Petauroides*, the greater flying phalanger, is closely related to *Pseudochirus*. It is characterized by the presence of a flying membrane, a fold of skin connecting the fore and hind limbs. *Petauroides* lives in high trees, from which it can launch itself into space, the membrane enabling the animal to glide a considerable distance before it reaches the ground. Le Souef and Burrell recount one such flight which spanned a distance of eighty yards.

The kangaroo, *Macropus* (Pl. XI), is well-known to people the world over because of its locomotor specializations. Leaping is also characteristic of *Perameles*, the bandicoot (Pl. XII). The method of progression employed by the bandicoot is very similar to that of the rabbit. Another similarity between the two animals lies in the fact that they both live in shallow burrows.

Fossorial adaptation is very competently represented by the wombat, *Phascolomys* (Pl. XIII). The wombat lives in large burrows which reach lengths of ten to fifteen feet. The work of excavating is carried on with remarkable speed.

*Phascolarctos*, the koala or marsupial bear (Pl. XIV), is completely arboreal in its habits. It is exceedingly sluggish. During the day it rests, curled up in the fork of a tree; at night it arouses to climb and feed.

The Tasmanian devil, *Sarcophilus*, spends most of its time on the ground. It lies under cover during the day, hunting in the afternoon and evening. It is not a very active animal, ambling leisurely after its prey.

The specific determinations of the animals studied are as follows: *Didelphys virginiana*, *Pseudochirus lemuroides*, *Petauroides volans*, *Macropus rufogriseus*, *Perameles macura*, *Phascolomys ursinus*, *Phascolarctos cinereus adustus*, *Sarcophilus ursinus*.

The present study was undertaken at the suggestion of Dr. W. K. Gregory, to whom profound gratitude is due for continued guidance dur-

ing its prosecution. The material dissected comes largely from the collections made for The American Museum of Natural History by Mr. H. C. Raven, to whom grateful acknowledgement is made for continued interest and encouragement during the progress of the work.

## PRELIMINARY ANALYSIS OF LOCOMOTION

When we consider the movement of the hind limb in locomotion we recognize that it consists of two well-defined parts or strokes, during one of which the limb is propelling the animal and during the other is being carried forward to a new point of vantage. The propulsive stroke is therefore followed by a recovery stroke. Each of these strokes has two phases, so we may divide each cycle of movement of the limb into four phases, as follows:

PROPULSIVE STROKE (Figs. 1 and 11 A, B)

Phase 1.—From the time the foot strikes the ground until the line of support (the line from the acetabulum to the point of contact with the ground) is vertical.

Phase 2.—From the end of phase 1 until the foot is lifted.

RECOVERY STROKE (Figs. 1 and 11 C, D)

Phase 1.—From the end of the propulsive stroke until the center of gravity of the limb is perpendicularly beneath the acetabulum.

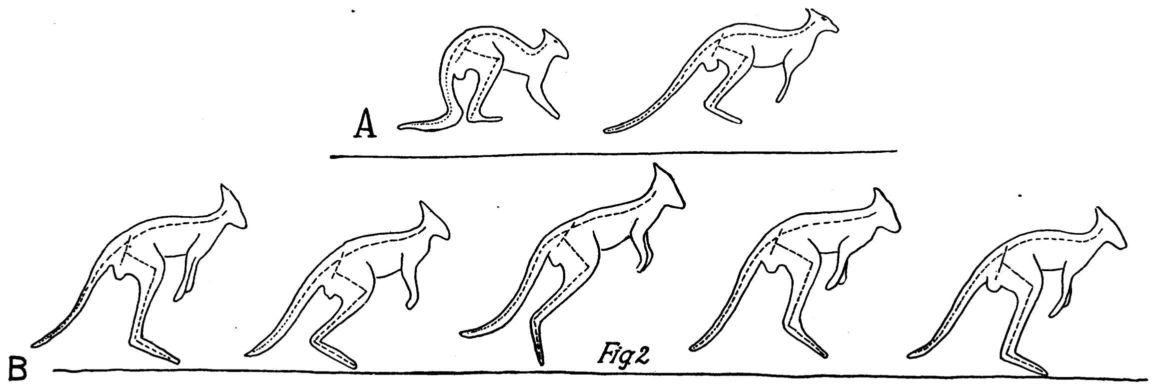
Phase 2.—From the end of phase 1 until the foot is planted on the ground.

A detailed account of the action of the muscles in all four phases of different types of locomotion is given in a later section.

## THE PELVIC MUSCLES IN THEIR RELATION TO LOCOMOTION

### FACTORS GOVERNING THE ACTION OF THE MUSCLES

The structure of the muscles is dependent on several factors. With the length of the muscle determined in general by the optimum points of origin and insertion, the internal structure must be such as to produce the required force and the necessary range of contraction. The distance through which a muscle can contract is a direct function of the length of its fibers, estimates of the amount of shortening varying from one-sixth to one-third the length at rest, while the force which a muscle can exert depends on the number of fibers, or the cross-sectional area of all the fibers. The work which a muscle is capable of performing is proportional to its force (a constant times the cross-sections of all its fibers) multiplied by its range of contraction (a constant times the length of its fibers). In other words, the work a muscle can perform is proportional to its volume,



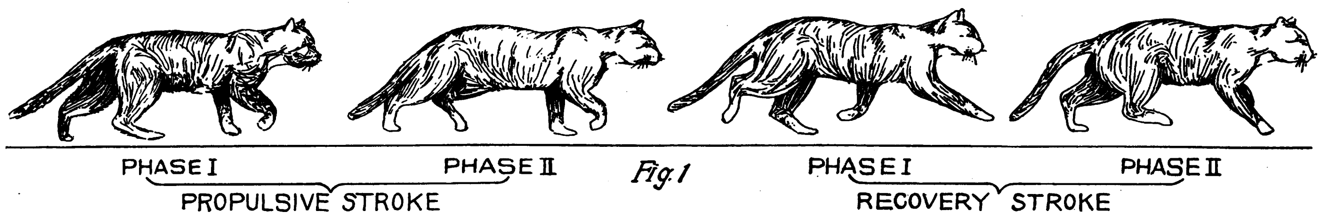




Fig. 1. The four phases of quadrupedal locomotion.
Illustrated by the right hind leg of the cat, pictured while trotting. (Adapted from a series of photographs in Muybridge, p. 225.)

Fig. 2. The leap of the kangaroo.
*a*, initiation of the leap from rest; *b*, one leap of a series. (Adapted from Muybridge, p. 207.)

while the force it can exert is proportional to volume divided by length of fiber. In comparing muscles this relation is only strictly true when the contractility of the muscle tissues is identical and the amount of connective tissue is the same. The force exerted by the fibers also depends on the angle they make with the tendon of insertion, being proportional to the cosine of this angle. This factor may usually be disregarded, since the angle is very small.

The first factor in determining the shape of a muscle is, then, the location of its points of origin and insertion. These points are usually situated so as to give the best mechanical advantage. Secondly, the fibers constituting the muscle have their length correlated with the distance which the muscle must shorten in contraction and their number with the force necessary. The third factor is that of the mutual relations of the muscles. Being as closely packed as they are, it is impossible for each muscle to have the shape which would be best if it had no neighbors. In view of well-established general principles of the locomotory apparatus we may assume, at least provisionally, that each muscle has a structure which fits its function and interferes as little as possible with its companions.

The situation of the points of attachment (origin and insertion) is largely governed by the leverage that is advantageous to the action of the muscle. The proximal point of attachment is usually considered the "origin" and the distal point the "insertion." Whether one, the other, neither or both are fixed depends on what movements the animal is performing. The longer the lever-arm of the muscle compared to that of the opposing weight the greater is the power of the muscle, but the smaller is the speed of the movement accomplished. The angle of insertion of the muscle is also important. An insertion at right angles to the lever gives the maximum power; the smaller angles give greater speed but the component of force available for movement of the lever (that is, the component at right angles to it) is less.

Muscles which are stretched beyond their resting length before contraction develop greater tension upon excitation. This condition actually obtains for many of the muscles in the normal processes of locomotion. A muscle also can do more work if its load is diminishing as it contracts. In the case of some muscles this is accomplished by the lengthening of the lever-arm as the angle of insertion increases during the action of the muscle. This is beautifully illustrated in the case of the gluteus medius and femoro-coccygeus, both of which gain increased leverage on the femur as extension continues.

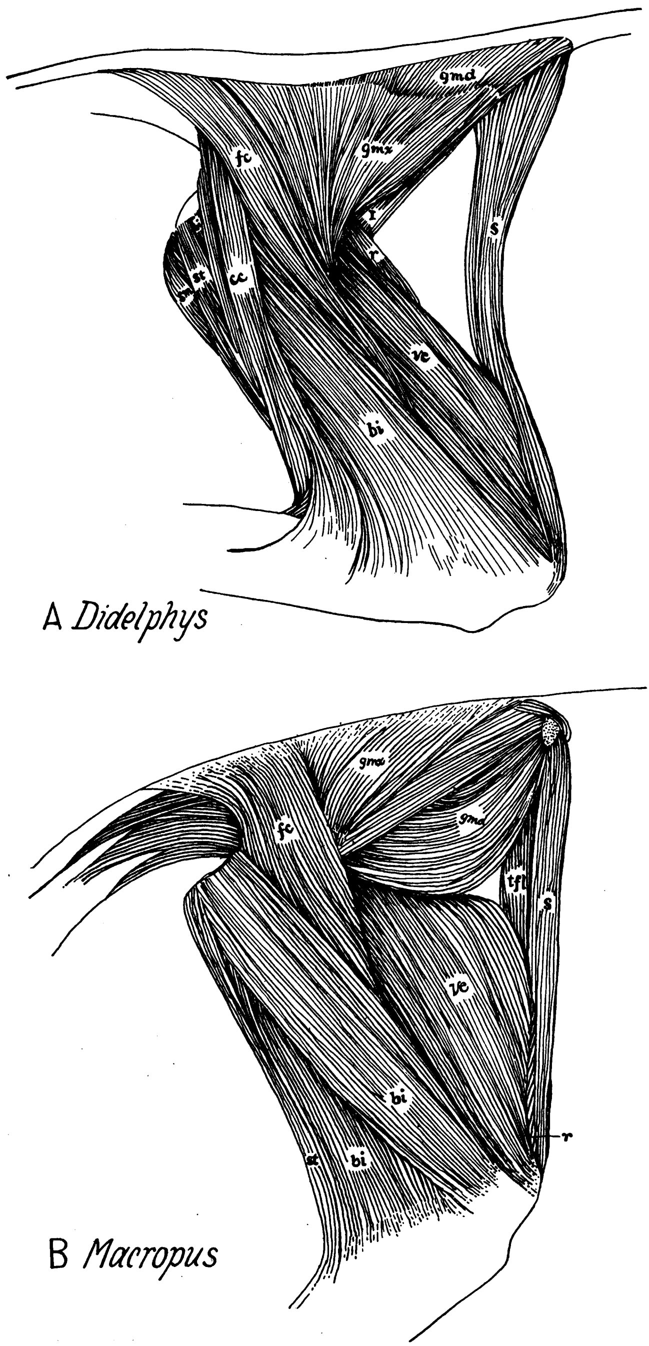



Fig. 3. Musculature of the hip and thigh, lateral view.
(See page 202 for key to abbreviations of names of muscles.)

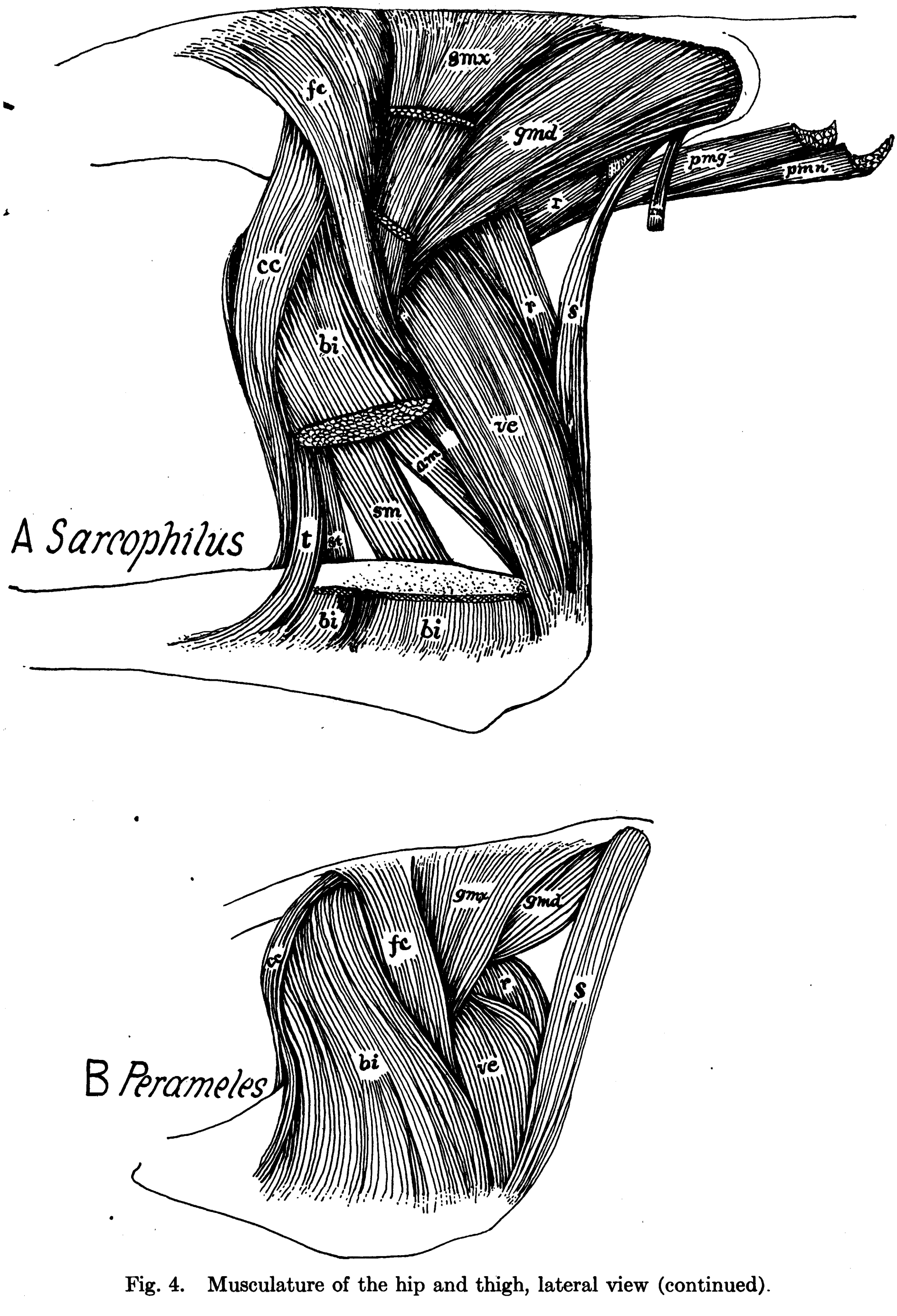



Fig. 4. Musculature of the hip and thigh, lateral view (continued).

