

THE FUNCTIONAL MORPHOLOGY
OF THE HIND LIMB OF THE
DOMESTIC PIGEON,
COLUMBA LIVIA

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INTRODUCTION

FUNCTIONAL MORPHOLOGISTS work at many levels from subcellular to that of whole organisms. Of particular importance to vertebrate morphologists and evolutionists whose interests lie with whole organisms is the study of bone-muscle systems, and aside from investigations on the feeding mechanism, no bone-muscle system has generated so much attention as that associated with locomotion. Morphologists have published an impressive amount on the locomotor mechanisms of vertebrates, including birds, and the basic findings of these studies have been reviewed by J. Gray (1968). For obvious reasons, functional investigations of birds have tended to concentrate on the forelimbs. Nevertheless, hind-limb anatomy of birds is probably better known than forelimb anatomy because of the importance placed on certain features of hind-limb muscles as taxonomic characters.

A functional approach to the avian hind limb can form the basis for several kinds of studies that are of interest to evolutionary biologists. For example, many families of birds have undergone adaptive radiations in hind-limb locomotor habits, and the kinds of adaptations equal, if not surpass, the diversity of intrafamilial radiations in the forelimbs. Furthermore, the fossil record of some groups of birds is rapidly increasing, and most of this material is from the hind limb. Functional studies of Recent forms should enable us to interpret the observable structural changes of fossils in terms of adaptations for different patterns of locomotion. Birds can also provide additional data relevant to the interpretation of adaptations for bipedalism seen in various groups of vertebrates.

Previous functional analyses of the avian hind limb have been based mainly on observations of the skeleton and on the origins and insertions of muscles. These studies provide a foundation on which to consider other aspects of avian locomotion, such as joint structure and function, ligaments, detailed muscle structure, muscle physiology, and biomechanics. At its inception, the present study was envisioned as a comparative functional analysis of several closely related species. It soon became apparent, however, that a more detailed approach to hind-limb function-

al analysis was needed, one that incorporated recent advances in muscle structure and function and which considered locomotor patterns with respect to joint structure and function. Hence, the plan for a comparative study was abandoned and concentration on examination of a single species was undertaken. It was my hope that the knowledge gained from the study of a single species could then be used to make future comparisons between species more meaningful.

Descriptive investigations will not be considered further here, as the extensive literature on avian hind-limb anatomy has been reviewed by Hudson (1937), Holmes (1963), and George and Berger (1966).

Functional studies of hind-limb locomotion are difficult to characterize because so many different approaches have been used. Perhaps the first important paper was that of Stolpe (1932). Although his treatment of muscle structure and function was limited, he emphasized the anatomy and functional interpretation of joints and stressed their importance in locomotion studies. To my knowledge, since Stolpe, no other avian anatomist has included a discussion of joints in his work on hind-limb locomotion. In an excellent study of the feet of birds Steinbacher (1935) considered ligaments and intra-articular structures, but his was not an investigation of locomotion per se.

Subsequent to Stolpe's paper, two major contributions to hind-limb locomotion were provided by Miller (1937) on the Hawaiian Goose (*Nesochen sandvicensis*) and Fisher (1946) on the cathartid vultures. Additional studies are those of Burt (1930) on woodpeckers; Wilcox (1952) on the loon *Gavia immer*; Berger (1952) on cuckoos; and Owre (1967) on the anhinga (*Anhinga anhinga*) and cormorant (*Phalacrocorax carbo*). These workers inferred their functional conclusions from data on osteology and on muscle origins and insertions. Information about detailed fiber arrangement, length and number of fibers, and muscle physiology was generally not included, and the muscles were compared in terms of weight and/or volume, which are parameters of limited reliability.

The plan of the present study is to discuss first

the structure and function of the various leg joints. The joints of the foot will receive less attention as they have been treated in detail by Steinbacher (1935). A description of the muscles with emphasis placed on the fiber arrangement and histological structure follows. The section on functional analysis of the muscles deals with the action of each muscle in terms of relative amount of force produced, degree of muscle excursion, speed of contraction, and kinds of movements which are produced around the joints. An analysis of locomotion patterns, using high-speed cinematography is then given, and the actual movements of the bird are discussed. Finally, these data, together with data on muscle function, are used to examine the locomotor patterns from the standpoint of the relative contribution of each muscle, including the time each muscle is functioning during the locomotor cycle.

Except for the motion-picture analysis, this study involves little experimentation. However, experimentation itself cannot be carried out if there is a vacuum of information about structure and function of the joints and muscles. The present paper is a contribution toward providing some of the basic functional data that are indispensable for experimental studies on avian hind-limb locomotion.

MATERIALS AND METHODS

The descriptions and functional conclusions presented herein are based on a study of the Domestic pigeon, *Columba livia*. The organization and goals of my study greatly limited the kinds of birds that could be used, and the pigeon was chosen as being nearly the ideal organism, for several reasons. First, it was available in abundant supply and easily kept in captivity. Second, because the emphasis of this study is primarily functional, it was mandatory that fresh material be accessible whenever needed. Third, the pigeon is of a workable size in that it is not so small as to make difficult the kind of morphological observations that were required, nor is it too large, in which case such aspects as joint histology would have been more formidable. Fourth, live pigeons were easily handled, and were excellent subjects for high-speed motion picture analysis. Finally, the locomotor pattern of the pigeon is of a rather general type and

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provides a good basis on which future comparative work can be undertaken.

The gross morphology of muscles and joints was studied with the aid of a Wild M5 dissecting microscope (6-50 power). More than 40 fresh and preserved specimens were utilized. An exact count of specimens was not kept as this varied greatly with the subject being studied. Certain joints, such as the hip, were far less complex morphologically than the knee or intertarsal joints, and accordingly fewer dissections were made. It must be emphasized that all conclusions about the functional roles of muscles or of joint structures are based solely on fresh material. The functional interpretation of preserved joint material is very misleading as the kinds and extent of movement of joint structures is greatly reduced. Also, the possible functions of various muscles are sometimes easily misinterpreted if fresh material is not used.

Approximately 1100 histological slides were made of the hind-limb joints. These included sections of at least eight hip, 11 knee, 18 intertarsal, six tarsometatarsal, and 16 interphalangeal joints. The joints were decalcified for varying lengths of time by means of the formic acid-sodium citrate method, which preserves histological details with long periods of decalcification. In all cases the skin and much of the muscle tissue were removed to facilitate decalcification. The results varied greatly from joint to joint and with the age of the bird. For adult birds it was found that the joints had to be decalcified for at least 40 to 50 days (with repeated changes of the solution) before good sections could be cut. The knee and intertarsal joints required slightly longer. Toward the end of the study RDO rapid decalcifier (DuPage Kinetic Laboratories, Downer's Grove, Illinois) was used with varying degrees of success. Good results were obtained after 24 to 48 hours of decalcification. Because the tissues were large, the times for dehydration and clearing had to be lengthened. The tissues were embedded in paraplast in a vacuum-oven for about five or six hours. The joints were then sectioned at 10 to 15 microns and mounted. They were stained with Mallory's triple connective tissue stain and with Verhoeff's elastic stain.

Approximately 425 slides were made of cross sections of the hind-limb muscles. The muscle tissue was fixed in Carnoy's fixative for about 18 hours. After short changes of absolute alcohol, the tissues were cleared, embedded in paraplast, and sectioned at 5 to 7 microns. The muscles were stained with Mallory's triple connective tissue stain and with a modified trichrome stain (Engel and Cunningham, 1963; Engel and Brooke, 1966, p. 55). The trichrome stain was found best for differentiating the fibrils in cross section.

The locomotor patterns of living birds were photographed at 250 frames per second using a Hycam 400 high-speed motion picture camera (16 mm.) and DuPont 932A ultra speed rapid reversal film. The patterns were then studied by single-frame projection using a photo-optical data analyzer 224-A (L-W Photo, Inc., Van

Nuys, California). A speed of 250 frames per second was found satisfactory for analyzing the motion of most of the limbs, although movement of the tarsometatarsal and interphalangeal joints was not completely stopped at this speed. With respect to the types of motion being studied, this was not considered a serious problem.

In order to photograph accurately the movements of the femur at the hip joint and the femur and tibiotarsus at the knee joint, the feathers of the posterior half of the bird were removed. The hip, intertarsal, and tarsometatarsal joints were then marked with black ink. The knee joint cannot be marked because the skin is very loose, but in analyzing the movies, the position of the knee joint was extrapolated with a fairly high degree of accuracy from the hip and intertarsal joints.

It was also discovered that the motion around the hip and knee joints could not be studied in detail unless the wings were tied over the back of the bird (removing the primaries was not sufficient). Most of the birds quickly learned to walk with their wings in this position, and the resulting locomotion did not appear to differ greatly from nonexperimental birds. Although it was hoped that such modification of experimental birds could be avoided, the movements of several elements could not be studied without it.

The locomotion of the birds had to be modified again when photographing certain aspects of the "landing" movements. It was not possible to construct the elaborate apparatus that Fisher used to study landing in flying pigeons (Fisher, 1956a, 1956b) nor was it considered necessary to do so. Hand-held birds were dropped from 1 to 2 feet heights and photographed. As in the walking experiments, the birds learned to land properly balanced. The experimental birds differed from normal birds in that the wings could not serve as a braking force, and thus the former group landed with much greater force. With respect to the results of the present study, this pattern of landing was not disadvantageous, but instead it emphasized the role of the joints and muscles in the landing process.

All the illustrations were drawn with the aid of a camera lucida.

STRUCTURE OF THE PELVIS AND HIND-LIMB ELEMENTS

TO PROVIDE A BASIS for discussing the structure and function of the joints and muscles, the osteological features of the pelvis and hind-limb elements are described briefly. Only those features associated with the attachments of muscles, ligaments, and other connective tissues are mentioned. Other structures not relevant to the results of this study are omitted. The terminology is that of Howard (1929), and her paper may be consulted for illustrations of the features discussed below.

PELVIS

The preacetabular ilium is about the same length as the postacetabular portion. The former is flattened, moderately cup-shaped, and lies in a plane horizontal to the longitudinal axis of the vertebral column. The anterior iliac crest is well defined and is greatly rounded (nearly circular) anteriorly. The preacetabular ilium comes to lie in a more vertical plane posteriorly. The postacetabular ilium is divided into dorsal and ventral parts by the posterior iliac crest. Ventral to this crest and dorsal to the ischium, the ilium forms a lateral iliac fossa (Holmes, 1963, p. 369), which is situated slightly more mediad than the crest itself. Dorsal to the crest and extending to the junction with the synsacrocaudal vertebrae, the postacetabular ilium is raised and bulbous-shaped but becomes more depressed posteriorly. The ischium begins narrow at the level of the ilio-ischiatic fenestra, broadens slightly posterior to it, and then tapers to a fine point. The posterior part of the ischium is connected to the pubis by fibrous connective tissue. The obturator foramen is not ossified posteriorly. The ilio-ischiatic fenestra is long and narrow, and extends posteriorly to the level of the posterior end of the lateral iliac fossa. The antitrochanter is moderately developed with its surface directed anteroventrally. The pubis is long and thin, extending posteriorly beyond the ischium about one-fourth of its total length.

On the inside of the pelvis, the only important feature is the deep depression of the ischium posterior to the obturator foramen. The depression becomes shallower posteriorly.

There are seven free caudal vertebrae (includ-

ing the pygostyle) posterior to the pelvic shield. Except for the last two, all have relatively well-developed transverse processes.

FEMUR

The head of the femur is well marked and separated from the neck by a noticeable groove. The pit for the attachment of the round ligament is deep, and the distal side of the head is also moderately excavated. The neck is short and stubby. A rounded trochanter projects noticeably proximad above the level of the neck. Distally, the trochanteric ridge is little developed. The obturator ridge is not well developed or distinguishable from the shaft. The latter is rounded posteroproximally and rather flattened anteroproximally. Distally, the shaft is rounded but becomes flattened both anteriorly and posteriorly near the condyles. The posterior intermuscular line is not well developed. As seen from the side, the internal condyle is somewhat irregular in shape. Its posterior edge is developed into a slightly rounded apex; the distal edge is produced into a distinctly rounded projection. The condyle is gently rounded posteriorly. The ligamental attachment of the internal condyle is rather large but not particularly deep. Anteriorly, the external condyle is gently rounded. Distally near its anterior side the external condyle possesses a slight depression. The posterior end of the condyle is well rounded and projects distinctly beyond the level of the fibular condyle. The latter is rounded only distally, the remainder of its posterior edge being straight and nearly parallel to the axis of the bone. In cross section the fibular groove is almost L-shaped rather than V-shaped. As seen from the distal end, the external condyle projects posteriorly well beyond the level of the internal condyle. The fibular condyle projects less posteriorly than does the internal condyle. The internal condyle projects anteriorly only slightly more than does the external condyle. The rotular groove is U-shaped, its walls nearly symmetrical (except for the larger size of the internal wall). As seen from the anterior side, the distal apex of the internal condyle is on the same anteroposterior level as the anterior part of the external condyle, but the

former projects distally much more than the latter. The posterior end of the external condyle, however, projects distally more than the corresponding portion of the internal condyle. The popliteal area is deep and distinctly separated from the surface of the internal condyle by a well-developed ridge.

TIBIOTARSUS

Seen in proximal view, the head of the tibiotarsus is longer anteroposteriorly than it is lateromedially. The inner and outer cnemial crests meet each other at an angle of approximately 75 to 80 degrees. The external articular surface is large and bulbous and separated from the outer cnemial crest by a broad U-shaped groove. Internally and posteriorly, the external articular surface is separated from the interarticular area by a shallow groove. The posterior border of the tibial head is formed into a slight apex, whereas the internal border is much more rounded. The interarticular ridge (new term) runs posteriorly from the rotular crest a short distance and is not well developed. Internal to the interarticular ridge, is a moderately developed depression. The head of the fibula is small, occupying slightly over one-fourth of the anteroposterior length of the tibial head.

The face of the inner cnemial crest and tibial head is almost flat, becoming rounded posteriorly with the tibial head not forming a lip over the face. Distal to the posterior border of the tibial head, the shaft is rather deeply excavated, and here the tibial head forms a lip over the shaft. Proximo-anteriorly, the shaft is nearly flat, being only slightly rounded. In the middle of the bone the anterior face of the shaft becomes rounded only to become flattened near the distal end of the bone. The internal face of the shaft is somewhat flattened anteriorly, becoming rounded as the posterior face is approached. The posterior face is flattened proximally and becomes rounded on about the distal half of the bone. The fibula extends distally about 80 per cent of the length of the tibia.

As seen from the side, the external condyle is rounded anteriorly and distally with the posterior profile being only slightly flattened. The external face of the condyle is moderately excavated. The anterior end of the condyle curves proximoposteriorly to meet the shaft at an angle approaching 90 degrees; posteriorly, the condyle grades smoothly into the main part of the shaft.

In a side view, the distal surface of the internal condyle is less strongly curved than that of the external condyle. The anterior end of the internal condyle is well rounded and gradually grades into the shaft. The posterior end of the condyle is gently curved and also meets the shaft gradually. The internal ligamental prominence is well developed, and the face of the condyle is moderately excavated distally and anteriorly to it.

Anteriorly, the external condyle is seen to project distally slightly more than does the internal condyle. The distal surface of the external condyle is rounded, becoming slightly less so, as it slopes to the intercondylar sulcus. The distal surface of the internal condyle is much more flattened, but becomes slightly rounded as it curves to the sulcus. The anterior intercondylar fossa is not deep, and it occupies about one-third of the anteroposterior length of the external condyle. A lateromedially directed ridge is present in the anterior intercondylar fossa. The supratendinal bridge lacks a bony tubercle externally and is oriented lateromedially so that it is perpendicular to the longitudinal axis of the shaft. Lateral to the supratendinal bridge, the shaft is somewhat broadened and slightly depressed. The tendinal groove is well marked, especially distally.

In a distal view, the internal condyle is seen to project anteriorly slightly more than does the external condyle. The posterior surfaces of both condyles project posteriorly to about the same level. The posterior intercondylar sulcus is moderately deep, the external wall being short and set at a sharp angle (about 50 degrees) to the sulcus, whereas the internal wall is nearly planar and is at an angle of approximately 25 to 30 degrees.

TARSOMETATARSUS

Seen in proximal view, the head of the tarsometatarsus is roughly triangular in shape. The external cotyla is slightly excavated and open, not cupped, anteriorly and posteriorly. The internal cotyla is decidedly more deeply excavated and cup-shaped, with a slight lip being formed anteriorly and a noticeable one present posteriorly. The outer side of the internal cotyla is much more elevated (lipped) than the outer side of the external cotyla. Both cotylae are about the same size with perhaps the external cotyla being slightly smaller. The cotylae are also

situated on almost the same horizontal plane, but the internal cotyla tends to be situated slightly more proximally relative to the external. The intercotylar prominence is broad, blunt, and directed somewhat anteriorly. The intercotylar area is depressed very little, hence the internal rims of the cotylae are not distinct. On the hypotarsus three calcaneal ridges are present, the most medial being the largest, and the most lateral the smallest. A closed canal is present at the base of the medial and middle ridges, and between these same ridges an open groove is situated more posteriorly. An open groove is also situated between the middle and lateral ridges. Another open groove is formed by the lateral ridge and the posterolateral edge of the external cotyla.

Anteriorly, the lateral side of the shaft is twisted forward, whereas the medial side is twisted backward. The anterior metatarsal groove is very shallow, being deepest in the area of the proximal ligamental attachment. The inner extensor groove is nearly as well developed as the anterior metatarsal groove. The anterior face of the shaft is somewhat flattened proximally and slightly rounded distally.

Medially, the side of the shaft and hypotarsus is deeply excavated, and this excavation becomes

progressively shallower as it goes distally. Still, a well-developed groove is formed down the medioposterior side of the shaft. Posterolaterally, below the hypotarsus, the shaft is only slightly depressed the length of the shaft. A well-pronounced ridge extends distally to the level of the metatarsal facet.