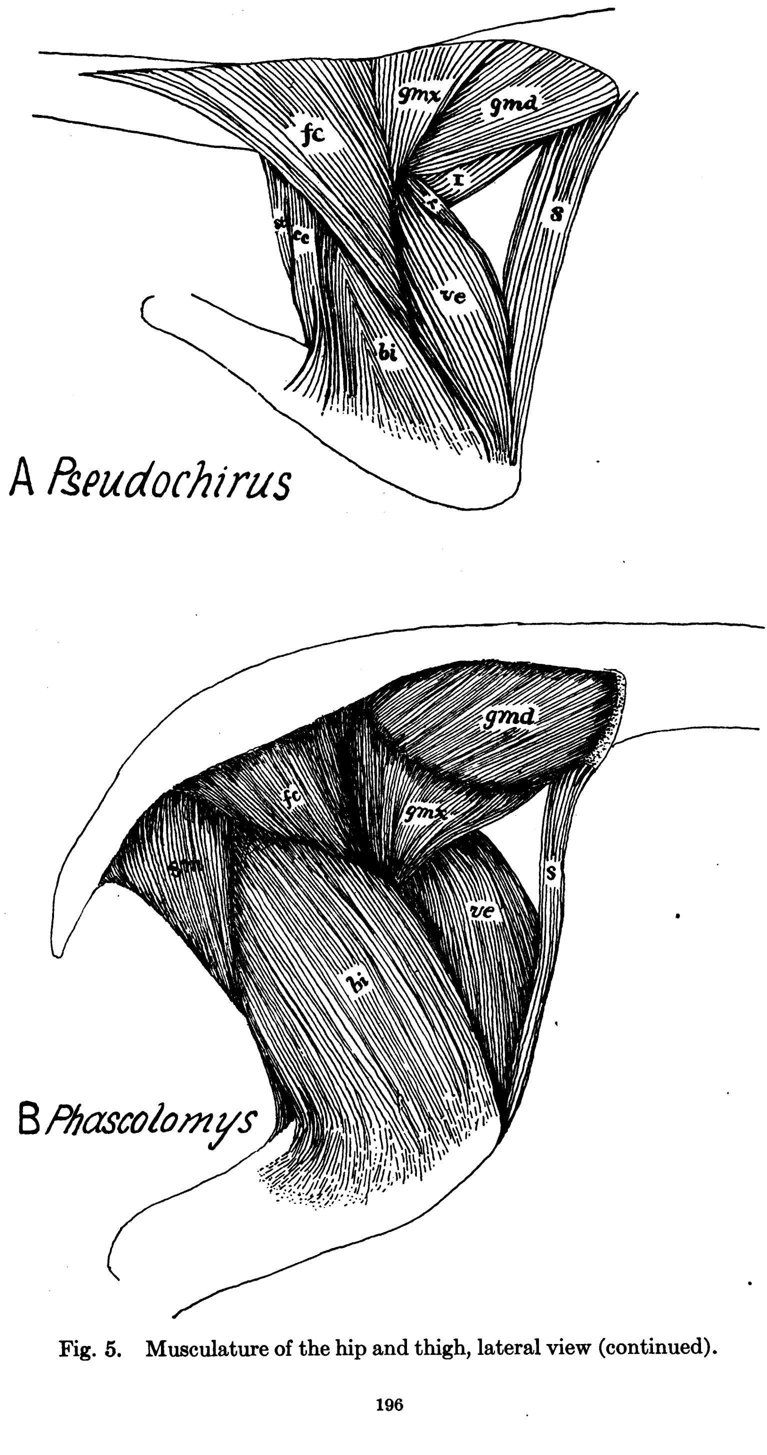



Fig. 5. Musculature of the hip and thigh, lateral view (continued).

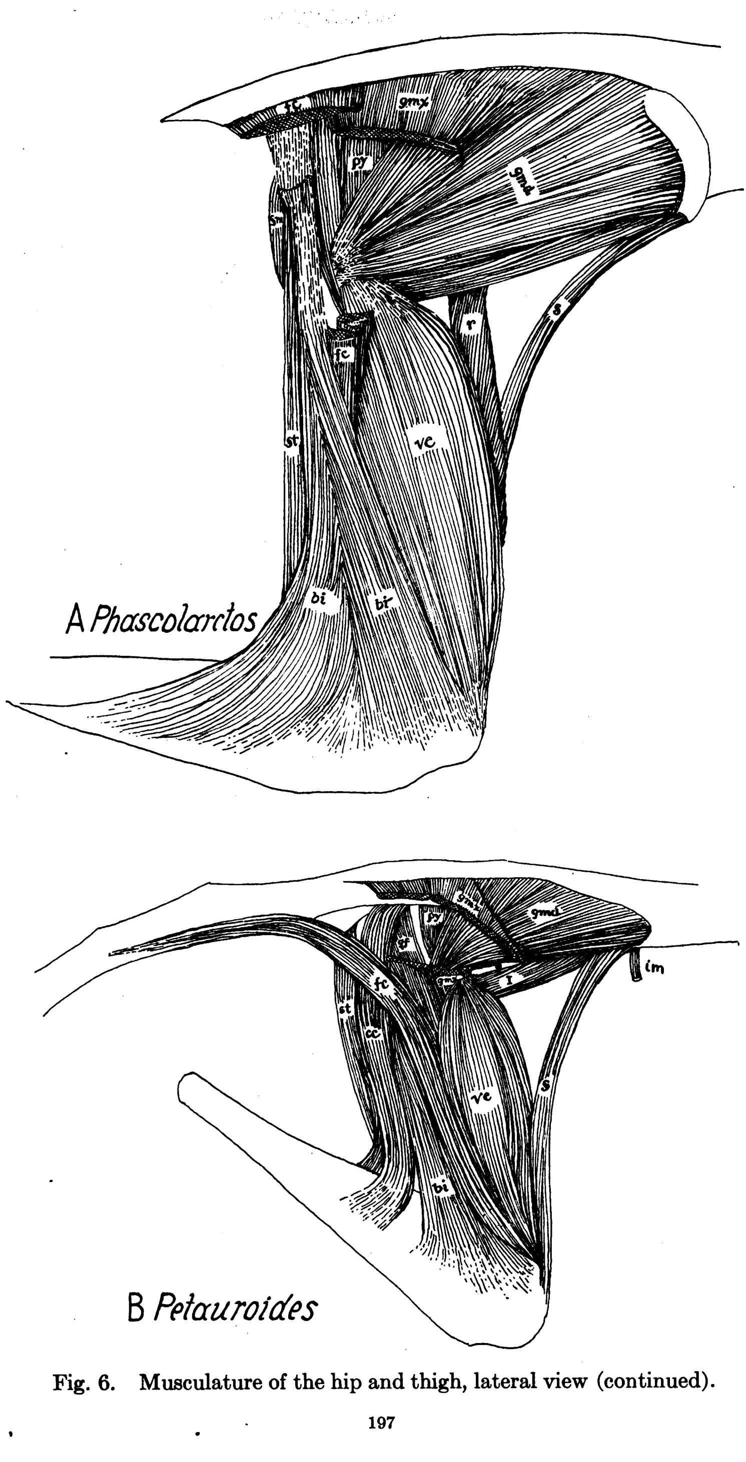



Fig. 6. Musculature of the hip and thigh, lateral view (continued).

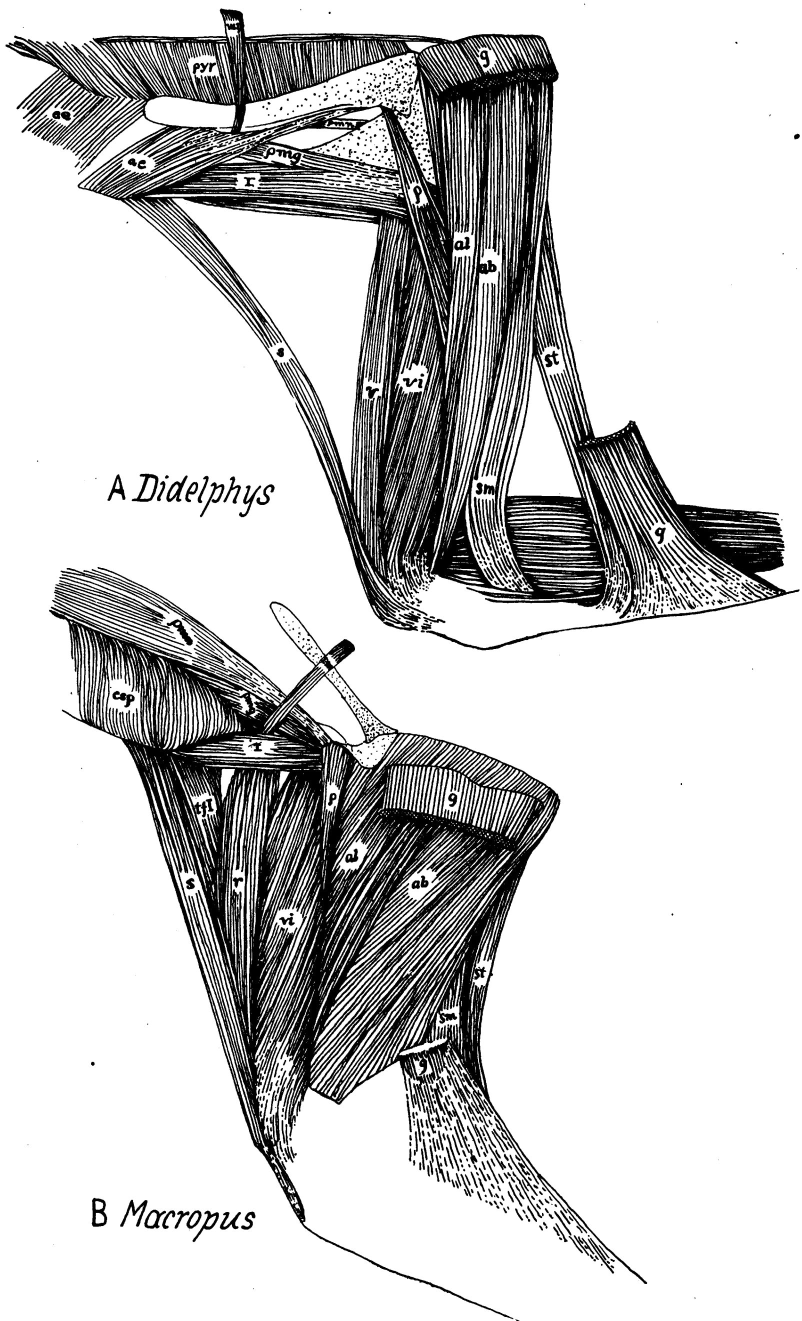



Fig. 7. Musculature of the hip and thigh, ventral view.

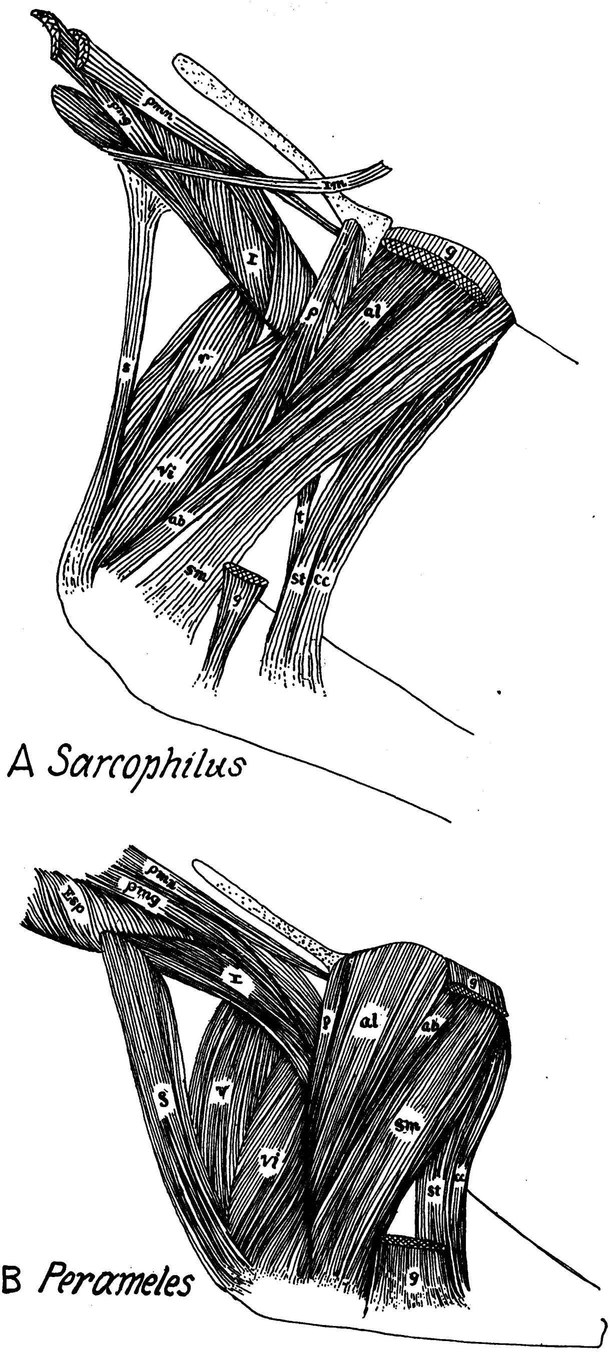



Fig. 8. Musculature of the hip and thigh, ventral view (continued).