The middle trochlea (III) is small and nearly circular in shape; its outer (lateral) portion is slightly larger in diameter than its inner (medial) portion. A well-marked groove extends around the middle of the trochlea. The outer trochlea (IV) extends distally about one-third of the distance of the middle trochlea. The anterior surface of the inner side of the outer trochlea is situated slightly more anteriorly than the middle trochlea. The lateral portion of the outer trochlea is turned posteriorly only a slight distance beyond the middle trochlea. The inner trochlea (II) also extends distally about one-third of the distance of the middle trochlea. In contrast to the outer trochlea, the inner is strongly turned posteriorly so that a little over two-thirds of the trochlea is posterior to the middle trochlea. The inner and outer trochleae have slight longitudinal grooves. The trochlea for the hallux (I) is broad, rounded, and tapers laterally to a rather blunt point.

STRUCTURE AND FUNCTION OF THE HIND-LIMB JOINTS HIP JOINT

THE HIP JOINT is by far the least complex structurally of the leg joints. It consists of two bony elements, the pelvis and femur, a joint capsule, and one or two ligamentous bands. Still, a detailed description of the joint does not exist, even though some authors have discussed certain aspects of its structure and function (Kaupp, 1918; Stolpe, 1932).

important role in limiting joint movement and will be described in detail. Stolpe (1932) commented briefly on the role of the capsule, but he did not give a description for any species.

Posteriorly, the capsule arises from the posterior end of the antitrochanter and from the ventral rim of the ilio-ischiatic fenestra. This part of the capsule is thick and strong, and attaches to the obturator ridge of the femur. Dorsally, the capsule originates from the antitrochanter and from the dorsal rim of the acetabulum, and attaches to the medial side of the well-developed trochanter. This portion of the capsule is thinner

MORPHOLOGY OF THE HIP JOINT

JOINT CAPSULE

The joint capsule (jc; figs. 1-4) plays an

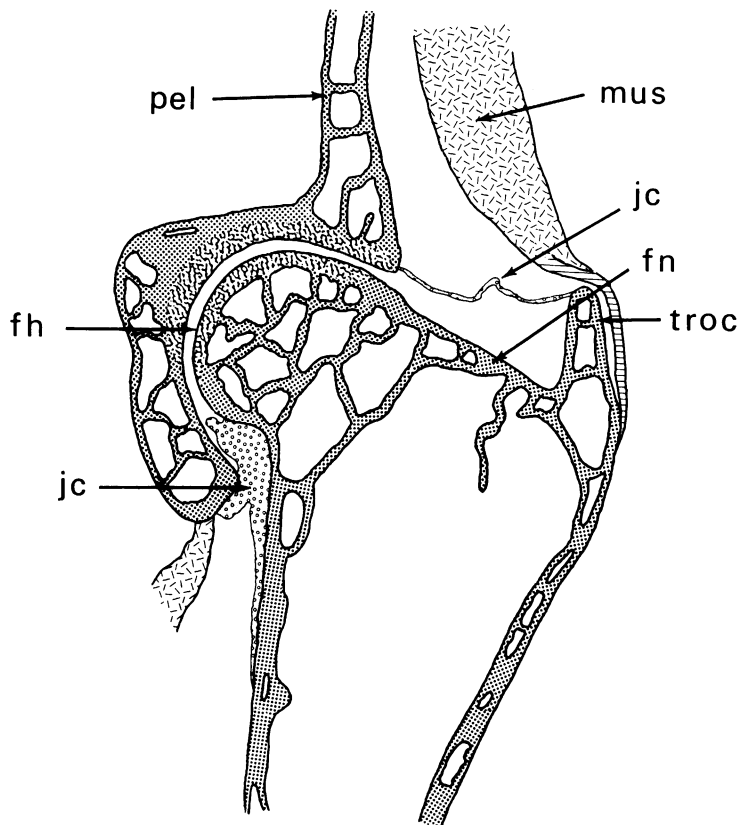


FIG. 1. Diagrammatic representation of histological frontal section through hip joint of *Columba livia*.

Abbreviations: fh, head of femur; fn, neck of femur; jc, joint capsule; mus, muscle; pel, pelvis; troc. trochanter.

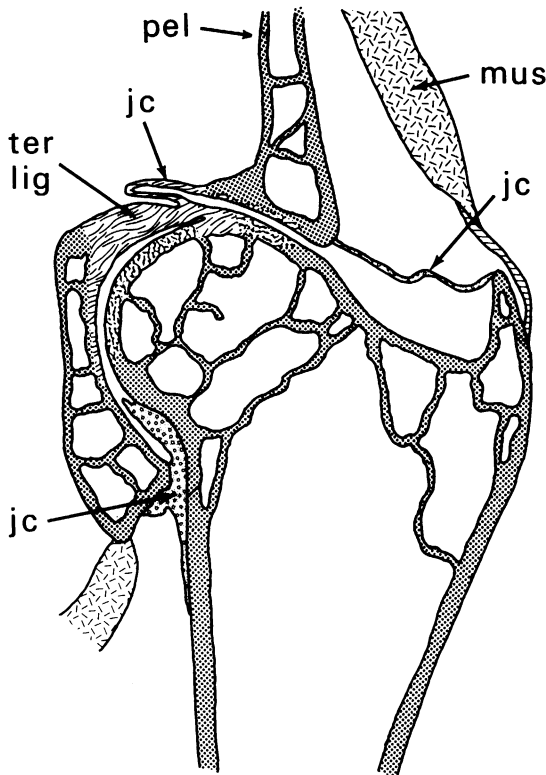


FIG. 2. Diagrammatic representation of histological frontal section through hip joint of *Columba livia* showing teres ligament.

Abbreviations: jc, joint capsule; mus. muscle; pel. pelvis; ter lig, teres ligament.

than the posterior part and is the weakest area of the capsule. The capsule on the anterior side of the joint arises from the anterior edge of the acetabulum and attaches to the femur along the anteroproximal edge of the shaft (at the base of the neck). In this area, the capsule is very short and fibrous. Ventrally, the capsule has its pelvic attachment on the ventral rim of the acetabulum and the dorsal part of the pubis. On the femur it attaches to the shaft just distal to the neck. The capsule of this region is very short and especially strong and heavy. The ventroanterior portion of the capsule is organized into a ligamentous-like structure, and well-defined, shiny bands of collagenous tissue are present within the capsule. This ligament is probably the "ligamentum ilio-sacrale" of Kaupp (1918, p. 65), but he did not include illustrations. Stolpe (1932) made no mention of the ligament.

TERES LIGAMENT

The teres l'gament (ter lig; fig. 2) arises from the dorsal portion of the head of the femur (fovea capitis; see Stolpe, 1932, p. 165). A short and broad ligament, it curves ventromedially to the anteroventral edge of the inner opening of the acetabulum.

POSTERIOR ACETABULAR LIGAMENT

Posterior to the teres ligament is a broad ligamentous-like connective tissue band, which is named here the posterior acetabular ligament. It attaches anteriorly to the teres ligament and to the posterior portion of the fovea capitis. Its pelvic attachment is to the posterior rim of the inner opening of the acetabulum.

The remaining portion of the inner opening of the acetabulum is covered by a thin membrane, which serves as the medial limit of the joint cavity. The dorsal portion is more fibrous than the ventral.

MICROANATOMY

JOINT CAPSULE: As noted above, the capsule surrounds the entire joint. Thus, when the joint is sectioned in a plane perpendicular to the longitudinal axis of the vertebral column, the capsule is exposed in two places. Dorsally, it is a very thin, fibrous band that runs from the dorsal lip of the acetabulum to the trochanter of the femur. Because it is thin and long, this portion of the capsule is usually lost during sectioning. Ventrally, the capsule is well developed. It broadly attaches to the ventral lip of the acetabulum and to the medial side of the femur. The femoral attachment extends from the ventralmost part of the articular surface of the head down the surface of the shaft about 3 or 4 mm. The fibers of the acetabular attachment are densely and regularly arranged, whereas the femoral attachment is less dense and more irregularly arranged. The tissue of the capsule is nearly all collagenous; no elastic tissue was found.

ARTICULAR SURFACE OF THE ACETABULUM: Anterior and posterior to the attachment of the teres ligament, the articular cartilage is present only on the dorsal part of the acetabulum (fig. 1); the ratio of chondrocytes to fibrous connective tissue becomes progressively smaller in a ventral direction. Dorsally, the cartilage does not extend laterally to the lip but terminates a short distance from that structure. The articular

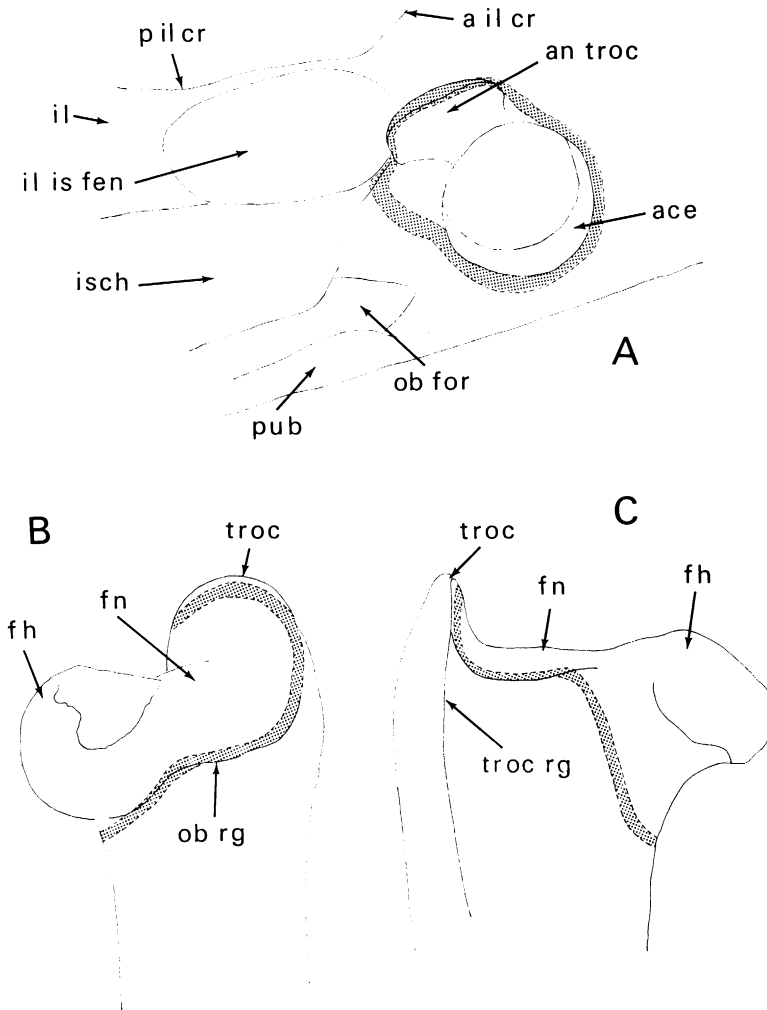


FIG. 3. Diagram showing places of attachment (stippling) of joint capsule of hip joint in *Columba livia*. A. Posterolateral view of the pelvis. B. Posteromedial view of the femur. C. Anterior view of the femur.

Abbreviations: ace, acetabulum; a il cr, anterior iliac crest; an troc, antitrochanter; fh, head of femur; fn, neck of femur; il, ilium; il is fen, ilioischiatric fenestra; isch., ischium; ob for, obturator foramen; ob rg, obturator ridge; p il cr, posterior iliac crest; pub, pubis; troc, trochanter; troc rg, trochanteric ridge.

surface overlying the bony (pelvic) portion of the acetabulum is more cartilaginous than that overlying the inner opening of the acetabulum. The latter has greater amounts of regularly arranged collagenous tissue interspersed between the chondrocytes. More medially in this region (nearer the inner opening), the tissue becomes wholly collagenous. The articular cartilage has a very thin, superficial zone com-

posed mainly of collagenous fibers with an apparently reduced number of flattened chondrocytes. Deep to the superficial zone the chondrocytes are rounder and seemingly more numerous. The chondrocytes do not have a noticeable orientation into rows as does the collagenous matrix.

In the area of the teres ligament the articular surface of the ventral part of the acetabulum has

been replaced completely by the ligament (fig. 2). Dorsally, the articular cartilage of the pelvis is composed of greater amounts of collagenous tissue.

ARTICULAR SURFACE OF THE FEMUR: The articular surface of the femur is quite different histologically from that of the acetabulum. The articular surface begins a short distance dorsal to the attachment of the ventral portion of the capsule and extends dorsally almost to the level of the lip of the acetabulum. A very thin, deeply staining zone is found superficially. This zone is mostly collagenous, chondrocytes not being apparent. Beneath this superficial zone is a thick zone composed of large rounded chondrocytes within moderate amounts of collagenous matrix. Neither the chondrocytes nor the matrix is oriented into rows. Deep to this thick zone is a poorly defined transitional area composed of greater amounts of collagenous tissue and smaller chondrocytes; this zone immediately overlies the bone. The chondrocytes of the femoral surface are larger than those of the acetabular surface, and the matrix of the former is irregularly arranged and not in well-defined columns. In the area of the teres ligament the structure of the articular surface does not change except that it is reduced in extent dorsally.

TERES LIGAMENT: This is a large, strong ligament composed almost wholly of collagenous tissue. The ventral edge, near its origin from the fovea capitis, is slightly cartilaginous.

The fact that the teres ligament inserts onto the ventral rim of the acetabulum is clearly evident in cross sections (fig. 2). Dorsally, a long, thin fibrous strand of tissue arises from the acetabulum, passes medially and then laterally, and attaches to the dorsal edge of the ligament; this strand represents the membrane covering the inner opening of the acetabulum (fig. 2). The membrane is clearly differentiated into two zones: (1) a lateral (facing the joint cavity), deeply staining layer of cuboidal cells, and (2) a medial (facing the abdominal cavity), wider, collagenous layer. The lateral thin zone represents the synovial membrane.

FUNCTIONAL ANALYSIS OF THE HIP JOINT

TYPES OF MOTION

Stolpe (1932, p. 175, fig. 23) seems to have been the only worker to define the axes of rotation in the avian hip joint. Such a task presents

the same problems as those found in other bipedal vertebrates, including man (see, for example, Rydell, 1966).

In order to analyze movement at the hip joint, the pelvis will be taken as the stationary element. Several basic movements of the femur on the pelvis are therefore possible.

a. **Protraction-retraction:** This motion takes place in a plane along the longitudinal axis of the femur and oriented in an anteroposterior direction. The axis of rotation (sometimes called the cervical axis) is through the longitudinal (lateromedial) axis of the center of the head and neck of the femur. Protraction is anterior movement of the femur, retraction is posterior movement (fig. 4).

b. **Rotation:** This describes an anterior or posterior spinning of the femoral shaft. Because the point of articulation of the head of the femur is displaced from the axis of the shaft, the axis of rotation does not coincide precisely with the longitudinal axis of the shaft. Instead it can be taken to lie along a line connecting the center of the articular surface of the femoral head and a point at the distal end of the bone midway between the condyles.

c. **Abduction-adduction:** Stolpe (1932, p. 175) considered this type of movement so uncommon that he did not discuss it in any detail. Whereas there are positions in which abduction-adduction is essentially absent, this type of motion is possible in conjunction with rotation. This motion takes place in a plane situated along the longitudinal axis of the femur and directed lateromedially. Abduction describes movement of the femur away from the body, adduction toward the body.

PROTRACTION-RETRACTION

The functional analysis of the hip joint is most simply understood if the fully protracted femur is considered to be the basic joint position. When the femur is fully protracted, all other motions—rotation, abduction, adduction—are reduced to a minimum. It is then possible to analyze these motions as the femur is being retracted.

All the structures are apparently organized so as to set a limit to the amount of protraction. With retraction, the joint structures become loose and only regain their tautness when the femur is retracted far beyond the position that could possibly be attained under any natural conditions. As the femur approaches the fully

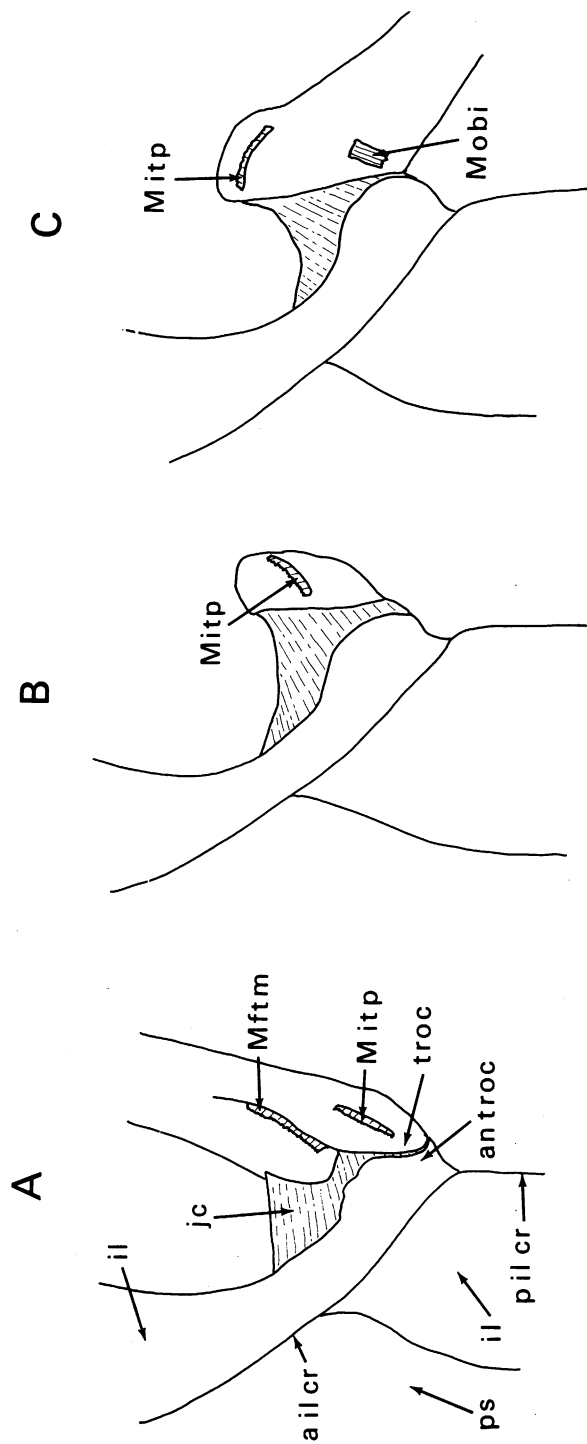


FIG. 4. Schematic diagram (dorsal view) of hip joint in *Columba livia* showing possible protraction-retraction movements of femur. A. Fully protracted position. B. Retraction underway. C. Fully retracted position.