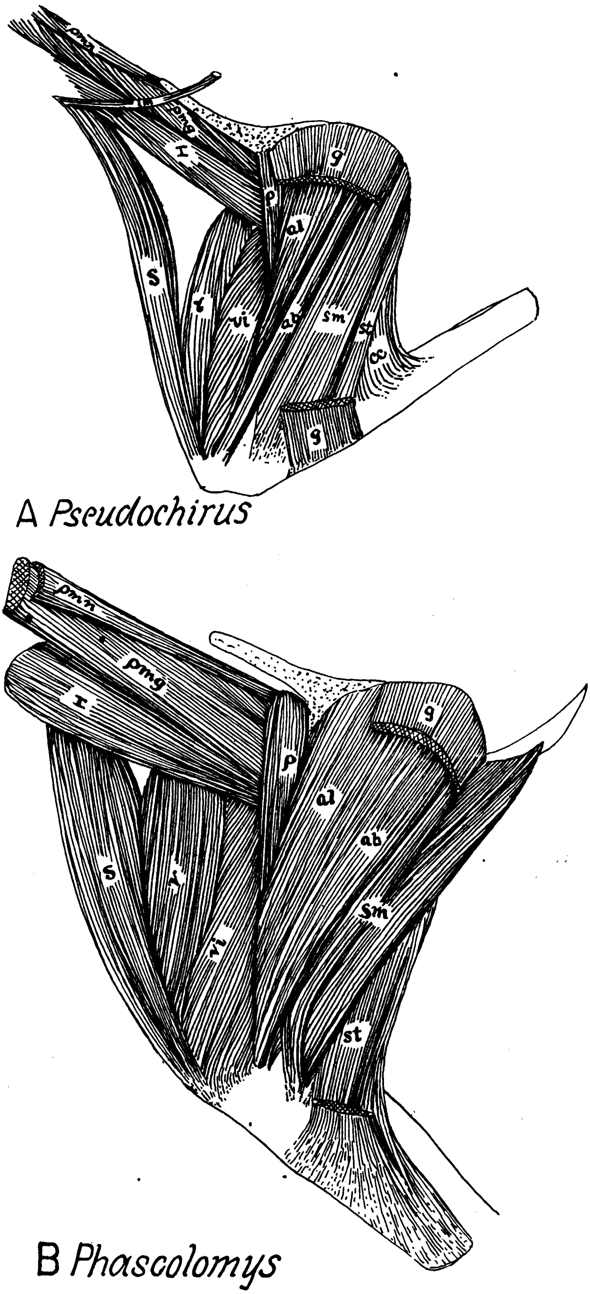



Fig. 9. Musculature of the hip and thigh, ventral view (continued).

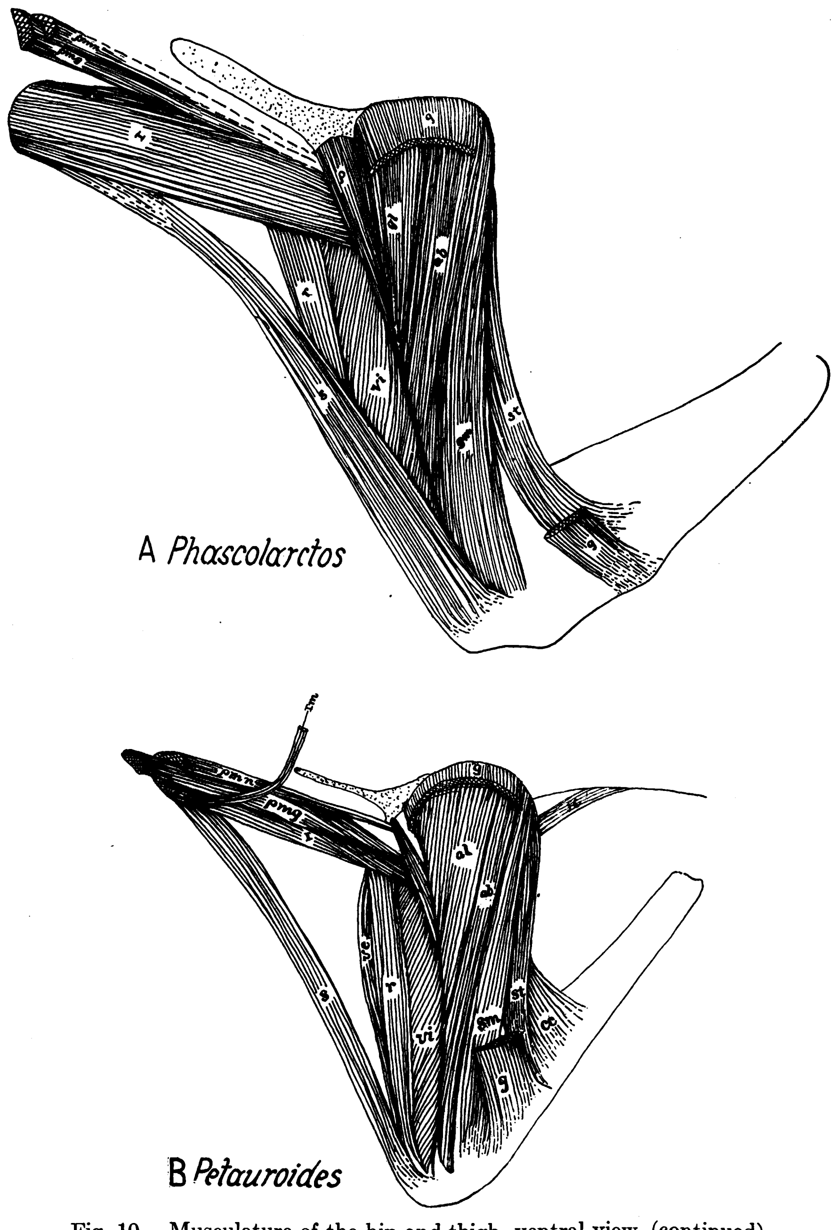



Fig. 10. Musculature of the hip and thigh, ventral view (continued).

## Key to Abbreviations of Names of Muscles

*bi* —biceps femoris
*cc* —cruro-coccygeus
*st* —semi-tendinosus
*sm* —semi-membranosus
*g* —gracilis
*t* —tenuissimus
*fc* —femoro-coccygeus
*gmx*—gluteus maximus
*gmd*—gluteus medius
*gmn*—gluteus minimus
*tfl* —tensor fascia lata
*if* —ilio-femoralis
*p* —pectineus
*al* —adductor longus
*ab* —adductor brevis
*am* —adductor magnus
*s* —sartorius
*r* —rectus femoris
*i* —iliacus
*pmg* —psoas magnus
*pmn* —psoas minor
*oe* —obturator externus
*oi* —obturator internus
*qf* —quadratus femoris
*gs, gms*—gemellus superior
*gi* —gemellus inferior
*gem* —gemelli (when undifferentiated)
*py* —pyriformis
*e, esp* —erector spinæ
*im* —ilio-marsupialis
*ae* —obliquus externus abdominis
*ai* —obliquus internus abdominis
*pyr* —pyramidalis
*ra* —rectus abdominis
*v* —vastus (when undifferentiated)
*ve* —vastus externus
*vi* —vastus internus

## Description of the Individual Muscles in a Generalized Type

The muscles are here described as they would be in a type which had not become specialized for any particular environment. Of all living marsupials the opossum, *Didelphys* (Figs. 3A, 7A), comes closest to being an incarnation of this type. The purpose of the description of the muscles is to present the essential facts concerned in the functioning of the muscles rather than to put on record the details of their morphology.

### Biceps Femoris (*bi*)

The short head of the biceps as found in human anatomy is uniformly wanting in the marsupials, unless Windle and Parsons are correct in assuming that it is represented by the tenuissimus.

Origin.—Fascia over the shank, sometimes extending up over the knee, attaching to the tibia and ligamentum patellæ.

Fibres.—About half as long as the muscle, arranged obliquely but at a very small angle.

Action.—Extension of the hip and, to less extent, flexion of the knee. Its power as a flexor depends on the lever-arm of its insertion. When acting alone it everts the shank.

### Cruro-coccygeus (*cc*)

Origin.—Tendon from transverse process of caudal vertebra.

The muscle is crossed by a tendinous inscription at the point where it comes in contact with the semi-tendinosus; both the cruro-coccygeus and semi-tendinosus send some fibers to each of the three common insertions.

Insertion.—(1) Medial border of the tibia by tendon and fascia attaching just distal to the insertion described under semi-tendinosus; it is covered in part by the tendon of the gracilis.

(2) A small slip along the posterior border of the biceps attaches to a continuation of the fascia which affords insertion for the biceps.

(3) Insertion on the medial side of the tibia described under semi-tendinosus.

Action.—The same as for the semi-tendinosus so far as the knee is concerned. The cruro-coccygeus, in addition, is of use to the animal in pulling his hind legs back when hanging by the tail. When acting singly the muscle is capable of flexing the tail laterally.

### Semi-tendinosus (*st*)

Origin.—Ischial tuberosity and anteriorly from the tendon of the biceps.

The muscle is crossed by a tendinous inscription not quite half-way down to the shank, where it comes in contact with the cruro-coccygeus. The two muscles inosculate—each one sends fibres to the three common insertions.

Insertion.—Chiefly by a tendon on the medial side of the tibia just proximal to the insertion of the gracilis. The other insertions receive most of their fibers from the cruro-coccygeus and are described under that muscle.

Action.—Flexion of the knee and, usually to a somewhat smaller degree, extension of the hip. The muscle would invert the tibia if the medial insertions could act alone and evert it very weakly if the lateral insertion could function singly; acting synchronously the rotatory tendencies neutralize each other.

SEMI-MEMBRANOSUS (*sm*)

Origin.—Posterior border of the ischium.

Insertion.—Tibia, by tendon passing beneath the collateral ligament.

Fibers.—Longitudinal.

Action.—Extension of the hip and, to less extent, flexion of the knee, since the leverage on the tibia is relatively small. The muscle also can invert the shank.

GRACILIS (*g*)

Origin.—Ventral and posterior borders of the pelvis (Fig. 7A).

Insertion.—By means of a tendon into the tibia about a third of the distance from the knee to the ankle.

Fibers.—Almost as long as the muscle.

Action.—The chief action of the gracilis is to flex the knee. With the tibia stationary the gracilis will extend the pelvis on the thigh, the power which it can exert in this action depending on the disposition of its area of origin, which is sometimes chiefly posterior to the acetabulum, sometimes chiefly beneath it. The gracilis is always an adductor of the limb, but it is much less powerful in that capacity than as a flexor of the knee, since it makes a very acute angle with the plane of the leg. Moreover, this angle becomes more acute as the limb is drawn under the body; the gracilis is therefore at its best as an adductor when the legs extend out from the body as in climbing trees. Acting alone the gracilis has a slight power of inversion of the tibia, but its leverage is very small.

FEMORO-COCCYGEUS (*fc*)

The femoro-coccygeus (Fig. 3A) is in many cases not clearly separable from the gluteus maximus, but it is functionally different, serving as an extensor of the hip.

Origin.—Chiefly from the transverse processes of caudal vertebræ but also slightly from the fascia over the caudal extensors.

Insertion.—The lateral border of the femur beginning on the great trochanter and extending distally for a variable distance.

Fibers.—Extend almost the entire length of the muscle.

Action.—Extension of the hip. Since the angle of insertion of the femoro-coccygeus on the femur is acute, the component of its force capable of causing rotation of the femur increases with extension of the thigh and is accompanied by a lengthening of the lever-arm. In this way the femoro-coccygeus works with increased mechanical advantage until the angle of insertion reaches its maximum shortly after the femur attains a vertical position. The femoro-coccygeus may abduct the thigh, but only weakly, since its insertion and point of passage over the ischium are nearly in the parasagittal plane in which the femur lies. In arboreal types the muscle may be of use in pulling the hind limbs toward the tail. It may also be used as a lateral flexor of the tail.

Gluteus Maximus (*gmx*)

The gluteus maximus is a thin fan-shaped sheet.

Origin.—Fascia over the gluteus medius and the caudal extensors; posteriorly slightly from the transverse processes of the caudal vertebræ.

Insertion.—Lateral border of great trochanter.

Fibers.—Longitudinal.

Action.—Abducts the thigh. The anterior part of the muscle has the power of inverting and slightly flexing the thigh. When the limb is fixed the gluteus maximus helps support the weight of the body as the other leg is lifted.

Gluteus Medius (*gmd*)

The gluteus medius is the largest of the glutei, a powerful muscle with a short range of action.

Origin.—Ilium and aponeurosis over vertebral muscles.

Insertion.—Tip of great trochanter by tendon.

Fibers.—Very short compared to the length of the muscle. Their attachment to the tendon of insertion is bipenniform, the fibers on the ventral side originating from the ilium, on the dorsal side from the fascia. Sometimes two laminæ are present.

Action.—The gluteus medius extends the hip and abducts and inverts the thigh. In walking these actions are all correlated, their combination resulting in a force exerted in the direction of progression of the animal instead of at an angle to it, since the pelvis is deflected to the right at the time the gluteus medius acts. The leverage for extension is increased by abduction and also becomes larger as extension progresses until the femur makes an angle of about 135° with the ilium, which is about the angle when the femur is vertical.

GLUTEUS MINIMUS (*gmn*)

The gluteus minimus is spread out in a fan-shaped sheet.

Origin.—Ilium.

Insertion.—Lateral border of the great trochanter.

Fibers.—Placed longitudinally and with a length almost equal to that of the muscle.

Action.—Chiefly inversion of the thigh, although a few of its posterior fibers may aid in abduction and extension.

ILIO-FEMORALIS (*if*)

The ilio-femoralis is a very minute cord-like muscle.

Origin.—Edge of the acetabulum slightly dorsal and posterior to the origin of the rectus.

Insertion.—Lesser trochanter, lateral to the ilio-psoas.

Fibers.—Longitudinal.

Action.—Very weak adduction and flexion of the thigh. Contraction of the muscle would keep the head of the femur in the acetabulum during extension and adduction. Coues (1872) points out that the ilio-femoralis is in the same position as the ligamentum ilio-femorale of human anatomy.

PECTINEUS (*p*)

Frequently the pectineus (Fig. 7A) consists of two separate parts.

Origin.—Typically on the epipubic bone, occasionally, as in *Macropus*, from the pectineal process.

Insertion.—Posterior surface of the femur from the lesser trochanter half-way down to the knee.

Fibers.—Longitudinal.

Action.—Adducts and everts the femur. It has no appreciable effect on the marsupial bone because of lack of leverage.

ADDUCTOR LONGUS (*al*)

Origin.—Ventral border of the pelvis.

Insertion.—Posterior border of the femur for almost its entire length distal to the lesser trochanter.

Fibers.—Longitudinal.

Action.—Adduction of the hip with eversion of the thigh. The angle of insertion increases as adduction proceeds, thus giving a better mechanical advantage to the muscle. The power of the muscle to extend the hip is slight, if any.

ADDUCTOR BREVIS (*ab*)

Origin.—Posterior border of the ischium.

Insertion.—Posterior border of the femur lateral to the adductor longus.

Fibers.—Longitudinal.

Action.—Extension of the hip, adduction and eversion of the thigh.

ADDUCTOR MAGNUS (*am*)

The name of this muscle (Fig. 11B) is misleading so far as the marsupials are concerned, because it is usually quite small.

Origin.—Posterior portion of the ischium near the ischial tuberosity.

Insertion.—Middle third of the posterior border of the femur medial to the femoro-coccygeus.

Fibers.—Longitudinal.

Action.—Extension of the hip and eversion of the thigh.

SARTORIUS (*s*)

The sartorius (Fig. 7A) is a long ribbon-like muscle.

Origin.—External border of the ilium near its anterior end.

Insertion.—Anterior and medial borders of the ligamentum patellæ.

Fibers.—Run longitudinally for almost the entire length of the muscle.

Action.—Chiefly flexing the thigh; it possesses a very short lever-arm for extension of the tibia, so that it could be of slight assistance to the rectus and vasti when thigh flexion is inhibited by the extensors of the hip. The chief function of the sartorius is to bring the femur forward during the recovery stroke of normal progression. At the beginning of this stroke the angle which the sartorius makes with the femur is relatively acute, favoring rapid movement; as flexion progresses the angle enlarges, thus increasing the component of the muscle force available for causing flexion. The situation of the origin far forward on the ilium is of some advantage, for it means that the vertical component of the muscle-pull is largest during the latter portion of the recovery stroke, as the limb is being lifted against gravity.

Rectus Femoris (*r*)

The rectus femoris is fusiform and is usually separable into at least two parts.

Origin.—Ilium in front of acetabulum.

Insertion.—Ligamentum patellæ. Sometimes the rectus unites with the vasti before inserting.

Fibers.—The fibers are short compared to the length of the muscle, originating and ending in tendon. They are so disposed as to be nearly parallel to the length of the muscle.

Action.—Flexion of the hip and extension of the knee. The leverage on the pelvis is slightly greater than that on the tibia. There is also this difference, that the lever-arm on the tibia, owing to the pulley of the rotular groove, does not change as the muscle contracts. In the propulsive stroke the hamstrings and gluteus medius prevent flexion of the hip while the knee is being extended, and in the recovery stroke the hamstrings prevent extension of the knee as the rectus assists in flexion of the thigh. The rectus has very little leverage in the first phase of recovery, since maximum extension of the femur brings the femoral axis almost directly in line with the origin of the rectus. During the second phase of the recovery stroke the rectus becomes increasingly powerful just as the leverage of the ilio-psoas is diminishing.

At the beginning of the second phase of the propulsive stroke, when the extensors of the knee are called into action, the rectus enjoys an advantage over the vasti in that it has been put under greater tension, due to the extension of the hip added to the flexion of the knee.

Iliacus (*i*)

Origin.—Ventral face of the ilium and in some forms partially from the ventral surfaces of sacral vertebræ.

Insertion.—Lesser trochanter, after fusing with the psoas major.

Fibers.—Short compared to the length of the muscle.

Action.—Flexion of the hip and eversion of the thigh.

Psoas Magnus (*pmg*)

Origin.—Ventral surfaces of the lumbar vertebræ.

Insertion.—By tendon with iliacus, with which it blends, into the lesser trochanter.

Fibers.—Relatively short compared to the length of the muscle.

Action.—Flexion of the hip, eversion of the thigh, flexion of the back.

PSOAS MINOR (*pmn*)

Origin.—Ventral surfaces of the lumbar vertebræ.

Insertion.—Pectineal process of the pubis.

Fibers.—Short and obliquely placed.

Action.—Flexes the vertebral column and extends the pelvis on the sacrum.

OBTURATOR EXTERNUS (*oe*)

Origin.—External rim of the obturator foramen (Plate IX A) and the membrane covering the foramen.

Insertion.—Digital fossa.

Fibers.—Length equal to that of the muscle, arranged in fan.

Action.—Eversion of the thigh, more powerful when the thigh is flexed, as the muscle is then pulling more at right angles to the axis of the femur. The obturator externus is a more powerful everter when the thigh is flexed and the obturator internus and gemelli when it is extended.

OBTURATOR INTERNUS (*oi*)

Origin.—Inner rim of the obturator foramen and membrane covering the foramen.

Insertion.—Tendon passing over the ischium as a pulley and inserting with the gemelli in the digital fossa.

Fibers.—As long as the muscle, excluding the tendon of insertion, and arranged in fan.

Action.—Abduction of the thigh accompanied by eversion, the latter being greater with the femur extended.

QUADRATUS FEMORIS (*qf*)

Origin.—Ischium near its dorsal border.

Insertion.—The posterior border of the trochanter major and extending down the femur for variable distances.

Fibers.—Extend the length of the muscle.

Action.—Extension of the hip and eversion of the thigh. The muscle possesses a good leverage for eversion; it is more powerful when the thigh is extended.

GEMELLI—SUPERIOR AND INFERIOR (*gs, gms, gi*)

Origin.—Dorsal border of ischium (Plate IX A) in region of sciatic notch.

Insertion.—With the obturator internus in the digital fossa.

Fibers.—Longitudinal.

Action.—Abduction and eversion of the thigh, the latter due especially to the inferior gemellus. The power to produce eversion is greater with the thigh extended, since that brings the femur more nearly at right angles to the direction of pull of the gemelli and internal obturator.

Pyriformis (*py*)

Whether the muscle described here as the pyriformis (Fig. 6) in marsupials is homologous with the muscle of the same name in mammals has recently been questioned by Appleton (1928). He considers that the muscle in marsupials represents the caudo-femoralis. Since the present paper deals entirely with marsupials, the homology of the muscle is not of immediate concern. It is hoped later to be able to contribute to the solution of the problem; for the present the name "pyriformis" will be retained.

Origin.—Transverse processes of caudal vertebræ.

Insertion.—Apex of trochanter major.

Fibers.—Longitudinal.

Action.—Abduction of the thigh. The pyriformis helps to support the weight of the opposite side when the limb of that side has been lifted off of the ground.

## Analysis of the Action of the Muscles in Different Types of Locomotion

### Walking Straight Forward on All-Fours

In considering the locomotion of mammals it will be simplest to take as our first case that of straight forward locomotion on four feet. We shall begin our analysis at the time when the animal has just planted its right hind foot on the ground. At that time the left leg is extended backward, the anterior end of the longitudinal axis of the pelvis is deflected to the left of the line of motion and the pelvis is rotated downward on the right side, slightly more posteriorly than anteriorly. The tibia makes approximately a right angle with the ground while the femur is flexed on the ilium.

The forward movement of the body is initiated by the contraction of the hamstring muscles (biceps, cruro-coccygeus, semi-membranosus, semi-tendinosus) and the femoro-coccygeus and to a slight extent the gracilis (Fig. 11A). The forward reach of the foot stretches these muscles so that they will develop a greater tension upon stimulation, thus starting the movement with greater efficiency. The contraction of these muscles

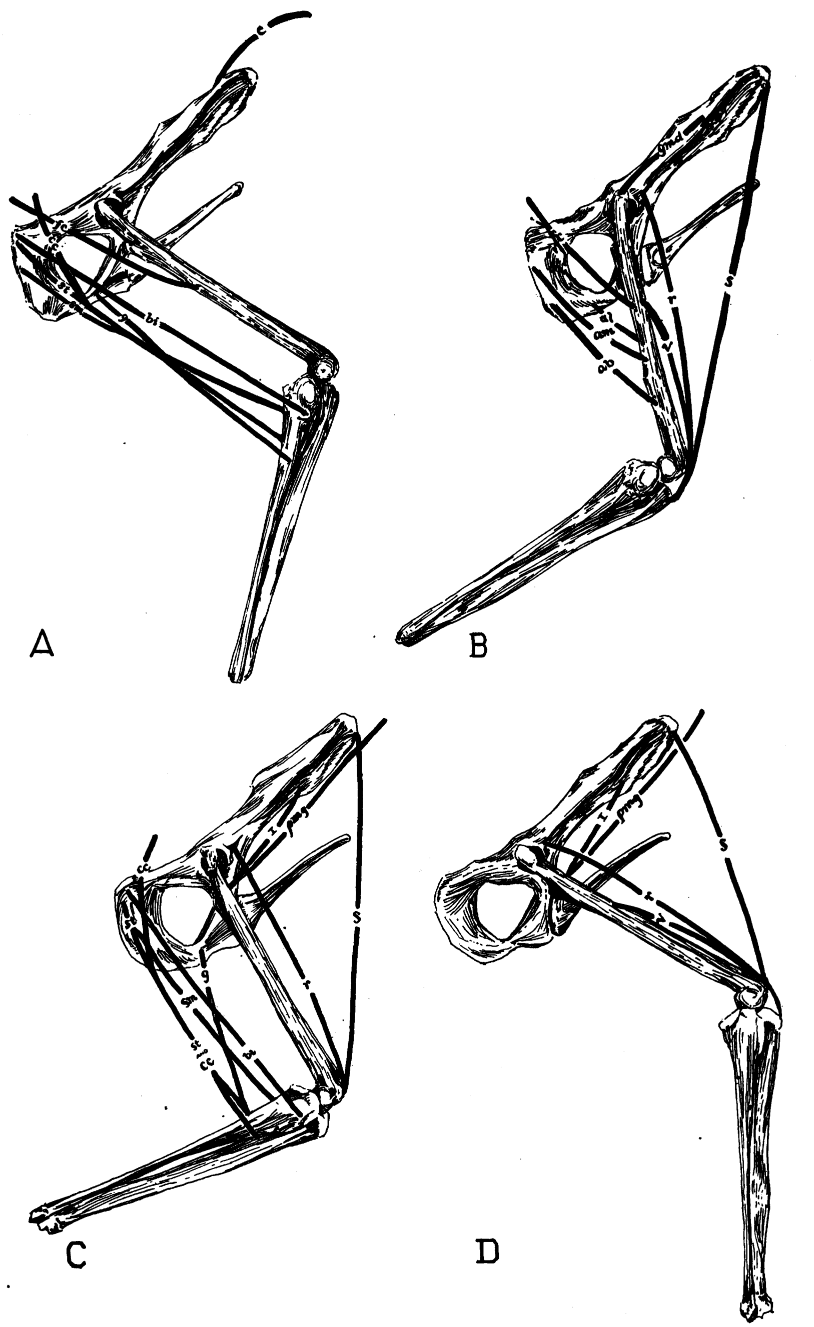



**Fig. 11.** The chief pelvic muscles acting in each of the four phases of locomotion. **_a_, propulsive stroke, phase 1; _b_, propulsive stroke, phase 2; _c_, recovery stroke, phase 1; _d_, recovery stroke, phase 2.**

elevates the anterior part of the body, the acetabulum acting as a fulcrum. The relatively large horizontal component of the contraction contributes to the forward movement of the body, which the left limb has just ceased to propagate. The slight flexion of the knee which occurs is brought about largely by the semi-tendinosus, cruro-coccygeus and gracilis, since their leverage on the shank is greater compared to their leverage on the pelvis than is that of the other hamstrings (the semimembranosus and biceps). The components for eversion and inversion of the tibia neutralize each other, since some of the hamstrings insert laterally, some medially.

The forward resultant of the action of the muscles mentioned above is augmented by the adductors, especially the adductor brevis and the adductor magnus. The lateral deflection of the longitudinal axis of the pelvis brings their line of action more nearly into the line of movement of the animal.

The erector spinæ, as well as other components of the spinal musculature, are also concerned in the elevation of the anterior part of the body. This elevation allows gravity to act. Since the hind limb above the joint between the metatarsals and phalanges is rigid, the fulcrum on which the body rotates in response to the pull of gravity is located in the foot. Consequently the body, while falling in response to gravity, is carried through an arc with the foot as its center and the hind limb as its radius. This arc has an appreciable forward component.

The adductors—longus, brevis and magnus—the pectineus, and the gracilis also function as adductors, tending to close the angle between the pelvis and the femur. This serves to rectify the sidewise tilt of the pelvis and also pulls the center line of the body over towards the right foot after the left foot has been raised from the ground. The gluteus medius begins its contraction, extending the femur on the pelvis and, with the aid of the gluteus minimus, drawing the longitudinal axis of the pelvis back into the sagittal plane.

Such is the situation up to the moment when the acetabulum has been brought vertically above the end of the metatarsals (Fig. 11 B.) The quadriceps, having been stretched to some degree by the flexion of the knee and the extension of the hip joint, is in a state which favors the maximum development of its power. The gluteus medius continues contracting, extending the hip. By its action and that of the gluteus minimus the longitudinal axis of the pelvis is pulled to the right. This brings the right leg more nearly into the line of progression, providing greater efficiency in the application of the locomotor impulse. It also brings the line of action of the gluteus medius more nearly into the line of movement. When the femur projects slightly outward from a parasagittal plane the inversion produced by the glutei medius and minimus may aid in forward movement. The extensors of the ankle play an important rôle in the latter part of the propulsion.

The gluteus maximus, femoro-coccygeus and pyriformis are instrumental in supporting the weight of the left side of the body after the left leg has been lifted.

In the recovery stroke of the leg the knee is bent by the hamstrings (Fig. 11 C). This is due partly to their passive rôle as connectives across two joints and would be greater in the case of the biceps and semi-membranosus, since they attach closer to the knee. The forward swing of the leg is partially a pendulum swing, due to gravity. The greater part of the muscular power for the flexion of the hip is supplied by the ilio-psoas, which with its short lever-arm can produce a rapid movement. There is a slight tendency for the ilio-psoas to evert the femur; this serves to keep the leg in an antero-posterior orientation, the long axis of the pelvis being deflected to the left at this time, as we noted above. The sartorius and rectus also aid in the flexion of the hip, extension of the knee being prevented by the hamstrings. The eversion of the femur caused by the ilio-psoas is aided by the obturators, gemelli and quadratus femoris; the latter muscle in some forms is continued down the femur as an extensor. In the last phase (Fig. 11 D) the knee is extended by the quadriceps and sartorius.

## Support of the Body While Standing

When mammals are resting they do not usually stand on all-fours but repose on their haunches. This removes the weight of the body from the hind limbs. When the animal is preparing for action or pausing on his way the body is supported in part by the hind limbs. Under these circumstances the muscles concerned in support are chiefly the one-joint extensors of the hip and knee—the gluteus medius and femoro-coccygeus and the quadriceps. The hamstrings assist the one-joint extensors of the hip in neutralizing the downward force of the anterior part of the body since the knee is kept rigid by the quadriceps. The adductors, gracilis and pectineus keep the legs from spreading under the weight of the body.