Abbreviations: a il cr, anterior iliac crest; an troc, antitrochanter; il, ilium; jc, joint capsule; M ftm, M. femorotibialis medius; M itp, M. iliopsoas; M obi, M. obturator internus; p il cr, posterior iliac crest; ps, pelvic shield; troc, trochanter.

protracted position, four parts of the joint begin to tighten and limit further anterior movement: (a) the obturator ridge moves posteroventrally and thus the joint capsule on the posterior side of the joint becomes taut, (b) the proximo-anterior surface of the shaft moves postero-dorsally and the anteroventral part of the capsule (including the "ligamentum ilio-sacrale") becomes taut, (c) the shaft is moving anteriorly and so the ventral part of the capsule becomes taut, and (d) the fovea capitis moves laterally away from the inside opening of the acetabulum, causing the teres and posterior acetabular ligament to tighten. All of these features function simultaneously to set a limit to the amount of protraction. With retraction, the preceding structures change position with the following results: (a) the obturator ridge moves anterodorsally and the posterior part of the capsule becomes loose, (b) the proximo-anterior surface of the shaft moves anteroventrally and the anteroventral part of the capsule becomes loose, (c) the shaft moves posteriorly and the ventral part of the capsule loosens, and (d) the fovea capitis moves medially toward the inside opening of the acetabulum, thus slackening the teres and posterior acetabular ligament.

At the fully protracted position the medial part of the trochanter of the femur articulates with the posterior portion of the antitrochanter (fig. 4A). As the femur retracts, the trochanter moves forward and loses contact with the antitrochanter (figs. 4B, C). The ventral surface of the antitrochanter then assumes an articulation with the posterior surface of the femoral neck.

LATERAL-MEDIAL ROTATION

In the fully protracted position only a very slight medial rotation is possible, whereas lateral rotation is prevented by the articulation of the trochanter against the antitrochanter. Thus, when the femur is fully protracted, the bone is also at its position of greatest lateral rotation. As the femur retracts it must rotate medially because of the configuration of the trochanter-antitrochanter surfaces (fig. 4B). With the slightest retraction, the femur can rotate medially, and once the trochanter is anterior to the

antitrochanter, a considerable amount of medial rotation is possible. With the muscles removed, an exposed fresh joint shows about 40 to 45 degrees of rotation beginning at the protracted position. Certainly much less rotation takes place in a living bird.

ABDUCTION-ADDUCTION

When the femur is fully protracted, no abduction is possible because of the trochanter-antitrochanter articulation and the ventral part of the capsule, and no adduction is possible because of the teres and posterior acetabular ligaments and the posterior part of the capsule (in some specimens a slight adduction was possible).

With steady retraction, increasing amounts of abduction-adduction are possible, the greatest amount taking place when the trochanter is anterior to the antitrochanter. In this position an arc of movement of as much as 20 to 35 degrees can take place (great variation is found even between the two joints of a single individual). This large amount of abduction-adduction probably does not occur under natural conditions of locomotion, because the femur would have to be retracted quite far before such abduction-adduction is possible.

KNEE JOINT

In my study of the avian knee joint, I have followed many of the methods and techniques developed by numerous workers in their investigations of the human knee joint (see, for example, Brantigan and Voshell, 1941; Last, 1948; Kaplan, 1957, 1962). These studies have proved to be of great value, and they have much to offer workers undertaking functional investigations in nonhuman vertebrates.

The avian knee joint exhibits a considerable range of motion during the locomotor cycle, but during most of this cycle the joint is in a flexed position. Many of the leg muscles and the joint structures themselves operate to maintain stable articulating conditions throughout the locomotor cycle. The functional morphology of the joint structures will be discussed in this section; the roles of the muscles are treated in a later section.

MORPHOLOGY OF THE KNEE JOINT

JOINT CAPSULE

On the medial side of the joint the capsule

attaches proximally to the femur about 5 or 6 mm. from its distal end (see figs. 5, 9, 10 for

illustrations of the joint capsule). The capsule in this area is thin and transparent but yet is moderately strong. Anteromedially, the capsule apparently passes somewhat posteriorly to the patellar ligament but becomes confluent with the tissue of the ligament and patellar fat pad. Here the capsule is thicker and stronger than it was more posteriorly. On the medialmost margin of the fat pad the capsule attaches to the distal base of the inner cnemial crest and continues posteriorly over the medial ligament. The tissue of the capsule appears somewhat distinct from the anterior edge of the medial ligament but is confluent with the posterior edge. On the tibiotarsus the capsule attaches a short distance below (distal to) the level of the articulating surface and to the distal edge of the overhanging lip of that surface. Posterior to the medial ligament, the capsule is confluent with the connective tissues associated with the origin of the medial head of *M. gastrocnemius*; hence, some fibers originate on the capsule. On the posterior side of the joint, the capsule covers the internal condyle and inserts into the popliteal area distal to the muscle insertions. Some fibers of these muscles arise from the tissue of the capsule. The capsule is connected by fibrous tissue to the medial meniscus posteriorly. The capsule covers the external condyle and attaches at its proximal base. At the same time, it has an extensive connection to the lateral meniscus. All along the posterior side of the joint the capsule continues to attach distally to the lip of the head of the tibiotarsus. On the posterolateral side of the joint the capsule becomes confluent with the common aponeurosis (aponeurosis 2; see muscle section below) of *M. flexor perforans et perforatus digiti II* and *M. flexor perforans et perforatus digiti III*, which lies immediately posterior to the lateral ligament. The capsule overlies the lateral ligament and anteriorly merges with the patellar ligament. In this region the capsule is intimately associated with an aponeurosis of origin (aponeurosis 5) for several flexor muscles of the toes.

LIGAMENTS

The knee joint of birds possibly contains more ligaments than that of any other vertebrate. Two of these ligaments are "outside" (or included in) the joint capsule, the remainder are not only inside the capsule but between the articular surfaces themselves.

The best discussion of ligaments of the avian

knee is by Haines (1942, pp. 283–285; fig. 7), who studied and illustrated the knee joint of *Gallus gallus*. Haines did not describe the ligaments in detail, nor did he discuss their function, but he did construct a terminology that is more useful than either Kaupp's laborious treatment (1918, pp. 65–69) based on veterinary names or Stolpe's (1932) superficial discussion of the ligaments. The following terminology is mainly that of Haines.

a. The lateral ligament ("ligamentum col-laterale fibulare" of Haines) (l lig; figs. 5–8, 10) runs from the lateral side of the proximal end of the fibula to the lateral side of the fibular condyle of the femur. The attachment on the femur is large, beginning on the side of the fibular condyle and extending proximally onto the lateral side of the shaft of the femur.

b. The medial ligament ("ligamentum col-laterale tibiale" of Haines) (m lig; figs. 5, 8, 10) is, like the lateral ligament, heavy and strong. It attaches to the medial side of the femur and runs to the side of the tibiotarsus about 7 mm. from its proximal end. The ligament is widest at the level of the articular surfaces. The posterior and medial edges of the ligament are attached to the medial meniscus, and a bursa is formed.

c. The meniscocollateral ligament (mc lig; figs. 5–7) is a short and narrow ligament connecting the anterior edge of the lateral ligament with the anterolateral corner of the lateral meniscus.

d. The meniscofibular ligament (mf lig; figs. 5, 6, 10) lies immediately distal to the preceding ligament. It is very short, broad, and strong, and runs from the anteromedial corner of the head of the fibula to the laterodistal side of the lateral meniscus.

e. The tibiofibular ligament (tf lig; figs. 6, 7) originates from the medial side of the fibula just distal and posterior to the preceding ligament. It runs medially and slightly anteriorly to insert onto the lateral side of the interarticular ridge. Some of the fibers at its origin may attach to the meniscofibular ligament and to the lateral meniscus. At its insertion some of the fibers of the tibiofibular ligament may intermingle with those of the anterior cruciate ligament.

Two ligaments arise from the anteromedial side of the lateral meniscus:

f. The more distally situated of the two ligaments is the anterior meniscotibial ligament (amt lig; figs. 6, 7). It runs medially across the

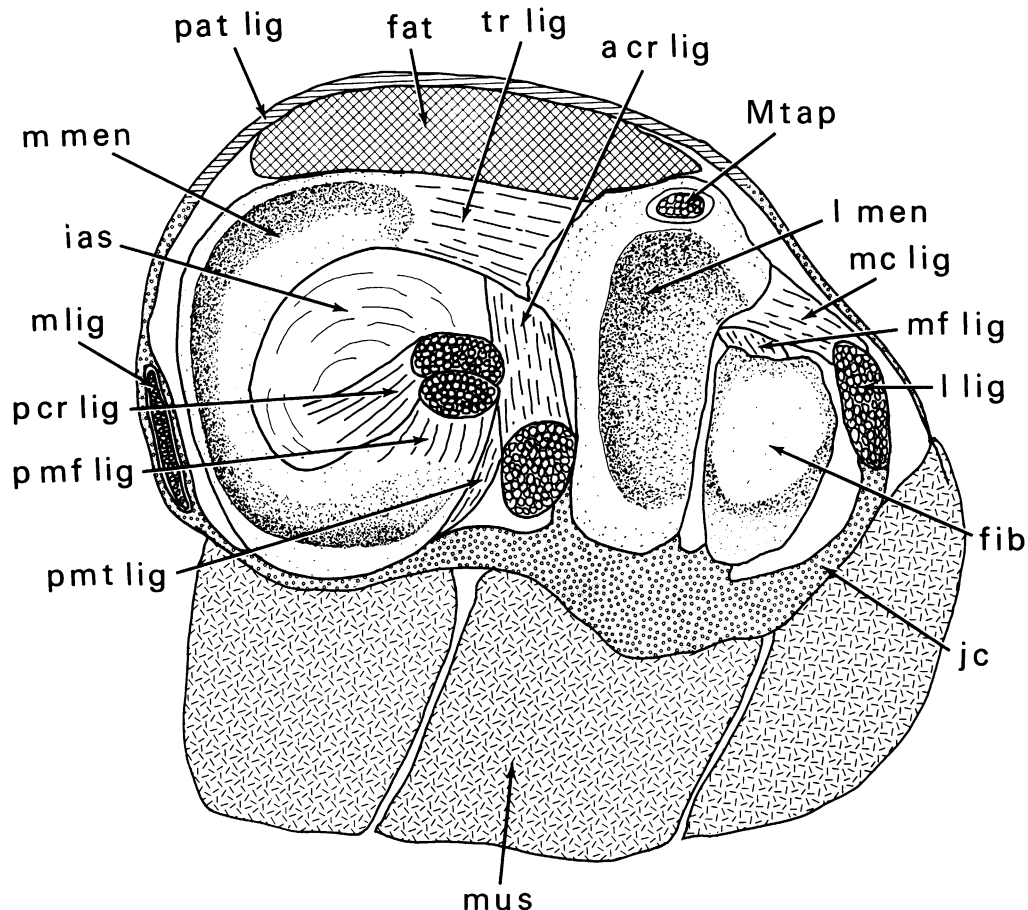


FIG. 5. Schematic diagram of proximal end of tibiotarsus showing knee joint structures in *Columba livia*.

Abbreviations: a cr lig, anterior cruciate ligament; fat, fat pad; fib, fibula; ias, internal articular surface; jc, joint capsule; l men, lateral meniscus; mc lig, meniscocollateral ligament; mf lig, meniscomfemoral ligament; m lig, medial ligament; m men, medial meniscus; M tap, M. tibialis anterior, posterior slip; mus, muscle; pat lig, patellar ligament; p cr lig, posterior cruciate ligament; p mf lig, posterior meniscomfemoral ligament; p mt lig, posterior meniscotibial ligament; tr lig, transverse ligament; l lig, lateral ligament.

joint and attaches to the head of the tibiotarsus anterior to the articular surface of the medial meniscus.

g. The transverse ligament (tr lig; figs. 5-7) arises from the lateral meniscus proximal to the anterior meniscotibial ligament. This strong and broad ligament passes medially to attach to the anterolateral edge of the medial meniscus. This and the preceding ligament join at their attachment to the lateral meniscus.

h. The anterior cruciate ligament (a cr lig; figs. 5-8, 10) arises from the anteriormost part of the posterior intercnemial ridge, passes posteri-

orly and attaches to the laterodistal part of the popliteal area of the femur (on the medial face of the lateral condyle) just distal to the attachment of the joint capsule. This large ligament is flattened at its ends and rounded in the central portion.

i. The posterior cruciate ligament (p cr lig; figs. 5, 6, 8) arises from the posterior part of the internal articular surface beneath the medial meniscus. It passes anterolaterally and proximally to attach to the lateral side of the distal end of the rotular groove of the femur. The ligament has a broad basal attachment to the tibiotarsus.

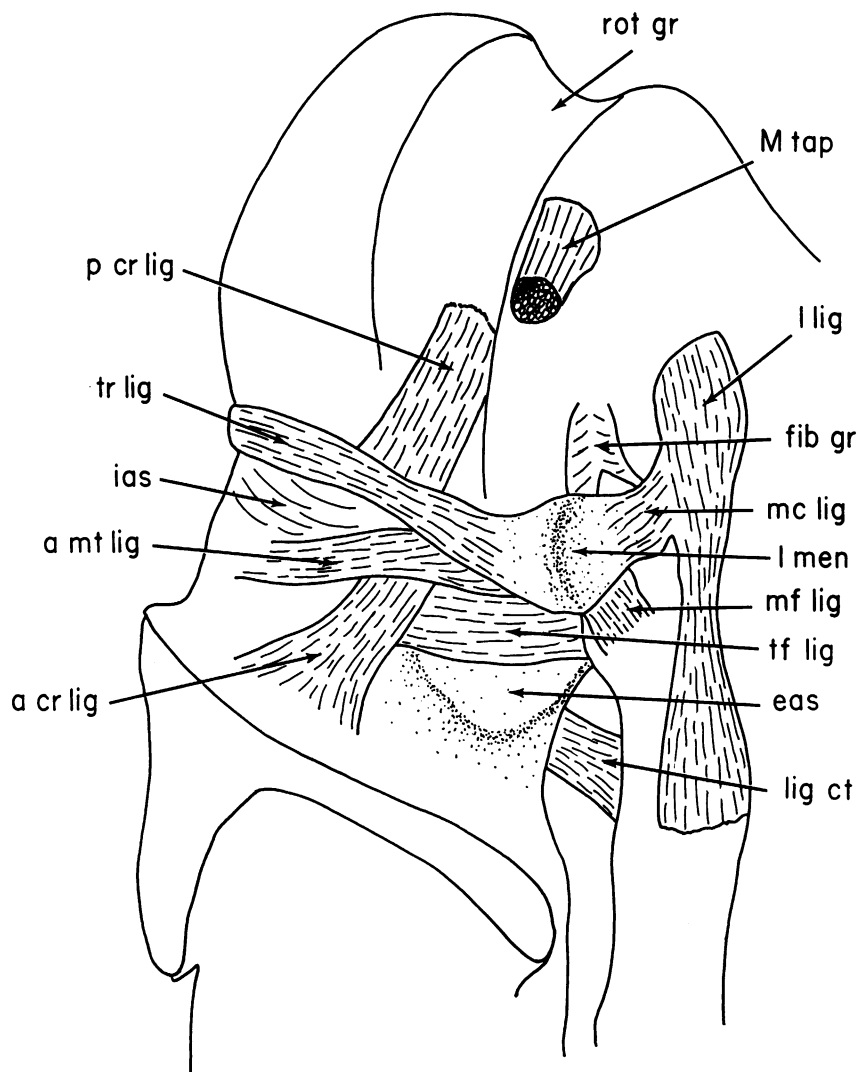


FIG. 6. Anterolateral view of knee joint of *Columba livia* in flexed position showing arrangement of ligaments.

Abbreviations: a cr lig, anterior cruciate ligament; a mt lig, anterior meniscotibial ligament; eas, external articular surface; fib gr, fibular groove; ias, internal articular surface; lig ct, ligamentous connective tissue; l lig, lateral ligament; l men, lateral meniscus; mc lig, meniscocollateral ligament; mf lig, menisofibular ligament; M tap, M. tibialis anterior, posterior slip; p cr lig, posterior cruciate ligament; rot gr, rotular groove; tf lig, tibiofibular ligament; tr lig, transverse ligament.

It is thick and strong along its lateral edge but flattened medially. This medial portion of the base serves as part of the surface of articulation for the medial condyle of the femur.

The posterolateral corner of the medial meniscus divides into two ligaments:

j. The more proximal one is the posterior

menisofemoral ligament (p mf lig; figs. 5, 8). It curves anteroproximally and attaches to the distolateral side of the rotular groove of the femur.

k. Distal to the preceding ligament is the posterior meniscotibial ligament (p mt lig; fig. 5). This branch curves anteriorly to attach to the lateral edge of the internal articular sur-

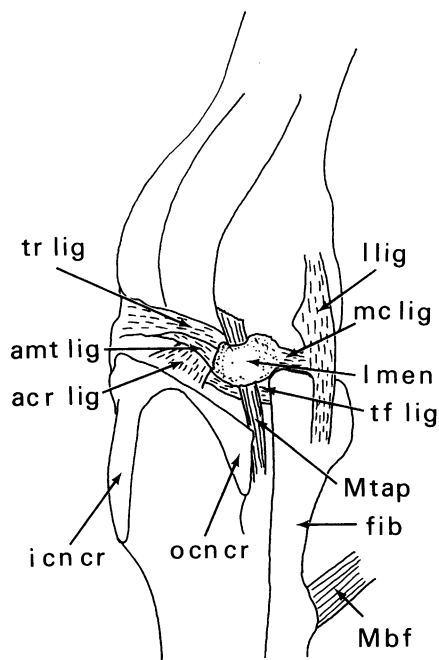


FIG. 7. Anterolateral view of knee joint of *Columba livia* in extended position showing arrangement of ligaments.

Abbreviations: a cr lig, anterior cruciate ligament; a mt lig, anterior meniscotibial ligament; fib, fibula; i cn cr, inner cnemial crest; l lig, lateral ligament; l men, lateral meniscus; M bf, M. biceps femoris; mc lig, meniscocollateral ligament; M tap, M. tibialis anterior, posterior slip; o cn cr, outer cnemial crest; tf lig, tibiofibular ligament; tr lig, transverse ligament.

face. Connective tissue connects this ligament with the anterior cruciate ligament.

MENISCI

The medial meniscus (m men; figs. 5, 9) is a large, crescent-shaped cartilaginous structure lying on the internal articular surface of the tibiotarsus. It is wide anteriorly and posteriorly but narrows medially. The outer edge is thicker than the inner so as to give the meniscus a triangular shape in cross section. Thick fibrous connective tissue adheres to the anterior side of the meniscus and connects it with the fibrous matrix of the fat pad and joint capsule. Medially the meniscus is joined to the capsule and medial ligament and posteriorly also to the capsule. Anteriorly, the meniscus is continuous with the transverse ligament and posteriorly with the posterior meniscofemoral and posterior meniscotibial ligaments.

Unlike the medial meniscus, the lateral meniscus (l men; figs. 5-7, 10) is not open in the center but is a solid, oblong, disclike structure. It lies in the depression between the head of the fibula and the external articular surface. The meniscus is thinnest in the center and thick peripherally. Anteriorly, it is especially thick where it serves as the point of attachment for four ligaments and where it possesses a groove for the tendon of origin of M. tibialis anticus. The lateral side, nearest the fibula, is thicker than the central part, but the former is situated much more distally because it is depressed between the fibula and tibiotarsus. This troughlike depression serves as the point of articulation for the external condyle of the femur. The anterior end of the trough has a much higher wall than the posterior end. Laterally, the bottom of the meniscus is connected to the medial side of the fibula (about 3 or 4 mm. from its proximal end) by a short, strong band of connective tissue. Posteriorly, the meniscus is joined to the joint capsule and to the posterior side of the fibula by a band of connective tissue.

A large mass of dense fibrous connective tissue is found posteriorly between the two menisci. It is continuous with the joint capsule and is intimately connected with the menisci. It has a strong, almost ligamentous, connection with the popliteal area of the femur and with the tibiotarsus by way of the joint capsule.

FAT PAD

The fat pad (fat; figs. 5, 9, 10) is large and extends the width of the joint posterior to the patellar ligament. The pad contains considerable amounts of fibrous matrix which is strongly connected to the tibiotarsus immediately posterior to the cnemial crests, the joint capsule medially and laterally, the patellar ligament and the several ligaments at the anterior end of the joint, and consequently, to the menisci. The pad extends proximally to about the level of the patella.

PATELLA AND PATELLAR LIGAMENT

The patella (pat; fig. 9) is a small, irregular-shaped sesamoid bone within the aponeuroses of insertion of M. femorotibialis and M. iliotibialis. It lies proximal to the articular condyles (when the joint is in an extended position). The patellar ligament is that part of the aponeuroses of insertion which continues distally beyond the patella.

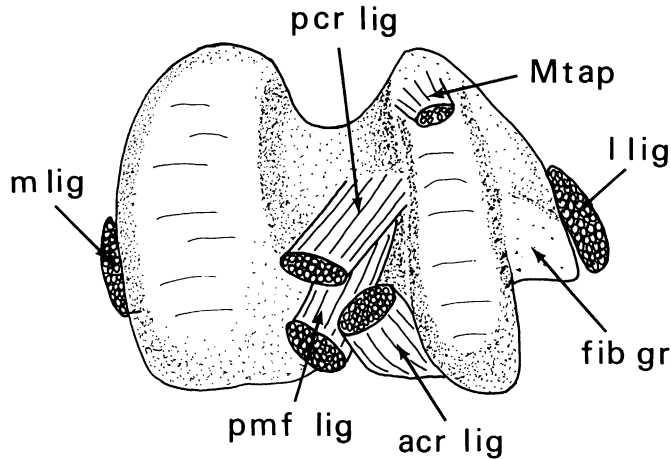


FIG. 8. View of the distal end of femur of *Columba livia* to show arrangement of ligaments.

Abbreviations : a cr lig, anterior cruciate ligament; fib gr, fibular groove; l lig, lateral ligament; m lig, medial ligament; M tap, M. tibialis anterior, posterior slip; p cr lig, posterior cruciate ligament; p mf lig, posterior menisofibular ligament.

to insert onto the anterior end of the tibiotarsus. The ligament forms the anterior end of the joint cavity.

MICROANATOMY

JOINT CAPSULE: In longitudinal section the only clearly definable portion of the capsule seen is that on the posterior side of the joint. In general it is a loosely organized structure. Proximally, the collagenous fibers are oriented in a proximodistal direction, but distally this orientation is less distinct and more nearly random. The proximal portion of the capsule is also more dense than is the distal portion, with the dense areas being situated posteriorly. Along the anterior surface of the capsule, facing inward to the joint cavity, is a narrow zone of very dense, deeply staining tissue. The zone is distinct from the more posterior parts of the capsule, especially in the central parts, but it becomes less distinct at the extreme proximal and distal ends. This zone corresponds to the synovial membrane portion of the capsule.

Anteriorly in longitudinal section, the patellar ligament forms the anterior boundary of the joint cavity. The fat pad, however, could serve as the anterior limit to most of the synovial fluid, and certain features of the pad suggest this to be the case (discussed below).

In cross section the capsule is continuous with portions of the patellar ligament. On the medial side the capsule passes posterior to the patellar ligament, and the fibers of the capsule intermingle with those of the ligament anteriorly and the fat pad posteriorly. Medially, the capsule differentiates into a medial ligament, the ligamentous portion being more densely and regularly organized. Posterior to the medial ligament the capsule continues around the joint. Some of the inner fibers of the capsule attach to the posteromedial surface of the tibiotarsus. On the posterior side of the joint the capsule becomes larger and at the same time much less dense. Only the portion of the capsule facing the joint cavity remains consistently dense. Here the capsule has rather extensive connections to the menisci and to the posteromedial edge of the fibula. Proximal to this position the capsule is confluent with the common aponeurosis of M. flexor perforans et perforatus digiti II and M. flexor perforans et perforatus digiti III. This thick aponeurosis is connected to the posterior side of the lateral ligament by a thin portion of the capsule. The capsule attaches along the lateral side of the ligament and remains much more distinct than the capsule and medial ligament. Anterolaterally, the capsule is directly continuous with the patellar ligament.

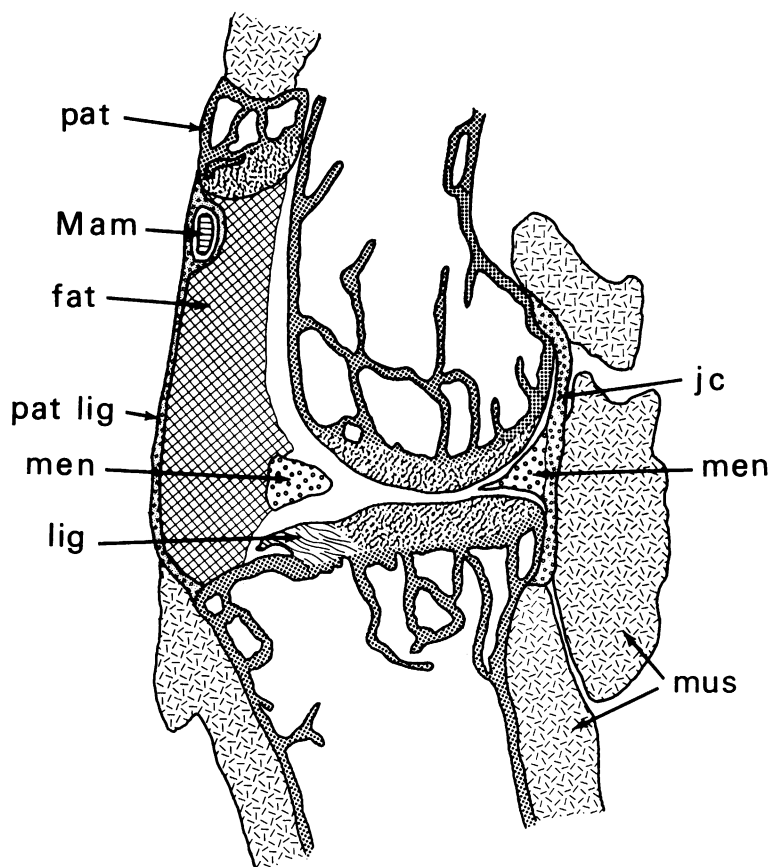


FIG. 9. Schematic diagram of histological sagittal section through knee joint of *Columba livia*.

Abbreviations: fat, fat pad; jc, joint capsule; lig, ligament; M am, M. ambiens; men, meniscus; mus, muscle; pat, patella; pat lig, patellar ligament.

MENISCI

LATERAL MENISCUS: A cross section through the head of the tibiotarsus (distal to the external condyle of the femur) reveals the most information about the histological structure of the lateral meniscus. The meniscus is a fibrocartilaginous structure, but the relative amounts of chondrocytes and collagenous tissue vary greatly within the meniscus. Centrally and medially, the meniscus is composed of large numbers of chondrocytes and substantial amounts of collagenous fibers. Although the fibers run in all directions, most of them are oriented anteroposteriorly. More laterally, the ratio of chondrocytes to fibers becomes smaller until at the lateralmost edge chondrocytes are almost absent. Posteriorly, chondrocytes decrease in number,

and a rather large portion of the posterior end of the meniscus is almost pure collagenous tissue. The anterior end of the meniscus is composed of proportionally greater amounts of fibrocartilage than is the posterior end. Chondrocytes are numerous anteriorly up to the canal for the tendon of M. tibialis anterior. Only medial and anterior to the canal is the meniscus wholly cartilaginous.

MEDIAL MENISCUS: As in the lateral meniscus, a cross section of the medial meniscus reveals that the proportion of chondrocytes and collagenous tissue changes within the meniscus. Centrally, chondrocytes and collagenous fibers are both found in nearly equal amounts. The fibers run mainly in an anteroposterior direction, but some are oriented lateromedially and

diagonally as well. Along the lateral edge of the meniscus (where it is thinnest) there is a thin, slightly deeper staining zone composed mainly of rounded chondrocytes. At the lateralmost edge there is a thinner, clear zone with hardly any chondrocytes. Medially, toward the medial ligament, the chondrocytes diminish in number so that a moderately broad area of the medial side of the meniscus is wholly collagenous. Anteriorly and laterally, the proportion of chondrocytes greatly increases. Medial to this area, the meniscus becomes wholly collagenous where it is confluent with the transverse ligament. Posteriorly, the number of chondrocytes decreases throughout the meniscus, although they still are most numerous laterally. Here also the clear zone along the lateral edge has disappeared. The meniscus becomes wholly collagenous where it is continuous with the posterior meniscofemoral and posterior meniscotibial ligaments.

FAT PAD

In longitudinal section, the fat pad extends from the surface of the tibiotarsus to the patella. A large amount of thin, loose fibrous connective tissue runs throughout the pad and is continuous with the tissue of the patellar ligament anteriorly the patella dorsally, and the menisci posteriorly.

The posterior edge of the pad consists of slightly greater amounts of fibrous tissue, and this tissue may effectively serve as the anterior edge of the joint cavity as far as the movement of the synovial fluid is concerned.

ARTICULAR SURFACES

In longitudinal section, the articular surface of the medial condyle is seen to be typical fibrocartilage. Large, rounded chondrocytes are present throughout except in a basal zone next

to the underlying bone. Here the chondrocytes become flattened. In no portion of the cartilage was a columnar arrangement of the chondrocytes found. The collagenous fibers are organized in an intertwining network with little distinct orientation, except for a slightly greater percentage of fibers that run in an antero-posterior direction. The thickness of the cartilage is greatest centrally and decreases anteriorly and posteriorly.

In this same region the condyle articulates with the internal articular surface of the tibiotarsus. The thickness of the latter is considerably greater than the corresponding surface of the femur. Rounded chondrocytes are present throughout except in a basal zone next to the bone and in a thin zone along the surface of the cartilage. In this thin zone the chondrocytes are reduced in number, smaller, and flattened. No such zone was noticed in the cartilage of the medial condyle. The chondrocytes are not oriented in columns. The collagenous fibers, while running in all directions, are somewhat oriented into columns directed perpendicular to the articular surface.

Longitudinal sections through the lateral condyle of the femur and the external articular surface of the tibiotarsus show essentially the same features as that described above.

A cross section at the level of the articular surfaces reveals that the articular cartilage of the lateral side of the femur is thickest in the region of the fibular groove and fibular condyle. The structure of the cartilage does not differ significantly from that already described.

The cartilage of the fibula is thickest anteriorly and dorsally and becomes thinner postero-medially. On the medial side the numbers of chondrocytes diminish, especially toward the surface.

FUNCTIONAL ANALYSIS OF THE KNEE JOINT

TYPES OF MOTION

In the discussion that follows on joint movement, the tibiotarsus will be considered as the stationary element unless noted otherwise. At the knee joint four separate types of motion can be defined:

a. Flexion-extension: This motion takes place in a plane oriented along the longitudinal axes of the bones and directed in an anteroposterior

direction. During flexion, the angle between the elements becomes smaller and in extension larger.

In a theoretical sense flexion and extension could take place by rolling, a motion in which equidistant points on the femur touch corresponding, equidistant points on the tibiotarsus. Pure rolling never takes place during the entire flexion-extension cycle but may occur during part of the cycle. Typically, flexion-extension is

brought about by a combination of rolling and anteroposterior translation (sliding) of the articular surfaces (see below). It would be difficult, if not impossible, to accurately measure the individual contributions that rolling and translation make to the flexion-extension cycle. Without the technique of radiography these two components could not be measured in an intact joint, and in a stripped joint the measurements would be meaningless. In the discussion below I will treat the functional morphology of the flexion-extension cycle in terms of the two movements independent of each other.

b. Lateral-medial rotation: The term rotation will be used to describe a spin of the femur about its longitudinal axis. Lateral rotation refers to a turning of the anterior end of the condyles (anterior end of rotular groove) toward the lateral (external) side of the leg as viewed from the proximal end of the femur. Medial rotation describes the turning of the anterior ends of the condyles toward the medial (internal) side of the leg.

c. Lateral-medial swing: A swing will be a motion that takes place in a plane oriented along the longitudinal axes of the bones and directed in a lateromedial direction. A lateral swing is one in which the proximal end of the femur moves laterally relative to the proximal end of the tibiotarsus, whereas a medial swing is one in which the proximal end moves medially.

d. Translation (sliding): Sliding of the femur on the tibiotarsus is in an anteroposterior or lateromedial direction.

FLEXION-EXTENSION

In a living bird the joint can be extended until the femur and tibiotarsus form an angle (measured posteriorly) of about 160 degrees. The joint can be flexed so that the tibiotarsus is nearly parallel with the femur, and if the two elements are moved in separate planes, they can be slightly crossed in some cases. Clearly then, the joint structures are not functioning to prevent flexion (but possibly to hinder it) but instead are organized to set a limit to the amount of extension.

Portions of the medial ligament may serve to limit extension. Lateral (deep) to the ligament the tibiotarsus projects slightly mediad. At the position of full extension only the posterior half of the fibers of the ligament cover this projection, and thus only these fibers are taut. At this time

the anterior fibers are loose. During flexion the ligament moves posteriorly relative to the tibiotarsus, thus causing the anterior fibers to overlies the projection and become taut. The relative degree of tautness of certain parts of the ligament is determined not only by the medial projection of the tibiotarsus but also by the relative curvatures of the two articular surfaces. The greatest portion of the ligament is taut at about 90 degrees and, as discussed later, this may be important in controlling the relative direction of movement of the two knee elements.

The lateral ligament also plays a complicated role during the flexion-extension cycle. At the position of greatest extension the ligament lies along the lateral side of the fibula. As flexion ensues, the fibular condyle of the femur rotates posteriorly over the head of the fibula. This movement tends to displace the condylar (femoral) attachment of the ligament posteriorly, and the ligament is "pulled" through an arc of about 35 to 40 degrees. Because the posterior portion of the articular surface of the fibula slopes proximally, the distance between the two ends of the lateral ligament increases slightly when the fibular condyle moves over the surface of the fibula during flexion. This mechanism insures that the lateral ligament is subjected to its greatest tensile forces at about 90 degrees. At an angle of flexion of between 90 to 100 degrees the direction of tension in the ligament is in line with the center of rotation of the joint elements, hence no torque producing forces are placed on the elements of the joint by the ligament (actually there are torques produced by the ligament that cause a lateral swing, but these will be ignored for the moment). Once the angle of flexion is decreased it is possible that the ligament, which can now release the energy stored within it, may provide some force to flex the joint farther. Even though this force is probably present, it is not necessarily true that the force is of significance when compared with the forces produced by muscles and gravity. The ligamental force probably is significant, however, in controlling the relative direction and magnitude of the movement of the femur and tibiotarsus (discussed in more detail below). Since the femur is moving posteromedially across the surface of the tibiotarsus during flexion, the lateral ligament pulls the fibula posteriorly. When the lateral ligament is cut, the mechanism described above is destroyed as is joint stability in general.