## Arboreal Life

Walking along the branch of a tree is remarkably similar in its general features to walking on the ground. There is a tendency for the legs to be more widely spread, increasing the functional significance of adduction and making the inversion of the femur available as a factor in propulsion. A striking example of large size of the gluteus minimus, the principal inverter of the femur, is found in the koala. When the branch on which the animal walks is inclined upwards the muscles involved in progression are the same as in ordinary walking; their magnitude compared to the mass of the body needs to be greater, since they are working against gravity. The proportion of the muscles to each other, however, remain essentially the same. The muscles for turning the body are of somewhat greater importance in arboreal life, since the opportunity for straightforward progress is more limited than in a terrestrial habitat. Prehensile tails are also developed in many of the tree-dwellers. Associated with the prehensile tail, as in *Pseudochirus*, is an increased development of the femoro-coccygeus. The advantage of this development is found in the aid it gives the animal in resuming a quadrupedal position after hanging from its tail.

## Gliding

Gliding animals are arboreal creatures which have the power of spreading their limbs so as to stretch the membrane which supports them as they glide through the air. Superimposed on the adaptations for arboreal life in such forms as *Petauroides*, we find an increased power of abduction of the femur and adequate power of extension of the hip and knee—the extension being similar to that in walking. This is accomplished by greater freedom of the head of the femur in the acetabulum and exceptional development of the muscles which abduct the femur—the pyriformis, gemelli and gluteus maximus.

## Leaping

Leaping, that of the kangaroo (Fig. 2) being taken as the example, differs from walking in that there is no lateral deflection of the pelvis and it undergoes no rotation about its longitudinal axis. The body is given a much greater forward thrust and a considerable elevation must be imparted to the body to keep it in the air while the horizontal component of the thrust carries it forward.

To attain these effects a powerful hind-limb musculature is necessary; compared to the total body-weight of the kangaroo the hind limb is very massive.

When we study the position of the hind limb of the kangaroo at the inception of the leap, we are impressed by the fact that the longitudinal axis of the body is nearly horizontal—a position similar to that in ordinary quadrupedal progression. The similarity is masked by the disparity in size of the fore and hind limbs. In contrast to the typical quadrupedal condition, the femur is more acutely flexed on the pelvis and the tibia more acutely flexed on the femur.

During the first phase of the forward movement, elevation of the body, some forward movement and flexion of the knee take place. Of these results the elevation of the anterior part of the body is by all odds the most important. It is accomplished by the hamstrings, femorococcygeus, gracilis, adductors and the erector spinæ. The latter muscle is very important in this connection; its function in leaping as well as in supporting the fore part of the body when the animal rests on its hind feet and tail correlates with its large size and large area of origin on the ilium.

At the beginning of the second phase of the propulsive stroke, during which the major portion of the impulse is transmitted, the longitudinal axis of the body is tilted upward at a considerable angle. As a result of this the forces which catapult the kangaroo into space are identical with those which cause forward horizontal movement in quadrupedal walking. The difference between the two cases lies in the direction of movement: in the case of the kangaroo this is more opposed to the pull of gravity and the muscles must therefore be more powerful. Larger muscles are also necessary due to the length of the leap and the fact that the efficiency of muscle is lower during rapid action.

The function of the extreme length of the tibia is of interest. During the first phase of locomotion its great length compared to the lever-arm of the hamstrings tends to increase the speed of the initial forward movement. During the second phase the tibia maintains the same angle with the ground, the propulsion taking place through extension of the hip and ankle. The length of the tibia is consequently impotent to affect the speed or force of the movement produced by the muscles in the second phase. On the other hand, it increases the radius of the arc through which the body falls in response to gravity.

The recovery stroke is similar to that found in quadrupedal locomotion. The two feet are brought close together as they approach the ground by the action of the ilio-psoas and the everters of the femur (obturators, gemelli, and quadratus femoris). The tibia is nearly vertical at the time of landing. The shock is largely absorbed by the extensors of the ankle; the hamstrings and erector spinæ are stretched by the fall of the anterior part of the body; as a result these muscles are in a state of tension ready to start the next saltation.

The simultaneous action of both hind limbs eliminates the lateral deflection of the pelvis in forward movement. In discussing quadrupedal walking we noted certain advantages which the animal enjoyed on account of the deflection, one of them being that the lines of action of the adductor muscles in the first phase and of the gluteus medius in the second were brought more nearly into the line of movement of the animal. In the kangaroo the line of action of the gluteus medius makes an angle of only twenty degrees with the sagittal plane compared with thirty degrees in *Didelphys*, as a result of the outward flare of the ilium. The area of origin of the gluteus medius approaches a frontal plane, thus decreasing the tendency of the muscle to invert the femur. In turning, the power would come largely from the gluteus minimus.

In the kangaroo the femur is more acutely flexed on the pelvis than in the ordinary tetrapod; even at its fullest extension it makes little more than a right angle with the ilium. One result of this is that the adductorial component of the pull of the muscles of the adductor group is decreased in favor of their function as extensors, since their leverage as adductors is greater when the femur is held farther back.

### Digging

When an animal digs with its fore feet, the function of the hind legs is to provide a resistance to the forward movement of the body which would normally follow a backward thrust of the fore limb. The muscle which is chiefly responsible for this resistance when the knee is stiffened by its extensors is the ilio-psoas, which keeps the hip from extending. In *Phascolomys* the ilio-psoas is very large. This muscle and the psoas minor also tend to arch the back; in a low tunnel this brings the back against the roof of the excavation. The hind legs are also of value in passing the detritus backwards; the muscles involved in this action are the same as those responsible for forward progression.

## Morphological Adaptations of the Muscles in the Types Studied

### Didelphys

Figs. 3A, 7A

The opossum possesses as generalized a muscle system as can be found among the living marsupials. It is well equipped for both arboreal and terrestrial life.

### Pseudochirus

Figs. 5A, 9A

The femoro-coccygeus is larger than in *Didelphys* and its origin extends farther back on the tail. This increases its power as a flexor of the tail, an important function especially when the animal is suspended from a limb by means of its tail and tries to regain a quadrupedal posture.

The hamstrings insert more distally on the tibia than in *Didelphys*, providing greater power in the first phase of the propulsive stroke but also decreasing the speed of the movement.

The gluteus medius is much smaller than in *Didelphys*, compensated, in a measure, by the large size of the femoro-coccygeus and the hamstrings. This condition is correlated with the slower movements of *Pseudochirus*, the femoro-coccygeus and hamstrings having longer levers and therefore producing less speed than the gluteus medius.

### Petauroides

Figs. 6B, 10B

The muscles of *Petauroides* were compared especially with *Pseudochirus*, a closely related purely arboreal form. This brought out the adaptations for gliding.

The posterior portion of the femoro-coccygeus has become widely separate from the anterior portion, having its origin on the seventh caudal vertebra. This increases its power as an extensor of the limb, especially after the limb has been brought close to the horizontal plane by abduction.

The quadratus femoris extends down to the knee. It is even longer than in *Pseudochirus*. Its origin is partially from the caudal vertebræ but not as much as in *Pseudochirus*.

The pyriformis is stronger than in *Pseudochirus*. This favors abduction of the thigh.

The superior gemellus is very strong, assisting the pyriformis.

The gluteus maximus is slightly stronger than in *Pseudochirus*.

### Macropus

Figs. 3B, 7B

The biceps in *Macropus* is very strong. Its fibers are relatively short, a fact which connotes a short range of contraction but great power. The insertion of the large anterior division of the biceps into the fascia over the condyle of the femur eliminates the action of this part of the muscle on the tibia but greatly increases its action as an extensor of the thigh. The posterior division of the muscle has a short leverage on the tibia, but the mass of this part of the muscle is only one-fifth that of the anterior part.

The cruro-coccygeus is absent in *Macropus rufogriseus,* but in a specimen of *Macropus rufus* a thin band of muscle was observed leading from the semi-tendinosus toward the vertebral column.

The semi-membranosus is a relatively weak muscle. Insertion on the condyle of the femur increases its power as an extensor of the femur and eliminates its action on the tibia.

The femoro-coccygeus is very powerful in the kangaroo. Due to its insertion at a very acute angle at the distal end of the femur, it is a rapid extensor of the hip.

The gluteus maximus is unusually large and placed with its fibers running obliquely backwards so that it assists in extension of the hip.

The component of the adductors capable of producing extension of the thigh is exceptionally large in the kangaroo, due to the great length of the pelvis back of the acetabulum and also to the fact that the femur is normally more flexed than in most animals, making a smaller angle with the ilium.

The rectus is large, with very short fibers. This makes it a powerful extensor of the knee with a short range of contraction.

The psoas minor is very large. It flexes the back and therefore acts as a check on the erector spinæ in balancing the body while the animal is supported by the hind legs. It also flexes the pelvis on the sacrum, which is of advantage in the recovery stroke.

The erector spinæ is extremely well developed. It lifts the anterior part of the body.

## Perameles

Figs. 4B, 8B

The muscles of *Perameles* are compared with those of *Macropus,* since they are both leaping forms. *Macropus,* however, is much more specialized in that direction.

The fibers are proportionately longer than in *Macropus.* The lever-arms are also longer; therefore the muscles of *Perameles* are more powerful, relative to their bulk, than those of *Macropus* but act with less speed.

The biceps is powerful in both *Perameles* and *Macropus,* but is larger in *Macropus.* In *Perameles* the insertion extends from the knee nearly to the ankle, quite a contrast to the proximal insertion in *Macropus.*

The size of the cruro-coccygeus in *Perameles* compensates for the small size of the semi-tendinosus. In *Macropus rufogriseus* no cruro-coccygeus is present, but in *Macropus rufus* a thin sheet of fibers extending dorsally from the semi-tendinosus represents this muscle.

The semi-membranosus is much more powerful in *Perameles* but its insertion is the same as in *Macropus*.

The femoro-coccygeus is only one-fifth as strong as in *Macropus*.

The gluteus maximus is not an extensor of the thigh in *Perameles* but is in *Macropus*.

The adductor brevis is not as large as in *Macropus*. The power of extension of the adductors is improved by the long ischium. Their power as adductors is lessened by the shallowness of the pelvis, which decreases the horizontal component of their pull.

The rectus is large, but not quite as large as in *Macropus*. Its fibers are short, but not as short, relatively, as in *Macropus*.

The psoas magnus is very large in *Perameles*, while the psoas minor is large in *Macropus*.

The semi-tendinosus has its origin under the biceps instead of posterior to it. This can be correlated with the large size of the cruro-coccygeus, which occupies the space immediately behind the biceps and also with the size of the biceps itself.

The semi-membranosus is large. It is a strong inverter of the shank, thus putting the foot into position for shoveling dirt or digging. It is assisted in this by the large medial slip of the semi-tendinosus.

The iliacus is very strong. This is a fossorial adaptation, as it prevents forward movement as the animal digs with its fore feet.

### Phascolarctos

Figs. 6A, 10A

The gluteus maximus assists in extension of the hip in addition to its usual function of abducting the thigh.

The adductors possess increased power for adduction of the thigh, compared to their power for extension, because of the shortness of the distance from their origins to the acetabulum.

### Phascolomys

Figs. 5B, 9B

The semi-membranosus has a very small leverage on the tibia.

The iliacus is large in mass and width, adapting it for lifting the leg against gravity.

The pyriformis has a large posterior division for eversion of the thigh and well-developed anterior division for abduction.

### Sarcophilus

Figs. 4A, 8A

The adductors are weak; there is no great need for adduction in terrestrial life.

The femoro-coccygeus fuses with the biceps, but also sends a separate tendon to the femur.

The tenuissimus is well developed.

The cruro-coccygeus inserts only on the medial side of the tibia. A branch of the semi-tendinosus joins it a short distance from the ischium by a tendinous inscription. Another branch of the semi-tendinosus has the usual medial insertion but receives no fibers from the cruro-coccygeus. There is no lateral insertion of the semi-tendinosus or cruro-coccygeus.

The iliacus and psoas magnus are of good size, but the psoas minor is very small.

The erector spinæ is quite large.

## ADAPTATIONS IN THE SHAPE OF THE PELVIS

### Factors Influencing the Shape of the Pelvis

In seeking to unravel the significance of the construction of the pelvis, we must first consider its morphological relation to the rest of the body. There are certain geometrical associations which influence the shape of the pelvis aside from its functions of supporting the animal and providing muscle leverage. In order to maintain its connection with the vertebral column and at the same time allow its two sides to meet ventrally, it is necessary for the pelvis to encircle the alimentary and urinogenital canals. Sufficient space must be allowed for the passage not only of the by-products of digestion but also of the young of the animal. In the case of the marsupials the young are of insignificant size at the time of birth, but the herbivorous diet of most of the animals necessitates a large pelvic outlet. The width of the trunk is also of importance in determining the width of the pelvis; here again herbivorous animals, having capacious trunks, have wide pelves.

The functions which the pelvis serves are those of static support and provision of lever-arms for the muscles. In the process of natural selection there would therefore tend to be developed in each type of animal a pelvic bone roughly modeled so as to fit the viscera and with finer detail so developed as to provide optimum support against gravity and leverage for locomotion.

SHAPE OF ILIUM.—The portion of the ilium which is situated between the acetabulum and the sacro-iliac joint transmits the force which propels the animal forward and is therefore very strong. The shape of the bone anterior to the sacro-iliac joint is determined chiefly by the sizes of the three muscle masses whose areas of origin form its three

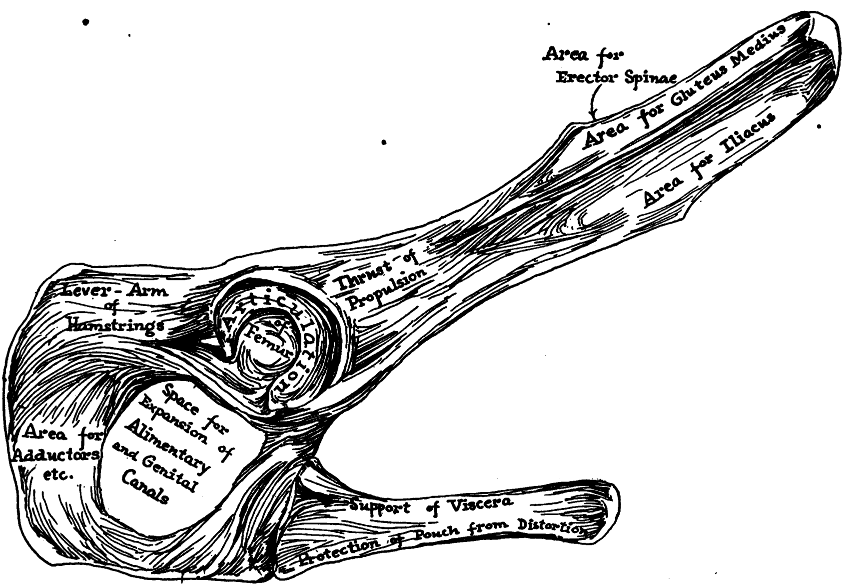



Fig. 12. Schematic diagram of pelvis, showing major function of the different parts.

borders—the erector spinæ mesially, the gluteus medius and the gluteus minimus dorso-laterally and the iliacus ventro-laterally. When the erector spinæ is small and the gluteus medius and iliacus are large and of sub-equal size, the result is an ilium flattened in the frontal plane, such as we find in *Phascolomys* (Plate IX G). When the iliacus has a relatively small origin on the ilium, while the gluteus medius and erector spinæ are both large, the ilium is flat but the plane is more nearly vertical, as in *Perameles* (Plate IX E).