The meniscocollateral ligament, being attached to the anterior edge of the lateral ligament, becomes taut during flexion as the lateral ligament moves posteriorly. The meniscocollateral ligament probably helps control movement of the lateral ligament and may contribute to pulling the lateral meniscus posteriorly.

The menisofibular ligament is relatively taut in all positions but certainly becomes more so as the fibula moves posteriorly during flexion. The ligament hinders this movement and probably also serves to stabilize the fibula against various forces which are transmitted across the joint surfaces.

The fibula is also stabilized by the tibiofibular ligament. As the joint flexes, the ligament is pulled posteriorly onto the rounded external articular surface and becomes taut. The ligament prevents the head of the fibula from being displaced laterally and thus broken when large forces are applied. The tibiofibular ligament seems to be a possible determinate of the arc of movement of the fibula. As the latter is pulled posteriorly, the ligament serves as the radius of this arc. At the very least, the ligament constrains the fibula to move within certain defined limits, depending on the length of the ligament. In an extended position of the joint the ligament is loose.

The anterior meniscotibial ligament is loose at the position of extension. As the joint flexes the ligament is pulled posterolaterally over the anterior cruciate ligament by the moving lateral meniscus. The ligament then becomes taut and prevents the meniscus and hence the fibula from moving laterally.

The transverse ligament seems to play a general role in keeping the flexion-extension cycle operating smoothly and in coordinating the lateral and medial menisci during movement. The transverse ligament becomes taut as flexion proceeds. During flexion, the ligament maintains the orientation of the anterior end of the medial meniscus, and this orientation is destroyed when the ligament is cut. If the ligament is cut, the medial condyle of the femur is allowed to rotate more mediad than it would normally do (this is especially true during extension). In general, a cut transverse ligament decreases the stability of the femur as it rotates. Another way in which the ligament may increase stability is through a connective tissue attachment with the medial ligament. When the

transverse ligament is cut, the medial ligament slides posteriorly a short distance. As the medial ligament contributes something to maintaining the anterior orientation of the femur, the proper functioning of the transverse ligament is important.

The anterior cruciate ligament becomes taut during extension and places a limit on this movement. The ligament also becomes slightly taut at the greatest position of flexion, but this is probably fortuitous and never reached under natural conditions.

The posterior cruciate ligament is most taut at full flexion; the ligament is not loose at full extension but does not seem to be limiting extension. It is difficult to envision this ligament preventing extension or flexion as other structures appear to function sooner. The posterior cruciate probably plays an important part in maintaining the orientation of the femur as it rotates.

The posterior menisofemoral ligament is relatively loose in the extended position but it becomes more taut with flexion. This is brought about because the medial meniscus is being displaced posteriorly by the medial condyle of the femur. The ligament thus functions apparently to keep the shape of the posterior part of the medial meniscus and to hinder its posterior movement. The same role can be postulated for the posterior meniscotibial ligament. It, too, is the most taut during flexion and probably maintains the position of the meniscus as the latter is being pushed posteriorly.

Perhaps the joint structure contributing the most to limiting extension is the joint capsule. The portion of the capsule over the posterior side of the joint is thick and fibrous, and as extension proceeds the condyles of the femur rotate into the capsule and extension is subsequently halted.

LATERAL-MEDIAL ROTATION

The amount of rotation at the knee joint is very difficult to measure, especially since some rotation is taking place during the flexion-extension cycle. Rotation becomes increasingly possible as the joint is flexed. In the fully extended position the joint capsule, medial and lateral ligaments, and many of the intra-articular ligaments are taut and thus hinder rotation. Even in the flexed position such structures as the lateral meniscus with its deep trough and the tibiofibular ligament, which is taut during flexion, would function to prevent rotation.

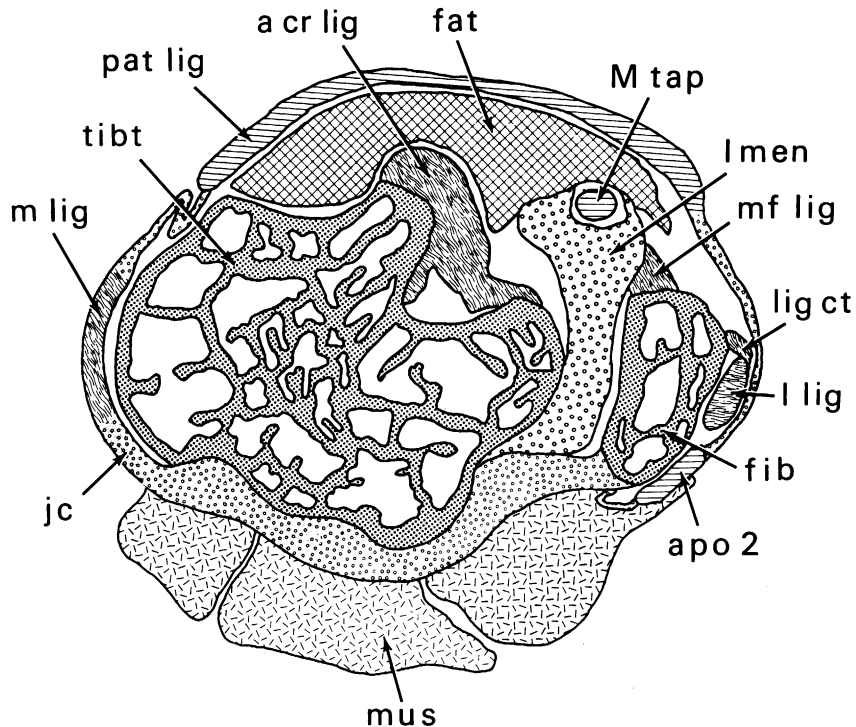


FIG. 10. Schematic diagram of histological cross section through knee joint of *Columba livia* at level of proximal end of tibiotarsus.

Abbreviations: a cr lig, anterior cruciate ligament; apo 2, aponeurosis 2; fat, fat pad; fib, fibula; jc, joint capsule; lig ct, ligamentous connective tissue; l lig, lateral ligament; l men, lateral meniscus; mf lig, meniscofibular ligament; m lig, medial ligament; M tap, M. tibialis anterior, posterior slip; mus, muscle; pat lig, patellar ligament; tib t, tibiotarsus.

LATERAL-MEDIAL SWING

Lateral-medial swing is a most important movement in the knee joint and follows a rather complicated pattern. Swinging in the knee joint is probably more a manifestation of the diagonal path that the femoral and tibiotarsal surfaces follow relative to one another rather than a deviation from a single plane of motion as it is in the intertarsal joint (see below). Swinging can be understood better if we consider the movements that take place as the tibiotarsus is extended. We will assume the joint to be in the fully flexed position and the femur to be the stationary element (as it essentially is during much of the locomotor cycle). In the flexed position the tibiotarsus and lower leg are oriented anteromedially ("toed-in"). As the knee joint is extended, the tibiotarsus slowly rotates laterally until the toes are oriented directly forward at the position of full extension. The rate of rotation of the tibio-

tarsus is less during the early stages of extension than it is during the later phases. The act of extending the leg, then, involves movement in all three planes, that is, flexion-extension, rotation, and swinging.

In the fully extended position lateral-medial swing is nearly absent. Both the lateral and medial ligaments would function to prevent such motion. The cruciate ligaments are taut and would likewise contribute to hindering swing.

As the joint is flexed, the loosening of the joint structures allows a greater amount of swing until at a point near greatest flexion the femur can swing through an arc of about 50 degrees. Most of this movement is in a medial direction because lateral swing is hindered by the medial ligament (recall that the medial ligament is taut at 90 degrees). The movable attachment of the lateral ligament to the fibula permits some additional medial swing.

The factors controlling the exact pathway of the femur across the surface of the tibiotarsus are unknown at present. The major influences seem to be the medial and lateral ligaments and the shape of the lateral meniscus-fibular surface and the external condyle-fibular condyle surface. When either the lateral or medial ligament is cut, the normal articular pathway is destroyed. There can be little doubt that the tension in these ligaments keeps the surfaces together so that the proper movement can take place, but this does not imply that these ligaments are the cause of the direction of movement. It is possible, however, that the changes in the amount of tensile force across the medial ligament during

the flexion-extension cycle could in themselves result in medial movement (swing) of the femur during flexion.

TRANSLATION

Of the types of motion possible in the knee joint, translation is undoubtedly the least important. In full extension translation in a latero-medial or anteroposterior direction is essentially absent, and as the joint is flexed the increase in translation is hardly noticeable. Almost all the joint structures are functioning at one time or another to prevent translation between the elements.

INTERTARSAL JOINT

The structure and function of the intertarsal joint have received as great attention from previous workers as has any other hind-limb joint. Langer (1859) discussed the configuration of the joint surfaces. Kaupp (1918, p. 69) briefly called attention to the joint ligaments, but it was

left to Stolpe (1932) to provide the first good description of the joint structures and to discuss their function. Barnett (1954a) compared the avian intertarsal joint with the human knee, but his treatment was of a general nature.

MORPHOLOGY OF THE INTERTARSAL JOINT

JOINT CAPSULE

The joint capsule (jc; figs. 11-14) is a complex structure in which gross and histological anatomy varies with its location around the joint. These structural differences give the capsule specific, and decidedly important, functional properties affecting joint movement.

Anteriorly on the tibiotarsus, the capsule attaches to the base of the external condyle. Posterolaterally the capsule merges with the fascia (probably should be considered part of the capsule) covering the tendon of *M. peroneus brevis*. Distally, the capsule entirely covers the external condyle and more laterally covers the lateral ligament as well. The capsule inserts distally on the anterior rim of the external cotyla. At this insertion the capsule includes the lateral cross ligament and the fibrous connective tissue that lies against, and in part is connected to, the lateral meniscus. Also, some fibrous strands of the capsule run into the anterior metatarsal groove and either insert directly on the tarsometatarsus in this area or are lost in the

surrounding connective tissue. Proximally, the capsule arises from the distal rim of the supratendinal bridge and covers the tendon of *M. extensor digitorum longus* as it emerges beneath the bridge. As the capsule passes distally in this region, it crosses the joint articulation and the intercotylar prominence and proceeds into the anterior metatarsal groove where it disappears into the large amount of loose connective tissue and fat found there.

Anteromedially, the capsule attaches at the proximal base of the internal condyle and covers the latter distally. On the medial side of the joint the capsule attaches to the surface of the internal condyle immediately anterior to the internal ligamentous prominence. Distal to the prominence the deeper portions of the capsule continue to insert onto the tibiotarsus, but the most superficial layer passes over the medial ligament. Posterior to the ligament the capsule is confluent with the broad ligamentous band attaching to the tibial cartilage. The capsule adheres closely to this fascia. The fascia (including

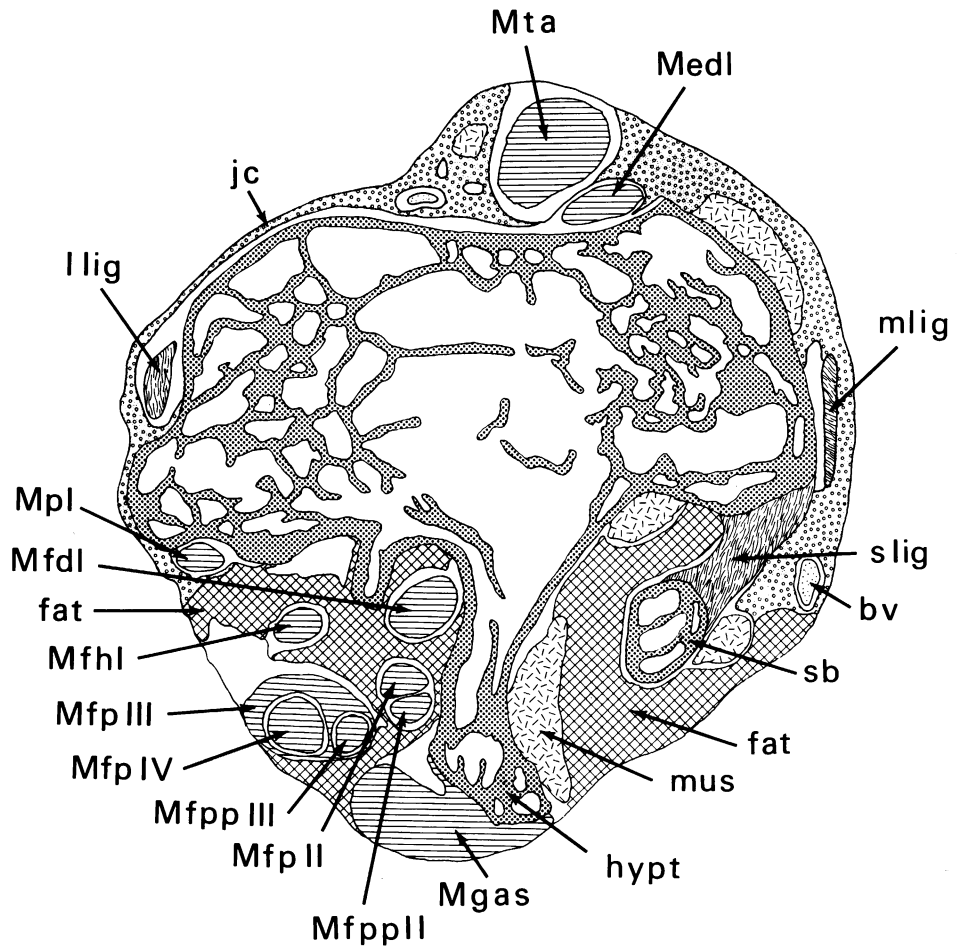


FIG. 11. Schematic diagram of histological cross section through intertarsal joint of *Columba livia* at level of proximal end of tarsometatarsus.

Abbreviations: bv, blood vessel; fat, fat pad; hypt, hypotarsus; jc, joint capsule; l lig, lateral ligament; M edl, M. extensor digitorum longus; M fdl, M. flexor digitorum longus; M fhl, M. flexor hallucis longus; M fpII, M. flexor perforatus digiti II; M fpIII, M. flexor perforatus digiti III; M fpIV, M. flexor perforatus digiti IV; M fppII, M. flexor perforatus et perforans digiti II; M fppIII, M. flexor perforatus et perforans digiti III; M gas, M. gastrocnemius; m lig, medial ligament; M pl, M. peroneus longus; M ta, M. tibialis anterior; mus, muscle; sb, intertarsal sesamoid bone; s lig, sesamoid ligament.

the capsule) is firmly bound to the side of the tibial cartilage. The capsule continues over the posterior side of the joint.

Distally the capsule joins with the fibrous connective tissue, including the medial meniscus, to insert onto the anterior rim of the internal cotyla.

On the lateral side of the joint the portion of the capsule covering the external condyle passes over the peroneus tendons to merge with the

ligamentous fascia that runs to the tibial cartilage. Portions of the capsule insert upon the rim of the external cotyla. Posterior to the peroneus tendons, the deep portions of the capsule are strongly bound to underlying connective tissue, the tibiotarsus itself, and the side of the tibial cartilage. The more superficial layers of the capsule surround the posterior side of the joint.

In some areas it is essentially impossible to de-

limit the boundaries of the capsule. This is true in the region of the anterior metatarsal groove and on the proximalmost or distalmost portions of the sides of the joint. There is a great amount of fibrous connective tissue covering the ligaments and tendons, and it cannot always be assumed that this also represents part of the capsule. The discussion of the microanatomy, below, should clarify many of the foregoing relationships.

LIGAMENTS

Numerous ligaments are associated with the intertarsal joint and are important during joint movement (Langer, 1859; Stolpe, 1932; Barnett, 1954a). Although the general features of their structure and function are known for several species of birds, a detailed description does not exist for any one species. Previous descriptions have emphasized the structure of the ligaments only with respect to the tarsometatarsus and tibiotarsus and have not stressed their relationships to other ligaments, the joint capsule, or the surrounding connective tissues. To this end it will be necessary to describe additional ligaments (or ligamentous connective tissues) which help to coordinate and integrate the functional aspects of the different joint structures. The ligaments of the intertarsal joint are as follows:

a. The lateral ligament (l lig; figs. 11, 12) is a broad and strong ligament situated beneath (medial to) the tendons of the peroneal muscles. The ligament extends from about the middle of the external face of the external condyle to the side of the external cotyla 1 or 2 mm. distad to its rim. The insertion on the tarsometatarsus is just disto-anterior to the insertion of the *M. peroneus brevis*.

Immediately anterior to the lateral ligament is another ligamentous band of connective tissue (called the accessory band by Barnett, 1954a). The accessory band is about one-half as wide as the lateral ligament and is noticeably thinner. It arises from the tibiotarsus slightly more distally than the lateral ligament and is joined to the latter by connective tissue. Some variation exists in the thickness of this tissue, and occasionally it appears that only one ligament is present. The accessory band does not insert upon the tarsometatarsus (if so, only a few fibers are involved) but turns medially at the level of the articular surfaces and contributes to the fibrous connective tissue anterior to the lateral meniscus.

The lateral ligament is separated from the lateral meniscus by a bursa. Proximoposteriorly, a triangular (fan-shaped) ligamentous band arises from the lateral ligament and passes posteriorly to merge with other connective tissue comprising the lateral tibial cartilage ligament.

b. The medial ligament (m lig; figs. 11, 12) arises as a narrow, strong band of fibrous tissue from the internal ligamental prominence and from the surface of the internal condyle immediately distal to the prominence. The ligament becomes broader and flatter as it crosses the articular surfaces. The ligament continues down the tarsometatarsus and inserts onto a ridge on the internal side of that bone. Actual insertion to the tarsometatarsus does not begin until a point about 4 mm. distal to the articular surfaces.