The flare of the ilia with respect to the vertebral column is a function of the size of the erector spinæ and also partly of the width of the trunk. The second factor is more clearly taken care of by the lateral extension or wing of the anterior end of the ilium, as in *Phascolomys* (Plate IX G). This brings the obliquus internus into correct position relative to the viscera; it also produces a more directly antero-posterior pull of the sartorius and iliacus.

SACRO-ILIAC ANGLE AND SACRO-ILIAC JOINT.—There is a definite correlation between the size of the sacro-iliac angle and the size of the area of origin of the erector spinæ. When the pelvis is as nearly parallel to the vertebral column (Plate X) as it is in marsupials in general, only the dorsal portion of the mesial surface is available as area of origin for the erector spinæ. In such forms as the kangaroo this condition is remedied by an increased sacro-iliac angle (Plate XI) and a more posterior position of the sacro-iliac joint (Plate IX D). The latter condition would decrease the size of the pelvic outlet, were it not for the tilting of the pelvis. In *Sacrophilus*, where the ilium makes a large angle with the vertebral column but the sacro-iliac joint is placed farther anteriorly, the ischium is again brought more nearly parallel to the backbone by a slight bend in the ilium (Plate IX H).

The sacro-iliac joint is a diarthrosis in the marsupials. As such it is capable of cushioning some of the shock as the foot lands on the ground, an important feature in forms like *Macropus* and *Perameles*. The peculiar elongate shape of the joint in *Phascolomys* (Plate IX G) is in harmony with the flattened shape of the ilium and is adapted to withstand dorso-ventral rotation of the pelvis. In this it is abetted by the ligamentous connection between the vertebral column and the ischium.

ISCHIUM.—The dorsal ramus of the ischium provides the lever-arm for the action of the hamstrings, and partially of the adductors, on the body. As a result it is of heavy construction, resembling somewhat the portion of the ilium immediately in front of the acetabulum. The length of the lever-arm is directly correlated with the habit of the animal. In leaping forms, such as *Macropus* (Plate IX D) and *Perameles* (Plate IX E), it is long, to afford the increased power needed for leaping. In *Phascolomys* (Plate XIII) it is long, to give increased digging power to the hamstrings when the body is kept stationary.

The vertical ramus of the ischium provides area of origin for the adductor muscles and the semi-membranosus. The area of this portion of the ischium is roughly correlated with the size of these muscles. In forms with long femora, such as *Petauroides* (Plate IX C), the cross-section of the muscles is decreased in favor of length. It is therefore important that the length of the muscle as well as its area and angle of origin be considered in estimating its size. In the animals with long ischia and with the posterior border vertical instead of inclined downward and forward, the adductors originate farther back from the femur. They are then more powerful as extensors of the hip than they would be under the alternative condition.

SYMPHYSIS PUBIS.—The symphysis resists the lateral pulls of the adductors, gracilis and obturators. In forms with movable sacro-iliac joints it is necessary to have strong pubic symphyses. In the kangaroo, especially (Plate IX D), but also in *Perameles* (Plate IX E), the symphysis is weak; this is correlated with the synchrony of action of the muscles of the two sides in leaping, their pulls opposing each other. In *Phascolomys* (Plate IX G) the shortening of the symphysis posteriorly is necessary to provide a proper outlet for the pelvis, the size of the outlet being decreased by the attachment of the transverse processes of the vertebræ to the ischia. The shortness of the symphysis is compensated by greater thickness.

VERTICAL RAMUS OF THE PUBIS.—The vertical ramus of the pubis transmits part of the force of the adductors longus and brevis and the gracilis.

OBTURATOR FORAMEN.—The origin of the obturator muscles, both externus and internus, is around the edges of the obturator foramen. There would be no great advantage in having a muscle arising from the area occupied by the foramen; in some forms some fibers of the obturators arise from the membrane covering the foramen. The presence of the foramen is of distinct service to the animal during the passage of waste matter and progeny through the pelvis, because the space within the pelvis can be materially increased by the outward protrusion of the obturator internus and pubo-coccygeus through the foramen. The size of the obturator foramen depends largely on the areas of origin of the surrounding muscles.

ACETABULUM.—The acetabulum is one of the critical parts of the pelvis, as it transmits the force of propulsion from the femur to the body and also transmits the weight of the body to the femur. For this purpose it is strongly buttressed anteriorly. In arboreal forms, such as *Didelphys* (Plate IX A) and *Pseudochirus* (Plate IX B), the cup is more open, allowing greater freedom of movement of the head of the femur. In gliding forms, *Petauroides* (Plate IX C) for instance, this arboreal adaptation is amplified still further, especially to allow abduction. The acetabulum is strongly buttressed posteriorly to withstand the thrust of the femur in the first phase of progression in *Macropus* (Plate IX D) and in the first phase of digging in *Phascolomys* (Plate IX G). The shape of the acetabulum is modified in *Macropus* to conform to the lateral elongation of the head of the femur, thus producing a larger bearing surface at the expense of freedom of rotation.

MARSUPIAL BONES.—The marsupial or epipubic bones assist in the support of the abdomen. In this function they co-operate with the abdominal musculature which, when very strong, as in *Phascolomys* (Plate IX G), may bear the greater part of the burden. The marsupial bones are largest in *Phascolarctos* (Plate IX F), which has very capacious viscera and spends most of its time in the trees in a semi-vertical position, thus concentrating the pressure of the viscera on the pelvis and lower wall of the abdomen. In the forms studied the marsupial bones are smallest in *Pseudochirus* (Plate IX B) and *Petauroides* (Plate IX C), in both of which the abdomen is small.

The external oblique and internal oblique muscles insert on the marsupial bones. The contraction of these muscles compresses the abdomen. The marsupial bones protect the pouch in a measure from the effects of this contraction, at the same time aiding the compression of the viscera.

The view was advanced by Owen and supported by Coues (1872 pp. 83-84) that the most important function of the marsupial bone is that of increasing the effect of the ilio-marsupialis muscle, the homologue in the female of the cremaster in the male. This would seem a trifling function for a marsupial bone as broad and strong as that of the koala (Plate IX F). The condition in *Petauroides* (Fig 10 B) is very significant in this connection; the ilio-marsupialis lies entirely anterior to the marsupial bone. Observation of the forms dissected points to the conclusion that the ilio-marsupialis pursues a course from the ilium to the pouch, passing over the marsupial bone only if it happens to lie in the path of the muscle.

## ADAPTATIONS IN THE SHAPE OF THE PELIVS IN THE TYPES STUDIED

### DIDELPHYS (Plate IX A)

The opossum is a generalized form; the pelvis shows no marked specializations. The ilium is trihedral, a condition which is correlated with the large size of the gluteus medius in conjunction with well-developed iliacus and erector spinæ muscles. In *Pseudochirus* the ilium is not nearly as triangular in cross-section, the gluteus medius being small and its area of origin narrow. The acetabulum permits freedom of movement of the head of the femur but its border is not excavated dorsally to favor great abduction as it is in *Pseudochirus* and *Petauroides*.

### PSEUDOCHIRUS (Plate IX B)

The dorsal border of the ilium is narrower than in *Didelphys*, the gluteus medius being smaller and having a narrower area of origin.

The sacro-iliac angle is smaller than in *Didelphys* and the sacro-iliac joint is situated farther back.

The posterior border of the ischium is inclined forward and downward. This enlarges the outlet of the pelvis, compensating partly for the decrease in size caused by the small sacro-iliac angle.

The acetabulum is more open dorsally than in *Didelphys*, permitting greater freedom of movement of the femur. This is of advantage in arboreal life.

### PETAUROIDES (Plate IX C)

*Petauroides* was compared especially with *Pseudochirus*, a closely related non-flying arboreal type. The pelvis is not as deep as in *Pseudochirus;* this is responsible for the impression one gets upon cursory examination that *Petauroides* has an unusually long ilium. The muscles lying parallel to the femur do not need to have great diameters at their origins, because the relatively great length of the femur allows the muscle substance opportunity for longitudinal distribution.

The acetabulum of *Petauroides* is somewhat more open than that of *Pseudochirus*. *Pseudochirus* also has a very open acetabulum, a condition associated with its arboreal life. In *Petauroides* the acetabulum has a deeper notch dorsally than in *Pseudochirus*, allowing extreme abduction of the femur during gliding.

### MACROPUS (Plate IX D)

The ischium is long compared to the rest of the pelvis. This provides additional leverage for the hamstrings and adductors and incidentally a larger area for the origin of the adductor magnus. It also brings the pull of the adductors more nearly parallel to the body, thus increasing their power as extensors; this effect is heightened by the fact that the femur is normally more flexed than in ordinary walking types.

The sacro-iliac joint is situated far back on the ilium. This is necessitated by the large area for the insertion of the enormously developed erector spinæ.

The large ilio-sacral angle makes the entire medial surface of the ilium available for the attachment of the erector spinæ. The large angle increases the size of the pelvic outlet which would otherwise be small due to the posterior location of the sacro-iliac joint.

The ilia flare outward, chiefly to accommodate the erector spinæ but also the gluteus medius. This flare is also of value in bringing the pull of the glutei more nearly into the para-sagittal plane of the femur; this is especially important, since there is no lateral deflection of the pelvis in leaping, the legs acting synchronously. The pronounced down-curving of the transverse processes of the lumbar vertebræ is also correlated with the size of the erector spinæ.

The symphysis pubis is relatively weak. The gracili and in part the adductors of the two sides meet without the interposition of bone. This is possible because they pull against each other, both sides acting at the same time.

The pectineal process is well developed. It serves for the attachment of the psoas minor; if the process were not so long the psoas minor would interfere with the psoas major and the iliacus. The pectineal process also gives origin to the pectineus.

The area of origin of the rectus is well marked; the rectus is very large in the kangaroo, being concerned especially with the second phase of the propulsive stroke.

The acetabulum is well adapted for antero-posterior movement of the leg. The dorsal lip overhangs the cavity to a great extent. The acetabulum is buttressed chiefly in two places : (1) anteriorly, against the body weight and the pull of the glutei; (2) posteriorly, against the pull of the femoro-coccygeus, adductors and hamstrings. The incisure is nearly closed.

### PERAMELES (Plate IX E)

The ischium is very long, in proportion to the total length of the pelvis; it even exceeds *Macropus*. The advantages are the same as those enjoyed by *Macropus*. The fact that the ischium in *Perameles* is longer than that of *Macropus* proportionately may be correlated with the lack of a long tail in *Perameles*, the balancing of the body being left entirely to the muscles.

The sacro-iliac joint is situated far back on the ilium, allowing a large area of origin for the huge erector spinæ muscle.

The ilio-sacral angle is large. It is not as large as in *Macropus*, but the available area of origin for the erector spinæ is increased by the downward curvature of the transverse processes of the lumbar vertebræ. The pelvic outlet is enlarged by the width of the pelvis.

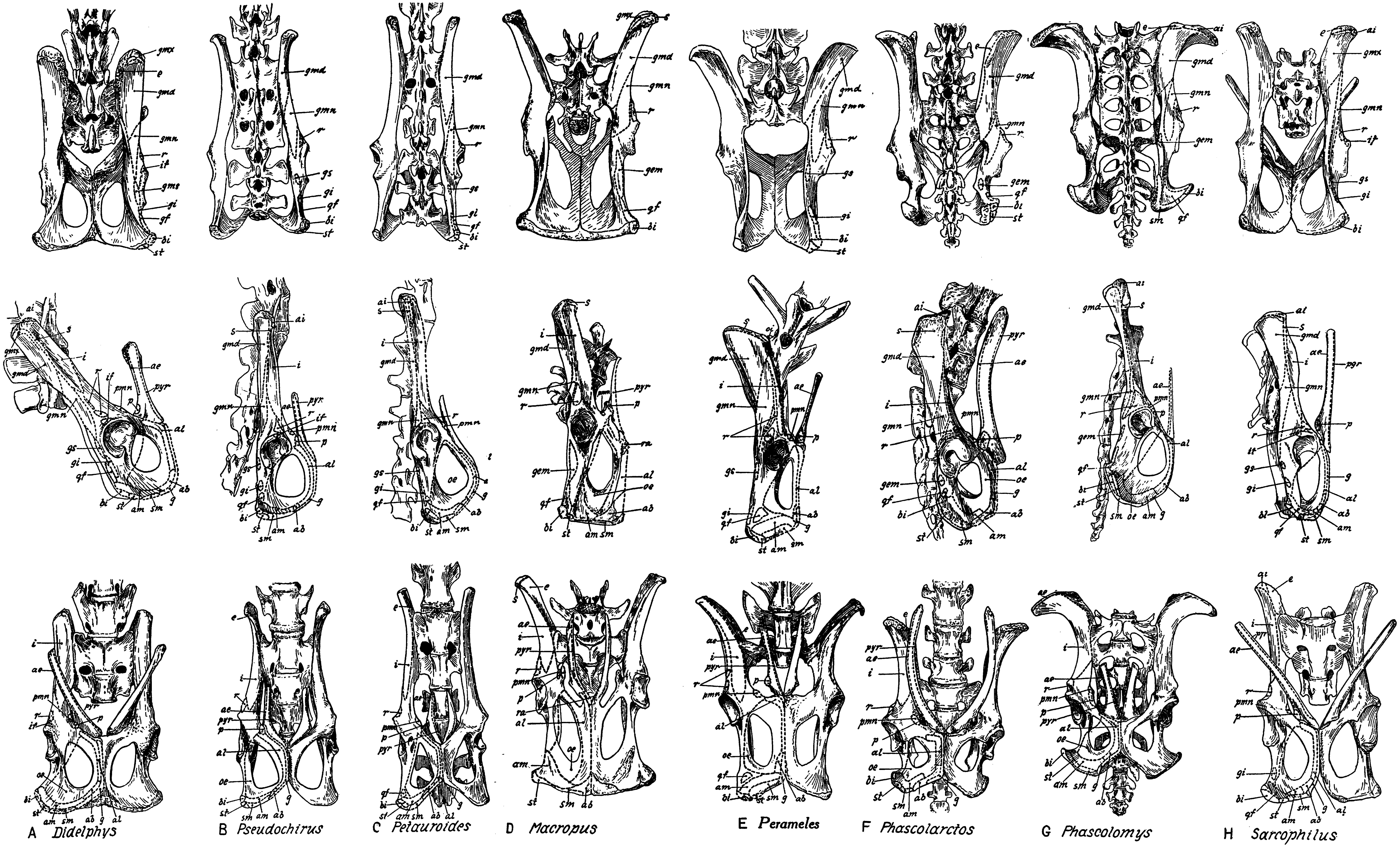



PLATE IX
Pelves in dorsal, lateral and ventral views.