On the proximoposterior border of the medial ligament a large fan-shaped band of connective tissue arises and passes posteriorly to connect with the tibial cartilage.

c. Another ligament, named here the internal medial ligament, lies just below (lateral to) the medial ligament. Although the internal medial ligament is in part a continuation of the joint capsule, it is sufficiently distinct in both structure and function to warrant a separate name. The thin, broad ligament arises from the surface of the internal condyle distal to the ligamental prominence and the attachment of the medial ligament. The internal medial ligament is short and inserts onto the outer rim of the internal cotyla slightly proximad to the attachment of the medial cross ligament (see below). Anteriorly the fibers are continuous with the joint capsule covering the internal condyle. Disto-anteriorly, the fibers of the internal medial ligament sometimes intermingle with those of the medial cross ligament. Posteriorly, some of the fibers are not attached to the tarsometatarsus but to a strong fibrous band which arises from the most posterior portion of the outer rim of the internal cotyla and which contributes to the deep portion of the medial tibial-cartilage ligament.

d. The medial tibial-cartilage ligament has been mentioned briefly in the discussion of the joint capsule. The morphology of this ligament is complex since portions are intimately associated with the joint capsule, whereas other parts are free from the capsule.

At the proximal end of the tibiotarsus, beginning approximately 5 mm. from the base of the internal condyle, the ligament arises from the

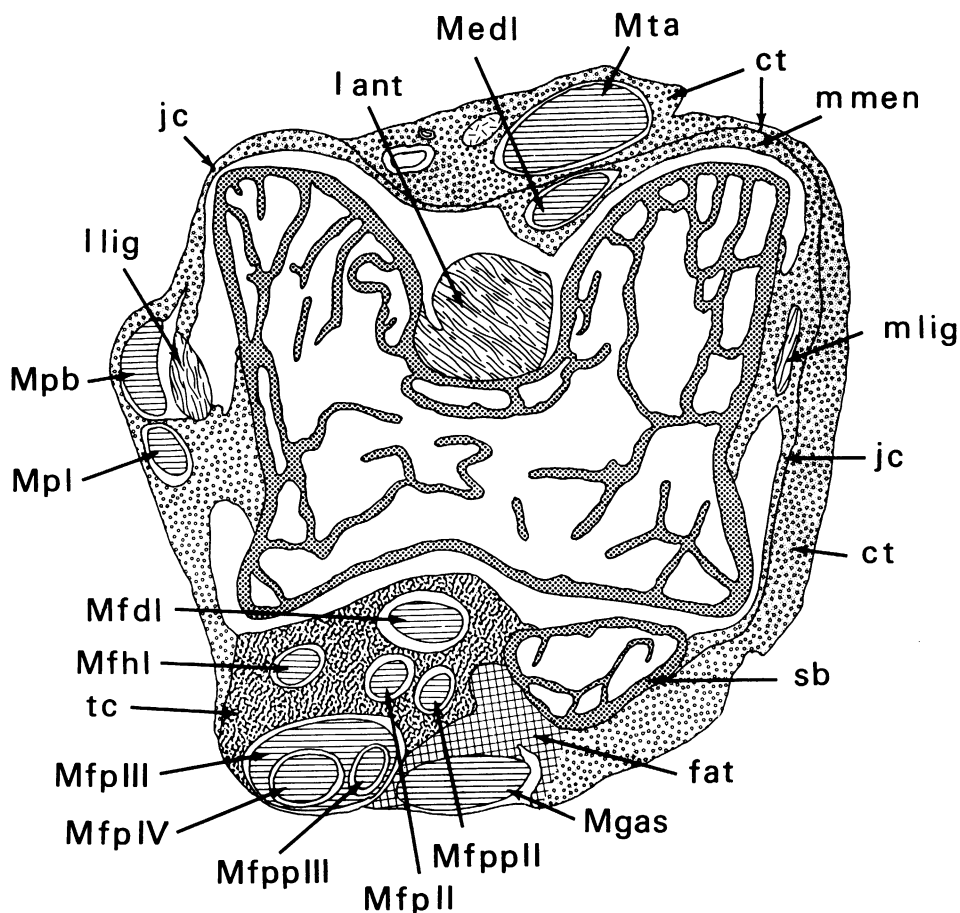


FIG. 12. Schematic diagram of histological cross section through intertarsal joint of *Columba livia* at level of distal end of tibiotarsus.

Abbreviations: ct, connective tissue; fat, fat pad; jc, joint capsule; l ant, ligamentum anticum; l lig, lateral ligament; M edl, M. extensor digitorum longus; N fdl, M. flexor digitorum longus; M fhl, M. flexor hallucis longus; M fpII, M. flexor perforatus digiti II; M fpIII, M. flexor perforatus digiti III; M fpIV, M. flexor perforatus digiti IV; M fppII, M. flexor perforatus et perforans digiti II; M fppIII, M. flexor perforatus et perforans digiti III; M gas, M. gastrocnemius; m lig, medial ligament; m men, medial meniscus; M pb, M. peroneus brevis; M pl, M. peroneus longus; sb, sesamoid bone; tc, tibial cartilage; M ta, M. tibialis anterior.

side of the bone near its anterior edge and also from the bone just proximad to the internal ligamental prominence. The origin from the medial ligament has already been described. The fibers that arise from the internal ligamental prominence lie just below the joint capsule and are intimately attached to it. The deeper fibers of the ligament arise from the internal condyle of the tibiotarsus posterior to the internal ligamental prominence and from the posteriormost areas of the outer rim of the internal cotyla. The

ligament attaches to the side of the tibial cartilage, but the superficial fibers pass over the posterior surface of the cartilage.

e. The lateral tibial-cartilage ligament is not as well defined as its medial counterpart. Proximally, the ligament takes origin from the proximoposterior border of the lateral ligament. These deeper fibers are covered, especially distally, by a mass of fibrous connective tissue, the latter of which includes the joint capsule. The deeper fibers originate directly from the external

condyle posterior to the attachment of the lateral ligament. Distally it is not possible to say whether any of the fibers of the ligament arise from the tarsometatarsus. In this region the overlying connective tissue is very thick, and the fibers are not regularly arranged. The ligament attaches to the side of the tibial cartilage.

f. The medial cross ligament ("mediales Kreuzband" of Stolpe, 1932, p. 171) arises, in part, from the side of the internal cotyla. In addition, fibers from the joint capsule contribute to the ligament. The medial cross ligament passes in front of the articular surfaces and then turns posteriorly. Medial to the tendon of *M. extensor digitorum longus* the ligament divides into two branches that surround the tendon. Distally, the fibers of both branches join together again on the lateral side of the tendon and become confluent with the joint capsule on that side. Proximally, the fibers of the superficial branch run posteriorly and attach to the supratendinal bridge of the tibiotarsus. The fibers of the deep branch turn into the anterior intercondylar fossa, lie against the internal condyle, and insert at the base of the distal opening of the supratendinal canal. In so doing, the deep branch forms a "runway" for the tendon of *M. extensor digitorum longus*.

g. The lateral cross ligament ("laterales Kreuzband" of Stolpe, 1932, p. 171) is less distinct than the medial cross ligament. It has its origin from the connective tissue attached to the anterior side of the lateral meniscus. This connective tissue is made up of fibers from the joint capsule and the accessory band of the lateral ligament. Although the cross ligament is indistinct at its origin, on the inner side of the lateral condyle the fibers are more dense and more regularly arranged. The more superficial fibers of the cross ligament insert onto the supratendinal bridge immediately lateral to the insertion of the superficial branch of the medial cross ligament. The deeper fibers insert at the medialmost part of the base of the external condyle.

The two cross ligaments are confluent with each other anteriorly by a thin portion of the joint capsule.

h. The ligamentum anticum ("intracapsular ligament" of Barnett, 1954a, p. 61) is short and strong. It passes from the tip of the intercotylar prominence to the distalmost portion of the anterior intercondylar fossa.

i. About 1 or 2 mm. lateral to the point

where the lateral meniscus attaches posteriorly to the tarsometatarsus, a ligament, the posterior meniscal ligament, arises from the dorsal surface of the meniscus. This thin, narrow ligament passes posteromedially to attach to the proximolateral base of the sesamoid bone. The posterior meniscal ligament is usually surrounded, above and below, by portions of the fat pad.

Most of the ligaments described above can be considered either as concentrations of fibrous connective tissue within the joint capsule or as derivations from it. Clear examples of the former are the medial and lateral cross ligaments and the tibial cartilage ligaments, all of which are not structurally distinct from the capsule in some places. The lateral and medial ligaments are fairly distinct from the capsule even though they might be connected to it in some way.

MENISCI

The lateral meniscus (1 men; fig. 13) attaches to the anterior rim of the external cotyla at the base of the intercotylar prominence. It then curves around the external and posterior rims of the cotyla to insert on to the most medial of two ridges that run obliquely backward from the intercotylar prominence.

In cross section the lateral meniscus is roughly triangular in shape throughout its entire length. Anteriorly, however, it is considerably flattened with the outer edge being only slightly elevated. Laterally and posterolaterally, the meniscus is greatly raised to form a wall around the cotyla. Posteriorly and posteromedially the meniscus again becomes flattened before its attachment to the medial ridge. In all portions of the cotyla, except perhaps the posterior part, the meniscus grades very smoothly into the surface of the cotyla. Indeed, sometimes the separation between the cotyla and meniscus is hardly noticeable.

At the anterior surface of the joint the lateral meniscus is joined to connective tissue that is continuous with the joint capsule. This union with the connective tissue is maintained until a position anterior to the lateral ligament. A bursa is interposed between the ligament and the meniscus. Posterior to the lateral ligament a branch of the capsule passes between the ligament and the tendon of *M. peroneus brevis* and attaches to the side of the lateral meniscus. On the posterolateral side of the cotyla a rather broad, fibrous band of connective tissue runs from the meniscus, behind the tendons of *M.*

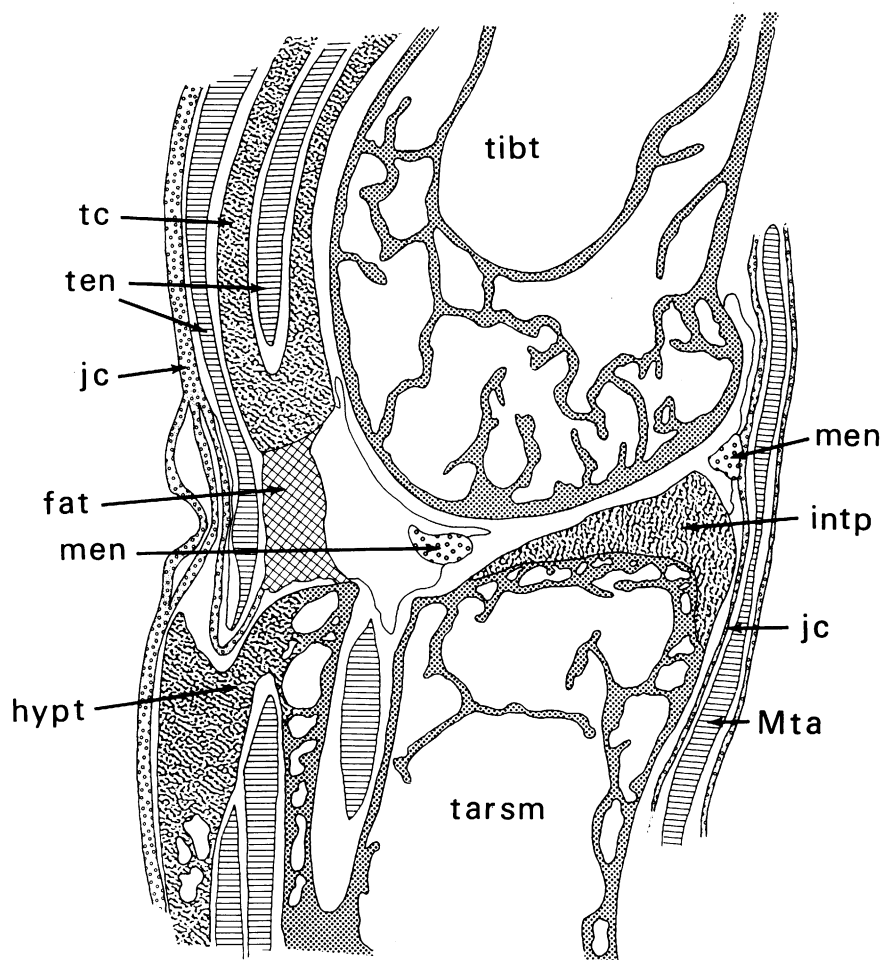


FIG. 13. Schematic diagram of histological parasagittal section through intertarsal joint of *Columba livia*.

Abbreviations: fat, fat pad; hypt, hypotarsus; intp, intercotylar prominence; jc, joint capsule; men, meniscus; M ta, M. tibialis anterior; tarsm, tarsometatarsus; tc, tibial cartilage; ten, flexor tendon; tib, tibiotarsus.

peroneus brevis and M. peroneus longus, and becomes confluent with the joint capsule.

The medial meniscus (m men; figs. 12, 14) is structurally quite different from the lateral meniscus and is much less complex. The medial meniscus originates from the outer rim of the internal cotyla. It passes around the anterior surface of the cotyla and terminates at the base of the intercotylar prominence. Unlike the lateral meniscus, the medial meniscus does not attach to the tarsometatarsus anteriorly. The joint capsule adheres closely to the outer side of the meniscus and at a point slightly lateral to the termination of the meniscus, the capsule divides

and surrounds the tendon of M. extensor digitorum longus.

Although the meniscus does form a wall to the anterior end of the cotyla, the meniscus itself is not truly triangular in shape. The meniscus does fit tightly against the cotyla.

FAT PAD

The fat pad (fat; figs. 11–13) is an irregularly lobed structure occupying a posterior position between the articular surfaces. The fat pad that is illustrated in most studies of the joint (Barnett, 1954a, p. 62; fig. 3) is, in reality, an anterior extension of the mass of fat between the end of

the tibial cartilage and the hypotarsus.

Between the articular surfaces there are two main lobes. The most proximal lobe is roughly oval in shape and is set at an oblique angle to the axis of the posterior intercondylar sulcus. This lobe is attached by strong connective tissue strands to the posterior edge of the lateral meniscus and to the dense fibrous tissue posterior

to the meniscus. The lobe is also connected to the posterior meniscal ligament and to part of the sesamoid bone.

A more distal lobe of the fat pad projects anteriorly beneath the posterior meniscal ligament.

Some variation exists in the shapes and sizes of the lobes, but it does not appear great.

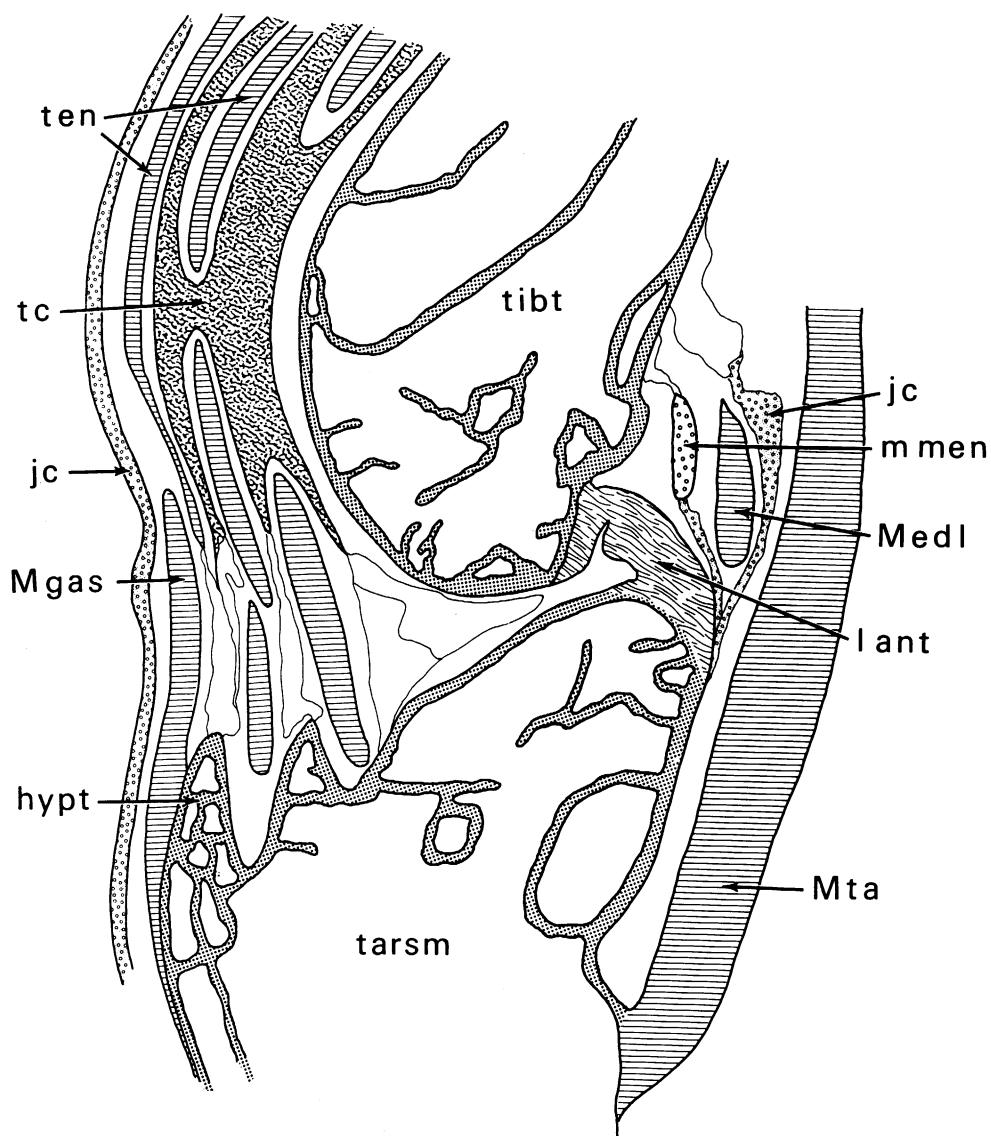


FIG. 14. Schematic diagram of histological midsagittal section through intertarsal joint of *Columba livia*.