The pelvis is wider than in *Macropus* in comparison with the width of the body. The pelvis is wider in *Perameles* than in *Macropus* when compared to the width of the body but not in relation to the length of the body. The proportion of the width of pelvis at the acetabulum to the length from the ischial tuberosity to the atlas is .17 in *Perameles* and .185 in *Macropus*. The kangaroo has a wider trunk proportionately, due to its herbivorous diet. The widening of the pelvis in *Perameles* is accomplished by increased width of the sacrum.

The ilia flare outward anteriorly as they do in *Macropus*, the advantages being the same.

The area for the origin of the glutei is not as horizontal as it is in *Macropus*. The iliacus has a smaller area of origin on the ilium, in *Perameles*, originating partly from the sacral and lumbar vertebræ. The shape of the ilium is therefore determined largely by the erector spinæ and gluteus medius.

The acetabulum is more generalized than in *Macropus*, the femur not being restricted to antero-posterior movement. The bandicoot is not nearly as highly specialized in its mode of locomotion as is the kangaroo.

### PHASCOLOMYS (Plate IX G)

The ilium has a very marked lateral flare anteriorly. The trunk is very wide; even with wing of the ilium as wide as it is, the sartorius barely misses the abdomen. The obliquus internus is very strong and has its origin from the wing of the ilium. The iliacus is extraordinarily large. The lateral extension of the ilium gives the gluteus medius a more nearly antero-posterior pull and brings the sartorius more nearly into the plane of the leg. This lateral extension is not due to the erector spinæ. The slight flare of the medial border facilitates the origin of the erector spinæ but would not be necessary.

The ilium is very flat in the frontal plane. The iliacus approaches the gluteus medius in size and the erector spinæ is not especially large.

The acetabulum is very strongly buttressed anteriorly to withstand the thrust of the leg in forward progression and in digging. It is less strongly buttressed posteriorly to withstand the forward pull of the body as the fore feet dig. The incisure is widely open.

The symphysis pubis is short. A strong symphysis pubis is not necessary when the pelvis is attached to the sacrum (Mijsberg, 1920, p. 588). The disappearance of the posterior part of the pubic symphysis increases the size of the posterior opening of the pelvis, which was greatly decreased by the attachment of the sacrum to the ischium.

A lateral projection is present on the ischial tuberosity. It gives origin to the major portion of the very large semi-membranosus. The lateral extension of the ischial tuberosity brings the pull of the biceps more nearly into a para-sagittal plane.

The great length of the ischium increases the antero-posterior component of the hamstrings, an adaptation of use in digging. The area of the dorsal portion of the posterior border of the ischium is increased, thus accommodating the hamstrings, the postero-ventral corner of the pelvis being cut off.

### Phascolarctos (Plate IX F)

*Phascolarctos* exhibits an outward flare of the ilia, but it is not nearly as marked as in *Phascolomys*. This may be correlated with the fact that the trunk is quite wide and the iliacus is large. The flare brings the sartorius more nearly into the plane of the leg. It is not due to the erector spinæ, the origin of which only extends three-fourths of the distance to the lateral extremity of the ilium. The area of origin of the erector spinæ is provided for by the large ilio-sacral angle.

The posterior position of the sacro-iliac joint and the large ilio-sacral angle provide a larger area of origin for the erector spinæ without producing an oblique pull as origin from the lateral extremity of the ilium would.

The symphysis is normal in length but is very thick. The stoutness of the symphysis enables it to withstand the strains of adduction.

The obturator foramen is small. The rest of the space is needed for muscle origin, since the ischium is short.

### Sarcophilus (Plate IX H)

The pelvis of *Sarcophilus* is very generalized.

The sacro-iliac angle is fairly large, providing area for the origin of the erector spinæ.

The ischium does not make as large an angle with the vertebral column as does the ilium. If the ischium made the same angle as the ilium it would increase the size of the pelvic outlet; this is not necessary, since the sacro-iliac joint is situated far anterior to the acetabulum.

The obturator foramen is large. The adductors are small, so they need only a small area of origin.

## SUMMARY

The movement of the hind limb in locomotion consists of two strokes, the propulsive and the recovery. Each of these strokes may be divided into two phases. During the first phase of the propulsive stroke the most important muscles are the hamstrings, which raise the anterior part of the body by means of their leverage on the acetabulum and pull the body forward, flexing the knee. During the second phase, which begins when the line of support of the limb has become vertical, the shank is extended on the thigh by the quadriceps femoris and the thigh is extended on the pelvis by the gluteus medius assisted by the femoro-coccygeus and the adductors. In the recovery stroke the knee is bent by the hamstrings and carried forward by the ilio-psoas and sartorius muscles, abetted by the rectus muscle and gravity. In the second phase of recovery the thigh is extended by the quadriceps. The lateral deflection of the longitudinal axis of the pelvis and the rotation of the pelvis about this axis during locomotion are advantageous in bringing the lines of action of the muscles more nearly parallel to the direction of movement of the animal.

Arboreal adaptation in pelvic structure consists largely of increased size of the muscles of adduction and a more open acetabulum, allowing more freedom of motion of the femur. These conditions are likewise found in arboreal forms adapted for "flying" or gliding; the gliding adaptation is characterized in addition by the power of extreme abduction of the femur, reflected in the large size of the pyriformis, gemelli and gluteus maximus and in the excavation of the dorsal margin of the acetabulum. To stretch the flying membrane the extensor musculature of the thigh is well developed.

Leaping forms are characterized by the large size of the hind limbs compared to the size of the body as a whole. The post-acetabular portion of the pelvis is relatively long to provide leverage for the hamstrings and also to increase the power of the adductors as extensors of the thigh, at the expense of their function as adductors. The erector spinæ is very large, its large area of attachment on the pelvis being associated with an outward flare of the ilium and a large ilio-sacral angle.

Fossorial adaptation depends largely on the habits of the particular animal studied, some forms pressing the dirt aside, some digging with their fore feet, others with their hind feet. In an animal like the wombat, which uses both the methods of pressing the dirt aside and of digging with its fore feet, the hind limb musculature as a whole is very powerful,

the hamstrings being especially well developed. The great length of the ischium increases the antero-posterior component of the pull of the hamstrings. The iliacus attains great size, serving to keep the animal from moving forward as it digs with its fore feet. The size of the iliacus is partially responsible for the broadness of the ilium. The sacrum has a ligamentous connection with the ischium.

The factors which influence the shape of the pelvis are not all concerned with the locomotor apparatus. The gross form of the pelvis is determined by its relation to the viscera. Its width is influenced by the width of the trunk. The size of the sacro-iliac angle and the position of the sacro-iliac joint are conditioned by the magnitude of the erector spinæ muscle and the necessity for an adequate pelvic outlet. The posterior border of the ischium in some animals is inclined forward and downward to compensate for an encroachment upon the size of the pelvic outlet on the part of the sarco-iliac joint or the sacrum. The obturator foramen permits of the distension of the alimentary and genital canals during the passing of material through the pelvis. The marsupial bones assist the abdominal musculature in the support of the viscera and protect the pouch from distortion during the contraction of those muscles.

## Explanation of Tables I and II

The following tables contain some of the measurements made in order to determine the relative importance of the different muscles in executing each of the movements concerned in locomotion. The measurements were intended for use in a qualitative rather than in an accurately quantitative analysis.

Table I lists the volumes of the muscles. These were obtained by computation from measurements of the muscles in the preserved specimens. This method was adopted because the rarity of the material precluded removing each muscle and weighing it or determining its volume by immersion. The results obtained are accurate enough for the purpose of this study; with more delicate determinations it would be possible to reach accurate quantitative measurements of the rôle of each muscle.

After the measurement of the muscles it was found desirable to know what proportion of the hind-limb musculature was made up by each of the muscles. The results are tabulated in terms of parts of one thousand. The variation in the importance of a given muscle in the different groups is brought out by this ratio.

Table II shows the lever-arms of the muscles of the hamstring group and the gracilis in their action on the ischium and also on the tibia. In the former case the lever-arm is measured from the origin of the muscle to the center of the acetabulum, in the latter from the insertion of the muscle to the center of rotation of the knee.

TABLE I

| | *Macropus* | | *Perameles* | | *Didelphys* | | *Pseudochirus* | | *Petauroides* | | *Phascolarctos* | | *Phascolomys* | | *Sarcophilus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | V | $R_m$ | V | $R_m$ | V | $R_m$ | V | $R_m$ | V | R | V | $R_m$ | V | $R_m$ | V | $R_m$ |
| Bi.—ant. | 37500 | 193 | 4160 | 103 | 810 | 24 | | | 560 | 22 | | | | | 4940 | 103 |
| post. | 6800 | 35 | 2400 | 60 | 1025 | 28 | 2205 | 113 | 280 | 11 | 6936 | 75 | 6552 | 137 | 1398 | 29 |
| Cc.—med. | | | 1234 | 31 | | | | | 1620 | 65 | | | | | 1372 | 29 |
| lat. | | | 319 | 8 | 685 | 19 | 844 | 43 | 567 | 23 | | | | | 410 | 9 |
| St.—med. | 8616 | 44 | | | | | | | | | | | 2772 | 58 | | |
| lat. | 1080 | 6 | 1049 | 26 | 1350 | 38 | 1127 | 58 | 1269 | 51 | 5100 | 55 | 438 | 9 | 2016 | 42 |
| Sm. | 8160 | 42 | 6290 | 156 | 7220 | 202 | 4180 | 212 | 3346 | 134 | 7560 | 82 | 7349 | 153 | 4500 | 94 |
| G. | 5180 | 27 | 1357 | 34 | 3024 | 86 | 2033 | 105 | 2520 | 101 | 5808 | 63 | 2550 | 53 | 6996 | 145 |
| Ten. | | | | | | | | | | | | | | | 729 | 15 |
| Fc. | 26500 | 137 | 1050 | 26 | 1100 | 31 | 1400 | 72 | 1536 | 62 | 5700 | 62 | 1240 | 26 | 1170 | 24 |
| Gmx. | 9207 | 48 | 672 | 17 | 760 | 21 | 253 | 13 | 975 | 39 | 3350 | 36 | 784 | 16 | 1480 | 31 |
| Gmd. | 25080 | 129 | 6113 | 152 | 6700 | 190 | 1660 | 85 | 1610 | 65 | 13220 | 143 | 7200 | 150 | 7500 | 156 |
| Gmn. | 2980 | 15 | 676 | 17 | 660 | 19 | 246 | 13 | 282 | 11 | 4498 | 48 | 458 | 9 | 1000 | 21 |
| Tfl. | 1440 | 7 | | | | | | | | | | | | | | |
| P. | 918 | 5 | 345 | 9 | 504 | 14 | 150 | 8 | 149 | 6 | 1920 | 21 | 937 | 20 | 527 | 11 |
| Al. | 11900 | 62 | 3300 | 62 | 2640 | 75 | 1150 | 59 | 3000 | 120 | 5400 | 59 | 900 | 19 | 1240 | 26 |
| Ab. | 11490 | 59 | 1370 | 34 | 1800 | 51 | 312 | 16 | 1400 | 56 | 6210 | 67 | 3300 | 71 | 2550 | 53 |
| Am. | 5965 | 31 | 1440 | 36 | 1680 | 48 | 1010 | 52 | 1080 | 43 | 7920 | 86 | 3000 | 63 | 464 | 10 |
| S. | 6270 | 32 | 1785 | 45 | 1260 | 36 | 595 | 31 | 720 | 29 | 1680 | 18 | 1800 | 38 | 1300 | 27 |
| R. | 20590 | 107 | 3450 | 86 | 1905 | 54 | 660 | 34 | 1380 | 55 | 6314 | 68 | 1663 | 35 | 3640 | 76 |
| I. | 3000 | 15 | 885 | 22 | 1260 | 36 | 805 | 41 | 1287 | 52 | 7155 | 77 | 5550 | 116 | 3240 | 68 |
| Pmg. | 1200 | 6 | 2340 | 58 | 940 | 27 | 810 | 42 | 1287 | 52 | 3660 | 40 | 1500 | 31 | 1535 | 32 |
| Pmn. | 9350 | 50 | 1200 | 30 | 952 | 27 | 324 | 17 | 450 | 18 | 3780 | 41 | 1122 | 23 | 800 | 17 |

In this table V represents the volume of the muscle in cubic millimeters and $R_m$ is the ratio of the volume of the individual muscle to the total volume of the musculature, excluding the psoas minor, expressed in terms of parts in one thousand.

## Table II

| Leverage | *Macropus* | | *Perameles* | | *Didelphys* | | *Pseudochirus* | | *Petauroides* | | *Phascolarctos* | | *Phascolomys* | | *Sarcophilus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ | $L_i$ | $L_t$ |
| Bi.—ant. | | 0 | | | | 8 | | | | 20 | | | | | | 19 |
| post. | 41 | 38 | 28 | 18 | 18 | 18 | 18 | 16 | 27 | 35 | 25 | 26 | 19 | 0 | 26 | 46 |
| Cc.—med. | | | | 30 | | | | | | 50 | | | | | 29 | 23 |
| lat. | | | 23 | 40 | 16 | 40 | 15 | 41 | 17 | 50 | | | | | 33 | 65 |
| St.—med. | | | | | | | | | | | | | | 26 | | |
| lat. | 50 | 50 | 31 | 29 | 21 | 27 | 21 | 32 | 29 | 42 | 30 | 44 | 21 | 17 | 28 | 53 |
| Sm. | 59 | 0 | 31 | 0 | 22 | 17 | 21 | 15 | 30 | 13 | 30 | 10 | 33 | 11 | 28 | 27 |
| G. | 40 | 30 | 24 | 20 | 8 | 34 | 8 | 26 | 0 | 32 | 10 | 44 | 17 | 26 | 14 | 18 |

$L_i$ is the length of the lever-arm on the ischium.
$L_t$ is the length of the lever-arm on the tibia.
All measurements are in millimeters.

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PLATES X TO XIV

PLATE X.—*Didelphys*.

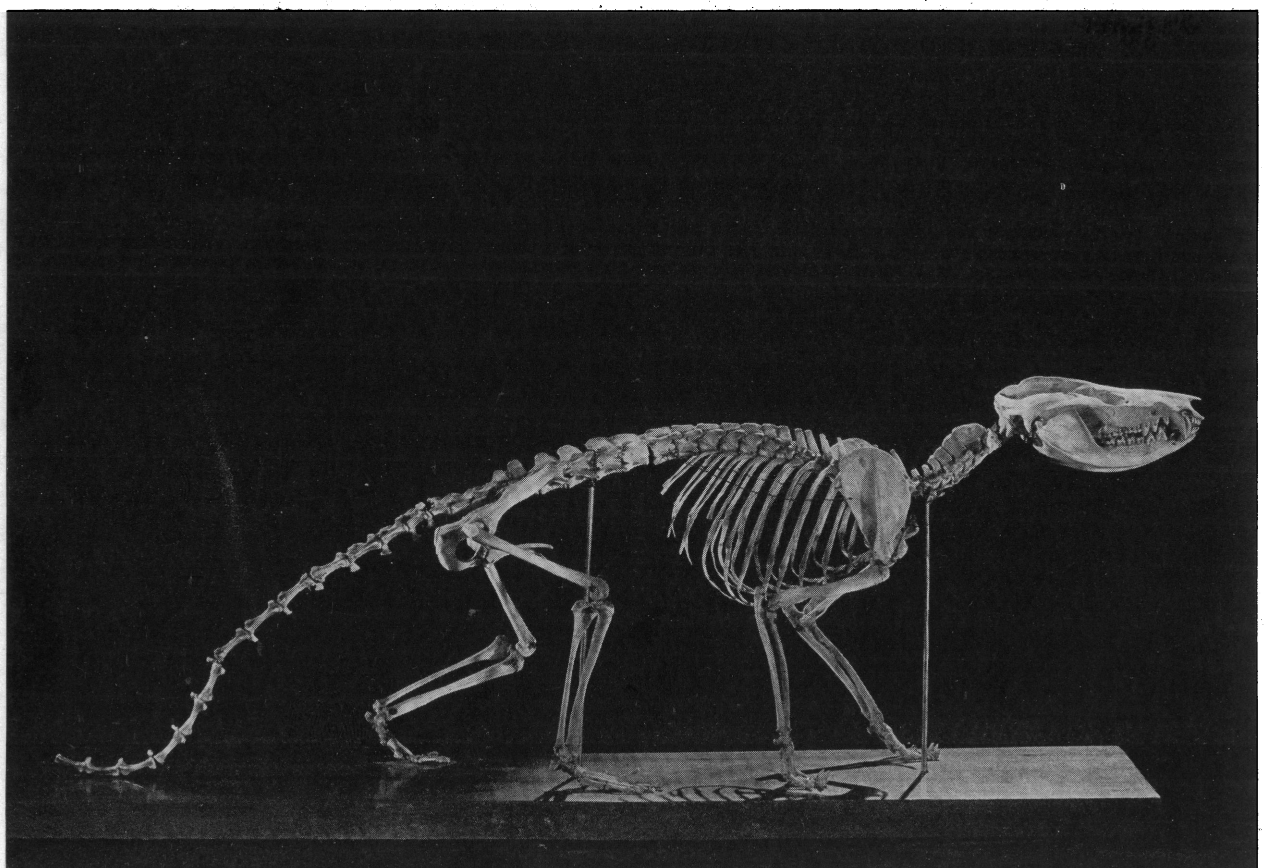

PLATE XI.—*Macropus.*

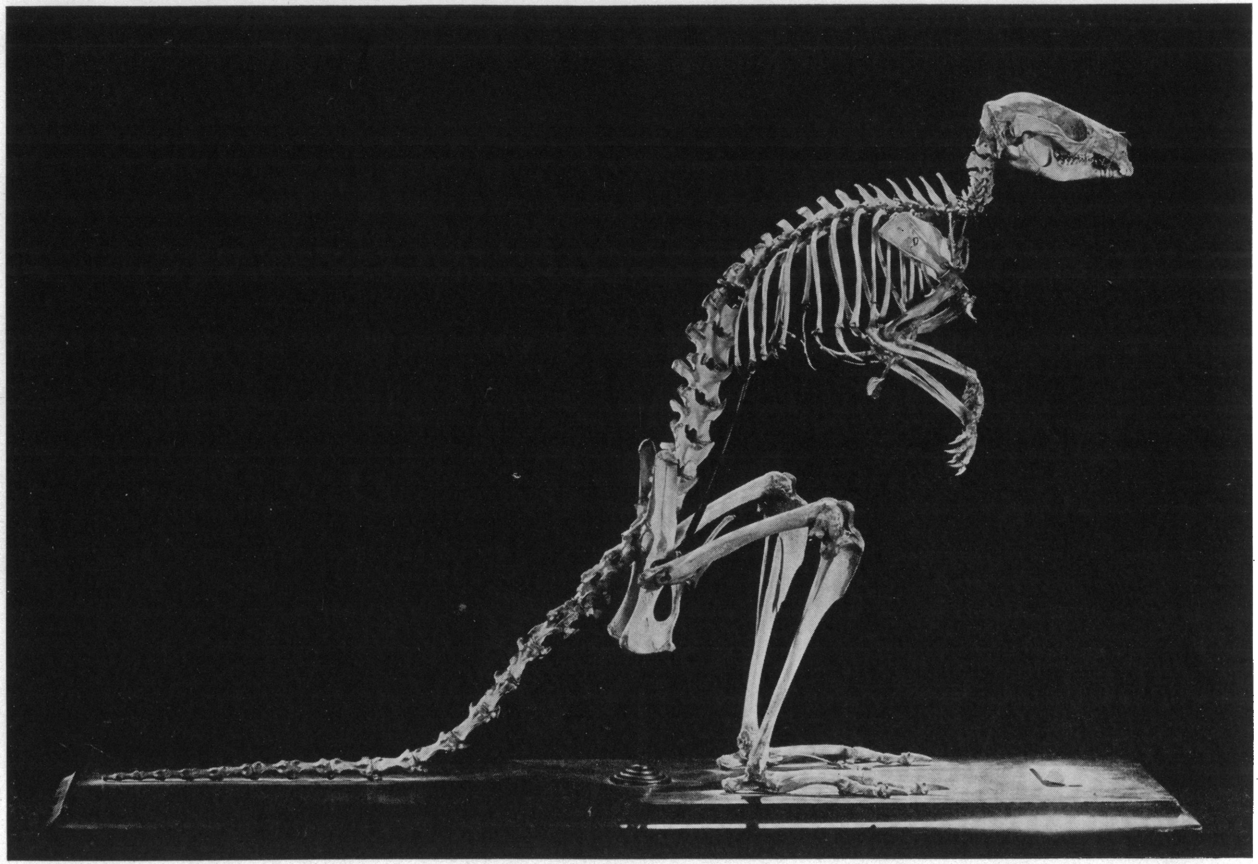

PLATE XII.—*Perameles.*

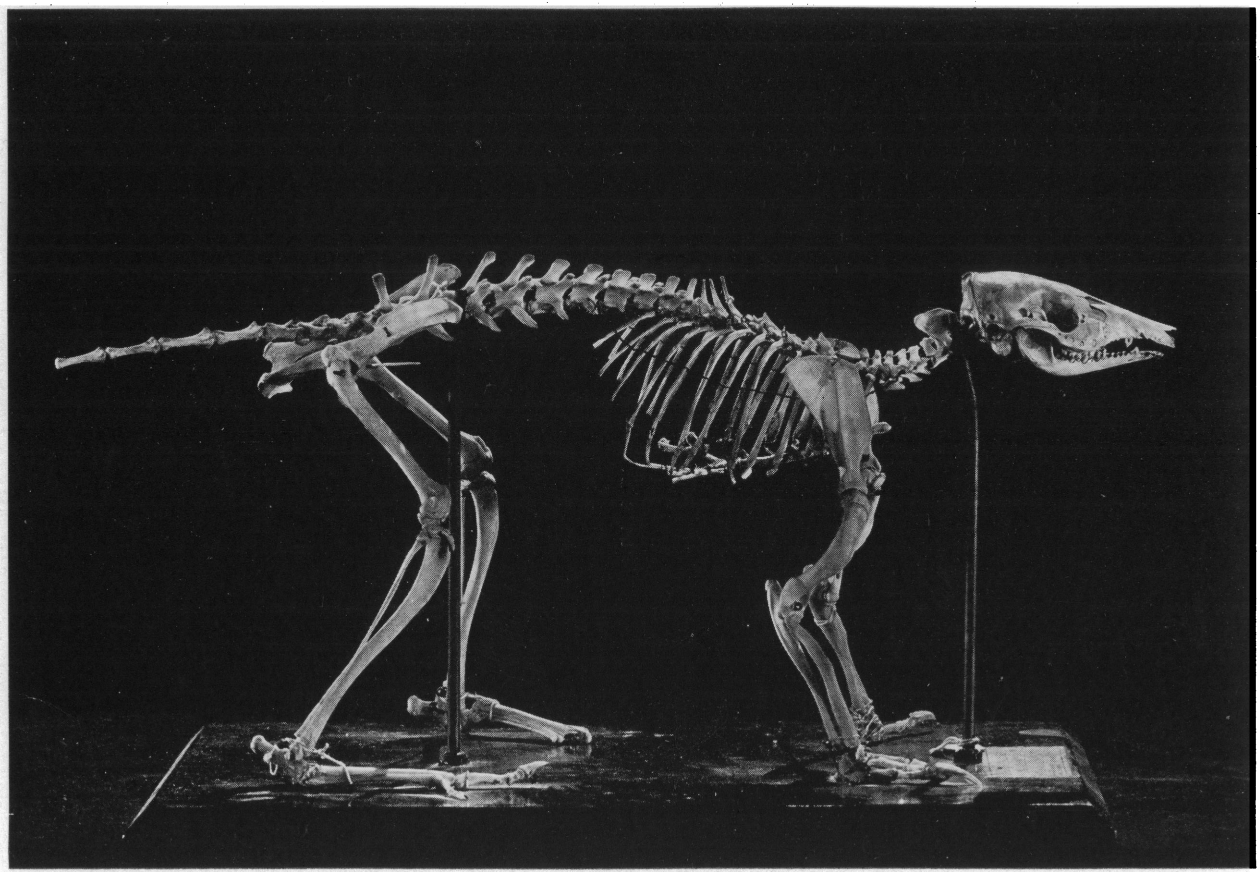

PLATE XIII.—*Phascolomys.*

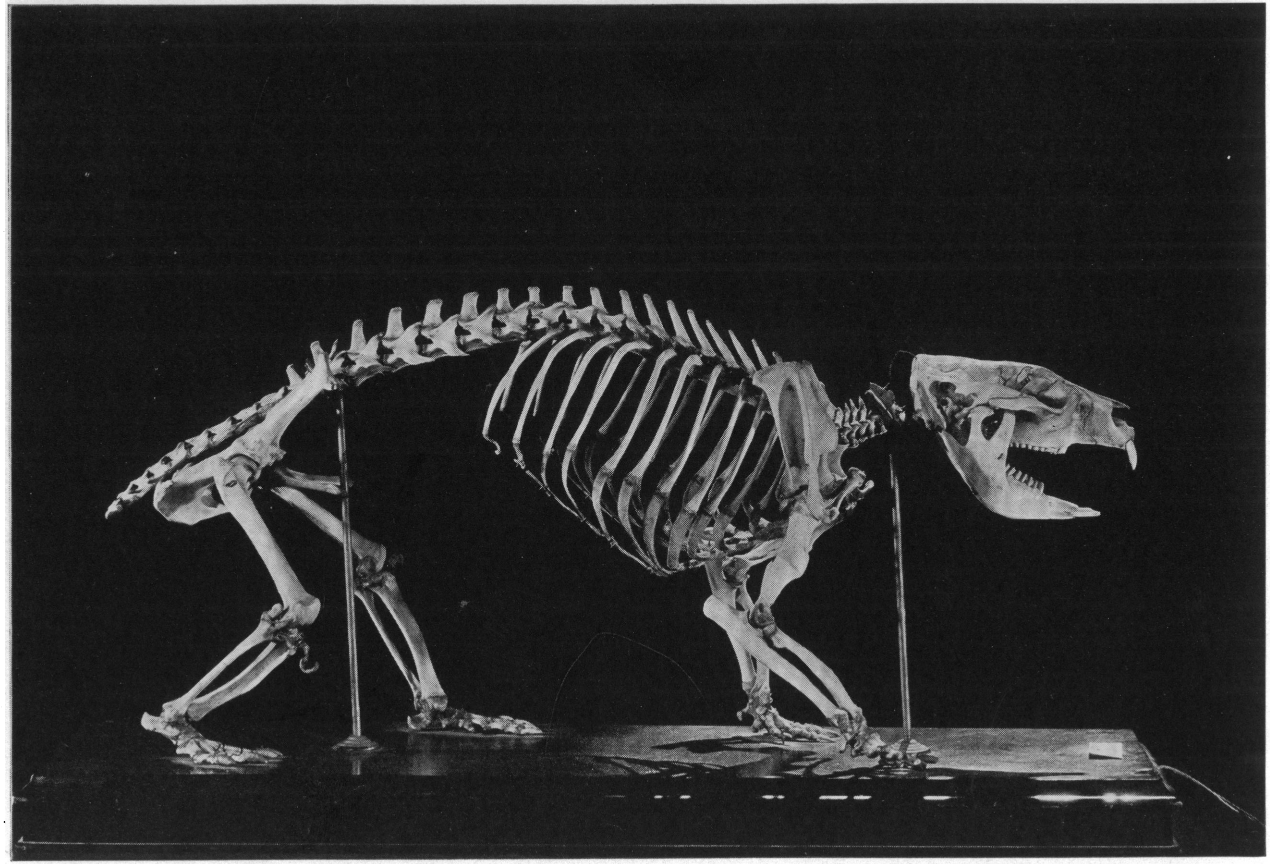

PLATE XIV.—*Phascolarctos*.