Abbreviations: hypt, hypotarsus; jc, joint capsule; l ant, ligamentum anticum; M edl, M. extensor digitorum longus; M gas, M. gastrocnemius; m men, medial meniscus; M ta, M. tibialis anterior; tarsm, tarsometatarsus; tc, tibial cartilage; ten, flexor tendon; tib, tibiotarsus.

TIBIAL CARTILAGE AND INTERTARSAL SESAMOID BONE

The tibial cartilage (tc; figs. 12–14) is a small, curved piece of cartilage situated proximal to the hypotarsus and lying against the tibiotarsal condyles. The anterior surface of the cartilage is very smooth and has two longitudinal, shallow grooves separated by a small ridge. The medial groove is about one and one-half times as wide as the lateral one. The grooves and ridge closely approximate the contour of the posterior intercondylar sulcus.

On the posterior surface of the cartilage the medial side has a broad and deep longitudinal groove for the tendon of *M. gastrocnemius*. The lateral side of the posterior surface also has a broad and deep groove for the tendon of *M. flexor perforatus digiti III* (and its two associated tendons). Anteriorly the cartilage is perforated by four canals for the other “flexor” tendons.

The intertarsal sesamoid bone (sb; figs. 11–12) is situated at the distomedial end of the tibial cartilage. In addition to its attachment with the posterior meniscal ligament, the sesamoid also has a short, broad, and heavy ligament running laterally from its inner (lateral) side to the anterodistal edge of the tibial cartilage. Proximally the sesamoid gradually becomes more cartilaginous and confluent with the tibial cartilage. At the distal end of the sesamoid a short ligament attaches to the posterior side of the tarsometatarsus below the rim of the internal cotyla.

MICROANATOMY

ARTICULAR CARTILAGE: Seen in cross section, the articular cartilage of the tibiotarsus varies in thickness with its position on the bone. Anteriorly, the cartilage is about equal in thickness over the main articular surface of both the condyles. The cartilage decreases in thickness as it passes into the anterior intercondylar fossa, and the chondrocytes become smaller. Likewise, the ratio of chondrocytes to interstitial substance decreases in the fossa, and at the deepest part the tissue is composed of great amounts of collagenous fibers.

Posteriorly, the articular cartilage decreases in thickness from the medial to the lateral side. This decrease is related to the fact that the articular cartilage that is in direct apposition to the sesamoid bone is thicker than that cartilage in apposition to the tibial cartilage. Medially the cartilage has a superficial, densely staining zone and a

lighter basal zone; only the densely staining zone persists laterally.

In cross section the collagenous fibers form a meshwork without any distinct orientation.

In sagittal section, other patterns of the articular cartilage are evident. At the anterior-most end of the condyles the cartilage is present only as a thin layer. The cartilage is thickest disto-anteriorly and gradually becomes thinner posteriorly. In the area of thickest cartilage, the chondrocytes are large and round basally, but toward the surface they become more compressed. The amount of collagenous interstitial substance increases toward the surface. Basally, the cartilage has thick bands of collagenous tissue running into the underlying bony matrix and oriented perpendicular to the articular surface. The structure of the bands is less distinct at the surface of the cartilage because of the bands heavy concentration, but there is a tendency for them to orient parallel to the joint surface.

Compared with that of the tibiotarsus, the articular cartilage of the tarsometatarsus is considerably thicker. When cut in longitudinal section, the cartilage is seen to be thickest in the central and anterior portions of the bone and less so posteriorly. The thickest portion of the cartilage is about five or six times as thick as that of the tibiotarsus. The chondrocytes seem smaller at the joint surface, but this may be the result of compression and flattening which takes place there. As with the cartilage of the tibiotarsus, the amount of fibrous interstitial substance is apparently greater at the surface. Basally, the collagenous tissue is oriented perpendicular to the articular surface, but this orientation becomes less distinct at the surface. Anteriorly, collagenous bundles are much more numerous undoubtedly as a response to the tensile forces applied to the tarsometatarsus by the ligamentum anticum.

JOINT CAPSULE: On the medial side of the sesamoid bone the collagenous bundles of the capsule are confluent with the matrix of the sesamoid, and the substance of this interface is oriented in an anterior direction nearly parallel to the capsule itself. More posteriorly, the capsule and sesamoid are more distinct and have less intermingling of their tissues. In a cross section at the level of the articular surfaces, the sesamoid is confluent with the tibial cartilage. At this level the joint capsule also is in some cases attached to the anterior side of the sesamoid bone but is thin

and distinct histologically from the bone. If cross sections are more distally situated, the capsule is absent from the anterior side and replaced by a thin layer of fibrocartilage.

The joint capsule is thick and dense as it curves around the posteromedial corner of the tibiotarsus. On the anteromedial side, however, the tissue of the capsule becomes less dense, and the inner portion has a broad attachment with the side of the tibiotarsus (here the "capsule" also includes the medial tibial cartilage ligament). Within the joint capsule the boundaries of the medial ligament are not easily delimited from the capsule, although the tissue of the ligament is more organized into bundles (cut in cross section) and not into anteroposteriorly directed fibers as is the capsule proper. Anteriorly over the internal condyle, the capsule has a dense internal layer and a rather loose outer layer. When the cross section is through the plane of the articulation, the dense zone (now recognized as the medial meniscus) becomes considerably larger. The meniscus is composed of a posterior, highly cartilaginous layer and a more anterior collagenous portion. The posterior portion consists of numerous chondrocytes with intervening collagenous bundles oriented in a lateromedial direction. The cartilage is thicker medially than it is laterally. Chondrocytes are absent anteriorly, and the meniscus here is composed entirely of lateromedially oriented collagenous bundles.

Medial to the tendon of *M. extensor digitorum longus* the capsule is thick and divides into two thinner layers which surround the tendon. On the lateral side of the tendon the capsule again becomes thick and dense but soon becomes thin laterally. Around the external condyle the capsule is composed of dense tissue, but this becomes slightly less dense shortly after it passes onto the lateral side of the tibiotarsus. The capsule of the lateral side (including the lateral tibial cartilage ligament) attaches to the tibiotarsus. The capsule of the lateral side is more distinct histologically from the peroneal tendons and lateral ligament than it was from the medial ligament. The tendons are enclosed within canals and are surrounded by the capsule. The anterior edge of the lateral ligament is confluent with the capsule, but the two structures are separated from each other more posteriorly.

Posterior to the peroneal tendons the capsule is moderately dense and becomes confluent with

the anterolateral edge of the tibial cartilage. If there are actually portions of the capsule present on the lateral side of the tibial cartilage, they are very thin and closely bound to it. A thin, dense strand of the capsule surrounds the posterior side of the joint, connecting the lateral edge of the tibial cartilage and the medial side of the sesamoid bone.

FAT PAD: As seen in longitudinal section, the fat pad attaches to the distal end of the tibial cartilage, the fibrous tissue of the cartilage being continuous with the fibrous tissue of the fat pad. Distally the pad attaches to the hypotarsus. Fat cells appear more numerous posteriorly, whereas anteriorly the pad is composed of greater quantities of very loose fibrous tissue.

A cross section at the level of the joint articulation (just distal to the tibial cartilage) reveals that the tendons are surrounded by the fat pad. The fibrous tissue of the pad is arranged into thin, densely organized layers encircling the tendons. Medially, the fat pad joins the sesamoid bone and posteromedially grades into the loose fibrous tissue lying external to the joint capsule. Laterally, the fat pad runs into the connective tissue comprising the joint capsule and into the tissue surrounding the capsule.

TIBIAL CARTILAGE: The tibial cartilage is typical fibrocartilage, consisting of many chondrocytes which are surrounded by a meshwork of collagenous bundles. In general, there is little definite orientation of the collagenous bundles. The outer edges of the cartilage and those portions forming the edges of the tendon canals are organized into thin, deeply staining layers. In these layers the chondrocytes are smaller, flattened, and less numerous than they are in the main portion of the cartilage.

In cross section, occasional proximodistally oriented collagenous bundles are found scattered throughout the cartilage. Although these are not clearly concentrated in any one area of the cartilage (except perhaps posteriorly near the sesamoid bone), they are seemingly situated nearer to the tendinal canals than to the middle of the cartilage itself.

TENDONS: All of the tendons, with the exception of that of *M. flexor perforatus digiti III*, consist of densely packed collagenous bundles. The latter tendon is structurally intermediate between the tibial cartilage and the more typical tendon. Numerous large collagenous bundles are scattered (not packed) within a cartilaginous

matrix and an intertwining network of collagenous strands. Unlike the tibial cartilage, the collagenous bundles are the dominant part of the tendon, and the chondrocytes occupy the spaces between the bundles. Laterally, the tendon consists almost entirely of the bundles, and the chondrocytes are lost. That portion of the tendon surrounding the canals for the tendons of *M. flexor perforans et perforatus digiti III* and *M. flexor perforatus digiti IV* is organized into a narrow, densely staining zone of flattened chon-

drocytes and circularly arranged (around the canal) collagenous strands.

The anterior edges of some tendons, notably those of *M. flexor perforans et perforatus digiti III*, *M. flexor perforatus digiti IV*, and *M. flexor digitorum longus*, consist of a thin zone of fibrocartilage. The chondrocytes are small and flattened, and thin strands of collagenous tissue are arranged circularly. In other respects these tendons have the typical structure of densely packed bundles.

FUNCTIONAL ANALYSIS OF THE INTERTARSAL JOINT

TYPES OF MOTION

Unless specified otherwise, all statements about the types of motion in the intertarsal joint are made with reference to a stationary tarsometatarsus. Like the tibiotarsus, the tarsometatarsus is also moving during locomotion relative to, say, the femur, but for this analysis, the tarsometatarsus is considered stationary.

As the types of motion in the intertarsal joint are the same as those of the knee, they can be defined with respect to the same axes and planes.

a. Flexion-extension: The angle of flexion-extension is measured as in the knee joint except that the measurement is along the anterior side of the joint.

b. Lateral-medial rotation: A lateral rotation refers to a turning of the anterior end of the tibiotarsal condyles toward the lateral surface of the leg; a medial rotation is a turning toward the medial surface of the leg.

c. Lateral-medial swing: A lateral swing will be one in which the proximal end of the tibiotarsus moves laterally; in a medial swing the tibiotarsus moves medially.

d. Translation: The same types—anteroposterior and lateromedial—are present as in the knee joint.

FLEXION-EXTENSION

Probably the most important limiting factor to flexion of the intertarsal joint during normal locomotion is the coordination of different groups of muscles. Detailed treatment of this aspect of joint function will be deferred to the discussion on muscles (see below).

That the muscles play the largest role in limiting joint flexion is reflected in the decided lack

of joint structures that could limit flexion. The medial ligament is loose throughout most of the flexion cycle, but at full flexion (when tibiotarsus and tarsometatarsus are parallel) some of the fibers become taut. Even then the ligament cannot be regarded as limiting flexion simply because the joint cannot be flexed farther. Similarly, the lateral and medial tibial cartilage ligaments possess some fibers that become taut at full flexion. In terms of the mechanics of the joint, it is impossible for the joint to be "hyperflexed." It is possible on living animals to flex the joint so that the tibiotarsus and tarsometatarsus lie against each other and are parallel. Obviously, however, this never happens in nature.

The joint can be extended to about 165 to 170 degrees in a living specimen before noticeable resistance is met; this point is termed "full extension" in the discussion below. Motion-picture analysis shows that this is also about the normal degree of extension during the act of walking. The joint can be forcibly extended farther, even slightly beyond 180 degrees in rare cases, but this amount of extension seldom occurs in nature. During walking, the joint is usually not flexed below a minimum of 50 to 60 degrees. Probably, flexion rarely reaches 30 or 40 degrees under natural conditions (this will be discussed in the section on motion-picture analysis).

Many joint structures are involved with limiting extension, and each is dealt with separately. In doing this I am not implying a more important role to any one structure for they all seem to function simultaneously.

As extension proceeds, the capsule covering the anterior surfaces of the external and internal

condyles is increasingly extended until it becomes taut at full extension. The portion of the capsule between the condyles does not become taut during extension. The capsule over the condyles is thick and strong, whereas between the condyles it is thin; the thickness of the capsule and the maximum amount of force being transmitted by the capsule are obviously correlated. When the capsules over the condyles are cut, some additional extension is possible, but it amounts to a few degrees at most.

The lateral ligament also functions to limit extension. Although it is at no time truly loose during the flexion-extension cycle, the ligament certainly is transmitting the greatest force at full extension, and as the joint begins to flex, the ligament becomes less taut. Cutting the lateral ligament does not appear to increase extension significantly, but it does have an effect on other kinds of movement (see below).

Like the lateral ligament, the medial ligament is very taut at full extension and slackens with the beginning of flexion. Furthermore, the ligament remains fairly taut in all positions of the joint. If the medial ligament is cut, somewhat more extension is possible.

Because it is broad and attached over a great area, the internal medial ligament has a somewhat more complex role in limiting extension. This ligament is taut only at the position of full extension. With flexion, the ligament becomes loose and remains so to a greater degree than does the medial ligament and at the same angle of flexion. The fibers of the internal medial ligament broadly insert onto the tibiotarsus and hence transmit force unevenly over the ligament at different times during the flexion-extension cycle. As the anterior end of the internal condyle moves forward during extension, the fibers of the ligament that insert in this area are the first to become taut and at full extension are transmitting more force than the posterior fibers. Some of the posterior fibers may not be taut at any part of the flexion-extension cycle.

The cross ligaments, as they are actually part of the joint capsule, become taut only when the joint is in full extension.

The lateral tibial-cartilage ligament is fan-shaped; hence the fibers will transmit force differentially during the flexion-extension cycle. At the position of full extension only about the distal one-third of the fibers are taut, whereas the proximal two-thirds of the fibers are very loose.

The fiber arrangement of the medial tibial-cartilage ligament is different from that of the preceding ligament. The distalmost portion of the ligament has fibers that are nearly at right angles to those located more posteriorly. Thus, at the position of full extension it is the more proximal fibers that are taut, whereas the distal fibers are loose or only slightly taut.

The ligamentum anticum is a strong ligament that plays an important role in limiting extension.

ROTATION

The amount of lateral or medial rotation is related to the position of the joint in the flexion-extension cycle. Considerable individual variation in the amount of rotation exists at any given position of flexion, and average figures are rather meaningless. There are, however, several generalities regarding the degree of rotation. Rotational movement is minimal when the joint is in the fully extended position. As flexion proceeds, rotation becomes increasingly possible and rotation through an arc of about 35 to 40 degrees takes place.

Lateral rotation of the tibiotarsus upon the tarsometatarsus is resisted by several joint structures. As the external condyle of the tibiotarsus rotates anteromedially over the external cotyla, the lateral ligament becomes taut and moves anteriorly a short distance. Simultaneously, the capsule covering the internal condyle becomes taut as does the medial cross ligament. One of the most important limiting factors is the internal medial ligament that becomes very taut with rotation. Twisting of the ligamentum anticum also probably plays a role in reducing lateral rotation. When the above structures are cut, either singularly or in combination, the amount of lateral rotation is increased.

Medial rotation of the tibiotarsus is prevented by the same types of structures as is lateral rotation. With medial rotation, the capsule over the external condyle and the lateral cross ligament become taut. The lateral ligament appears to resist medial rotation as it is taut and moves posteriorly relative to the external condyle. Interestingly, the medial ligament also resists medial motion (especially near full extension), and when it is cut the amount of this motion increases perceptively. The anteriormost fibers of the internal medial ligament contribute to limiting medial rotation. Again, the ligamentum

anticum no doubt resists rotation.

That lateral and medial rotation is significantly reduced at full extension can be easily explained in terms of the joint structures mentioned above. At full extension almost all of those structures that limit rotation are also limiting extension and are taut. Therefore, any tension applied to them by rotary forces would be immediately resisted. During flexion, the structures are loose and not transmitting force, and thus greater rotation is possible before they become taut.

LATERAL-MEDIAL SWINGING

At full extension essentially no swing takes place. As flexion proceeds, more swing occurs, but never is the amount more than 10 or 15 degrees.

The capsule over the internal condyle and the medial and internal medial ligaments function to prevent abnormal lateral swinging. The ligaments are especially important in preventing swinging movements when the joint is in the flexed position. During flexion the medial ligament is loose but becomes taut when the joint undergoes lateral swinging.

The corresponding features on the lateral side of the joint likewise resist medial swinging of the tibiotarsus. These features include the joint capsule over the external condyle, the accessory band, and the lateral ligament, all of which are taut with medial swinging.

The ligamentum anticum and, to a lesser degree, the cross ligaments contribute to resisting swinging.

TRANSLATION (SLIDING)

There is very little lateromedial sliding of the tibiotarsus even in a flexed position. In addition to the resistance offered by the shapes of the condyles and cotylae themselves, the ligamentum anticum and the joint capsule seem to be the most important features in limiting lateromedial sliding. Lateral sliding is prevented also by the short internal medial ligament. Lateromedial sliding is not affected significantly by cutting either the lateral or medial ligament. Considerably more anteroposterior sliding is possible than is lateromedial, but still the former is small in absolute distance. Sliding of the tibiotarsus in an anterior direction is greater than that in a posterior direction. As the tibiotarsus slides anteriorly, the capsule over the condyles

becomes taut, but motion of the tibiotarsus is halted before the capsule is fully taut. The ligamentum anticum prevents the forward sliding. Likewise, the ligamentum anticum is probably the major factor in limiting posteriorly directed sliding.

Somewhat greater sliding is possible in a flexed joint than in a fully extended one, since in the latter the taut joint structures contribute to preventing any motions of the tibiotarsus.

MENISCI

To study the movements of the menisci considerable dissection is required before they are exposed for observation. Structures that are intimately associated with the menisci, for example, the lateral ligament, some tendons, cross ligaments, and the joint capsule, sometimes have to be cut or modified so that the menisci can be seen. As a result of this procedure conclusions regarding the function of the menisci have to be made with great care.

During flexion, the anterior end of the external condyle moves distoposteriorly and hence slides over the posterior surface of the lateral meniscus surrounding the anterior rim of the external cotyla. Flexion of the tibiotarsus forces the meniscus forward, but because of its attachment posterolaterally to the joint capsule and to the tarsometatarsus, the meniscus is eventually prevented from moving forward. It can be suggested that the meniscus, in this case, helps to resist flexion of the tibiotarsus (other possible roles of menisci are reviewed later in the present paper). When the posterolateral attachment of the meniscus is cut, it does seem that flexion of the joint is easier simply because the meniscus can now move more anteriorly. It is clear that by cutting the attachment, the shape of the meniscus is destroyed.

The posterior meniscal ligament is apparently not involved in the above mechanism, and it is difficult to see what role this ligament plays in joint movement. It does become taut as the meniscus moves forward but is not situated so as to prevent the forward motion to any degree. The posterior meniscal ligament could function to prevent excessive lateral movement of the meniscus, or it could hinder medial movement of the sesamoid bone and consequently the tibial cartilage.

The medial meniscus does not have the same type of movement as does the lateral meniscus.

The former does not rest on the proximal surface of the cotyla as does the latter but is along the outer and anterior sides of the internal cotyla. Furthermore, the medial meniscus appears to be not much more than a feature strengthening the

joint capsule. It can be questioned whether the medial meniscus ever transmits much force, as it will be recalled that at its anterior end it is continuous with the very thin part of the joint capsule, covering the intercondylar area of the joint.

TARSOMETATARSAL-PHALANGEAL JOINTS

The articular structures of the avian foot have received little attention in the anatomical literature. Steinbacher (1935) studied the functional anatomy of the foot in a variety of birds. He included excellent discussions of the joint surfaces, joint ligaments, and tendons but did not mention the joint capsule in any detail. Schaffer's work (1903) remains the best treatment of the histological structure of the interphalangeal joints, although Lubosch (1910) also dealt briefly with this subject.

LIGAMENTS OF THE FOOT

In the following discussion I have not formally named the ligaments. It would be less efficient to apply lengthy, topographical or descriptive names than to give the ligaments letter designations. Steinbacher (1935) apparently believed this too as he also did not apply formal names. Furthermore, it seems best to wait until a comprehensive investigation of ligament homology is completed.

Three main ligaments are present on the ventral side of the foot in individuals of *Columba*:

1. Ligament a. This rather narrow ligament originates from the lateral side of trochlea IV just below the tendon of M. abductor digiti IV. It runs proximoposteriorly and attaches to the lateral process of metatarsal I and to the proximalmost portion of the lateral side of phalanx I.

As the hallux moves medially, the ligament becomes taut and prevents farther motion. Ligament a is important in restricting medial motion of the hallux and in protecting against accidental disruption of the tarsometatarsal-metatarsal I joint.

2. Ligament b. This ligament attaches to the proximalmost portion of the lateral side of phalanx I, digit IV. It curves ventrally around phalanx I and passes medially to attach to the proximalmost portion of the ventrolateral side of phalanx I, digit III. Ligament b then crosses

the bottom of the foot and attaches to the proximalmost part of the medial side of phalanx I, digit II. Ligament b is a broad ligamentous sheet, and the above represent its three major attachments. There are several less well-defined attachments. One is to the connective tissue associated with the insertion of ligament a to the lateral side of phalanx I, digit IV. Several strands of fibrous connective tissue connect ligament b with this area, and the attachment is strong. Ligament b is also connected to very strong fibrous connective tissue lying between the bases of digits II and III. The ligament has additional attachments with connective tissue between digits I and IV.

Between ligament b and the skin of the foot lies a large, fibrous, connective tissue pad. Much of this is loose and easily removed, but other parts are very tough and strongly connected to the surface of the underlying (but dorsal) ligament b. The pad provides a cushion and structural protection for the tendons of the tarsometatarsal-phalangeal joints. Ligament b almost certainly functions to separate the tendons from the connective tissue pad so that the former can operate freely. Only small amounts of very loose fat lie between the tendons and ligament b.

3. Ligament c. This ligament attaches to the anterior and medial sides of the metatarsal I-phalanx I joint. It runs to digit II and attaches to the medial side of the trochlea II-phalanx I joint. Ligament c is continuous laterally with the connective tissue attached to ligament b.

Ligament c acts to prevent the hallux from moving laterally and also limits the amount of extension of the hallux.

MORPHOLOGY OF THE JOINTS

The tarsometatarsal-phalangeal joints of *Columba* are all very similar in structure and will be described together.

JOINT CAPSULE: Anteriorly, the capsule attaches to the base of the trochlea and extends

distally to insert onto the postermost portion of the first phalanx of each digit. The capsule is thin anteriorly. The tendon of *M. extensor proprius digiti III* is incorporated into the joint capsule of the third digit. Laterally and medially the capsule arises from the posterior portion of the depressions on the sides of the trochlea. Here the capsule is thick and confluent with the side ligaments which run from the depressions of the trochleae to the sides of the proximal ends of the first phalanges. Posteriorly (ventrally) the capsule attaches to the sides of the subarticular cartilages.

SUBARTICULAR CARTILAGES: On the ventral side of each tarsometatarsal-phalangeal joint (except digit I) is a large cartilaginous structure. Distally, it is attached to the proximal end of the first phalanx. The cartilages are joined to the joint by the joint capsule. The proximal ends of the cartilages of digits III and IV serve as the points of insertion for the *M. lumbricalis*. The posterior (ventral) side of each cartilage has a large groove for the flexor tendons of the digit. A strong tendon sheath holds the tendons within the groove as they pass over the joint.

FUNCTIONAL ANALYSIS

MOVEMENTS OF THE JOINTS: The hallux can be extended parallel to the tarsometatarsus, then flexed forward about 160 to 170 degrees. The

hallux can also describe a lateromedial arc of about 90 to 100 degrees.

Digits II and IV can flex and extend through an arc of nearly 180 degrees. Digit III exhibits somewhat less flexion-extension movement (about 150 degrees) than the other digits.

Digit IV can move laterally through an arc of approximately 70 to 75 degrees, whereas digit II can move medially about 65 to 70 degrees. Digit III shows very little lateromedial movement, less than 10 degrees. Digits I, II, and IV exhibit significant amounts of rotational movement, but this is greatly reduced in digit III.

The degree of flexion in the intertarsal joint has some effect on the amount of movement at the tarsometatarsal-phalangeal joints. At full flexion of the intertarsal joint, dorsal movement of the digits is more restricted as might be expected. Also, lateral movement of digit IV and medial movement of digit II are reduced.

LIMITS TO MOVEMENT: Probably the greatest factor limiting movement at the tarsometatarsal joints is the action of the muscles. The shapes of the joint surfaces of the trochleae for digits II and IV obviously permit a greater freedom of movement than does the surface of the middle (III) trochlea. The movement of the third digit is confined more in the plane of flexion-extension.

The side ligaments limit the amount of movement in the lateromedial direction, and the

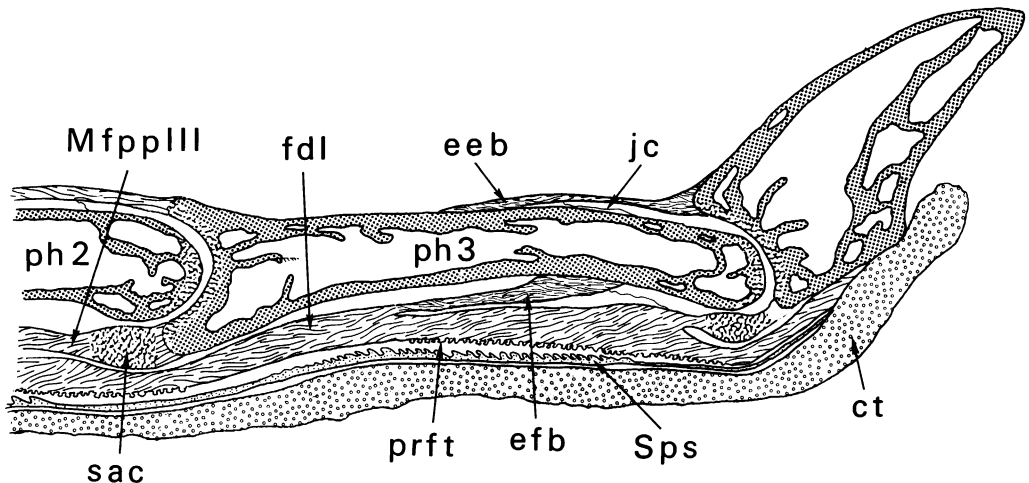


FIG. 15. Schematic diagram of histological saggital section through distal end of digit III of *Columba livia* to show interphalangeal joints.

Abbreviations: ct, connective tissue; eeb, elastic extensor band; efb, elastic flexor band; jc, joint capsule; M fdl, *M. flexor digitorum longus*; M fppIII, *M. flexor perforatus et perforans digiti III*; ph 2, phalanx 2; ph 3, phalanx 3; pr ft, protuberances on flexor tendon; sac, subarticular cartilage; Sps, "Sperrschneiden" of Schaffer, 1903.

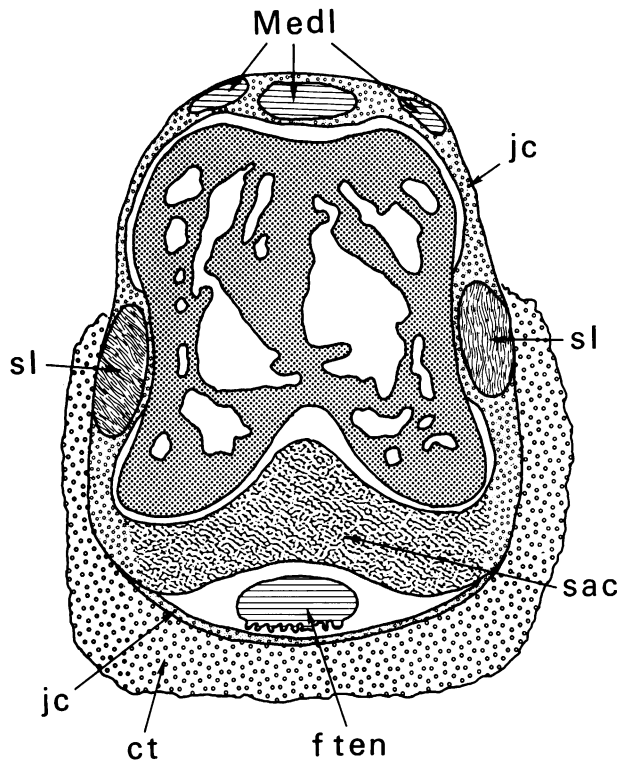


FIG. 16. Schematic diagram of histological cross section through an interphalangeal joint of *Columba livia*.

Abbreviations: ct, connective tissue; f ten, flexor tendon; jc, joint capsule; Medl, M. extensor digitorum longus; sac, subarticular cartilage; sl, side ligament.

movement is increased when a ligament is cut.

The joint capsule plays little role in effecting movements of the first phalanx of each digit. Anteriorly, the capsule is thin, and laterally, medially, and ventrally the capsule is "replaced" by the side ligaments and subarticular cartilages.

The latter clearly serve to form channels for the distribution of the flexor tendons. The cartilages of digits III and IV also increase the moment arm and hence the possible torque of M. lumbricalis. This is almost certainly a secondary role.

INTERPHALANGEAL JOINTS

MORPHOLOGY OF THE JOINT

The interphalangeal joints are all similar morphologically and need only be described once. Schaffer (1903) and Lubosch (1910) discussed the histology of the joints.

The joint capsule (jc; figs. 15, 16) is structurally similar to those of the tarsometatarsal joints. It arises from the base of the trochlea of the proximal phalanx and extends distally to insert onto the proximalmost edge of the next phalanx.

Laterally and medially the capsule is confluent with the side ligaments. The latter arise from the depressions on the sides of the trochleae and attach distally to the side of the next phalanx. Ventrally, the ligaments (capsule) are continuous with the sides of the subarticular cartilages. Dorsally, the capsule may incorporate one or more branches of the tendons of M. extensor digitorum longus. The branch of the tendon that inserts onto the distal phalanx of the joint is

intimately a part of the joint capsule. However, if the branch continues distally to the next interphalangeal joint, it is enclosed within a "canal" on the surface of the capsule.

The subarticular cartilage (sac; figs. 15, 16) is a fibrocartilaginous enlargement at the end of one of the flexor tendons; it is not a separate entity as in the tarsometatarsal joint. The "cartilages" are present at all interphalangeal joints, but they vary in size and in the amounts of chondrocytes present. These cartilages are the sesamoid bones mentioned by Richardson (1942, p. 350) and other authors. In *Columba* very little ossification takes place and is usually absent.

Associated with the last interphalangeal joint of each digit is the well-known elastic extensor band (eeb; fig. 15). The band runs from the

proximal end of the dorsal (anterior) side of the claw and attaches to the dorsal surface of the next proximal phalanx.

FUNCTIONAL ANALYSIS

MOVEMENTS OF THE INTERPHALANGEAL JOINT:

Considerable movements in all three planes are possible. Rotation around the long axes of the phalanges is also observable.

LIMITS TO MOVEMENTS: As in the tarsometatarsal joint, muscles probably play the major role of limiting motion; this is certainly true with flexion and extension. Lateral and medial swing is hindered by the side ligaments. Rotation is limited by the ligaments and the remaining parts of the capsule.

MORPHOLOGY OF THE HIND-LIMB MUSCLES

INTRODUCTION

THIS SECTION INCLUDES a description of the hind-limb muscles; a discussion of their functional analysis is deferred to the subsequent section. The description of each muscle is divided into three topics. First, under general description, the origins and insertions will be given. As much of these data have already been published (George and Berger, 1966, pp. 380-464), I will include only those aspects that are necessary for an understanding of the functional analysis. Several other workers (Haswell, 1880, 1883; Berlin, 1963) have examined the leg musculature of *Columba livia*, but these studies were restricted to a small portion of the total musculature or dealt with problems of taxonomic interest.

The second heading, fiber arrangement, includes data on the structure of the aponeuroses of origin and insertion, the pattern of the fibers in relation to the aponeuroses, the angle of pinnation, and the relative length of the fibers. It is necessary to point out that the use of the term "fiber" in morphological studies of bone-muscle systems is actually in reference to a muscle fasciculus, that is, a group of muscle fibers enclosed within a connective tissue sheath. Muscle fasciculi contain a variable number of muscle fibers, and these can sometimes pass from one fasciculus to another (Huber, 1916). Furthermore, it seems clear that muscle fibers do not necessarily extend the length of the fasciculus (Huber, 1916; Clark, 1931; van Harreveld, 1947). In the present study, I use the term "fiber" in its conventional meaning, fully realizing that a "fasciculus" is the correct morphological unit under consideration. Also, it will be assumed that the fibers extend the length of the fasciculus so that comparative measurements of fiber length will have some meaning in terms of whole muscle function. Unfortunately, histological studies that can provide information about the relation of fiber length to fasciculus length in pigeon hind-limb muscles are lacking. An additional assumption is that the number of fasciculi is a reliable index of the number of fibers.

Four major patterns of fiber arrangement are recognized. Quite obviously there are morpho-

logical intermediates between the different patterns, and a designation of a particular pattern is sometimes arbitrary. A muscle is considered to have a parallel arrangement when the fibers extend (or nearly extend) the length of the muscle, that is, from the origin to the insertion. Typically, aponeuroses of origin and insertion are lacking in parallel muscles. A unipinnate fiber arrangement is one in which the fibers are shorter than the length of the muscle (excluding tendinous portions). An aponeurosis of insertion is always present. An aponeurosis of origin may be, but is not necessarily, present. Although the fibers are arranged in parallel, their line of force is not parallel to the plane (or axis) of the tendon of insertion as is true in a parallel muscle. In a bipinnate muscle the fibers insert onto a central tendon from two sides. When considering small muscles, the distinction between a bipinnate and unipinnate arrangement is particularly difficult to define. If the tendon of insertion is narrow, the fiber pattern is bipinnate, whereas if the tendon is broad (approaches what might be called an aponeurosis), the pattern becomes more nearly unipinnate. The fourth fiber arrangement, radial, has fibers organized in a circle around a central tendon.

The angle of pinnation was measured by making a drawing using a camera lucida and then taking the measurement from the drawing. It was not possible to make accurate measurements of some muscles, either because the angle of pinnation was so small as to be almost parallel or because certain characteristics of the muscle such as size, shape, or the presence of tough aponeuroses permitted only arbitrary measurements to be taken. The angles of pinnation were measured on fresh specimens and on muscles that were assumed to be in their "normal resting position," that is, were not considered to be either stretched or contracted. It is sometimes difficult to recognize the "normal resting position" of a muscle, but the measurements are to be interpreted as general estimates. The angle of pinnation can vary tremendously within a muscle, and much more physiological and morphological work will need to be done on single

muscles to evaluate the significance of this variation. Measurements were made in different parts of the muscle (or along the central tendon if the muscle was bipinnate) and then averaged.

The lengths of fibers were measured on preserved muscles of legs that were fixed in a standing position. In the following descriptions the length of the fiber is expressed as a proportion of the total length of the muscle. The measurement expressed in this manner has several advantages. It allows an estimate of the fiber length of a muscle within a species irrespective of size. Later, when comparative studies are undertaken such a measurement will permit comparisons of muscles in birds of wholly different sizes and habits. Relative lengths of fibers can also be an indirect measurement of the angle of pinnation and of the relative number of fibers. The angle of pinnation would become smaller as the fiber length approaches that of the muscle. And, for a given shape of a muscle, more fibers can be added as the angle of pinnation increases. Absolute measurements of fiber length have a bearing on certain functional characteristics of muscle. However, absolute fiber lengths are not given in the descriptions as they are easily calculable from the measurements. Where absolute lengths are considered important, these will be discussed in the functional analysis. Measurements of the length of the muscle are for the maximum length of the contractile material and do not include aponeuroses or tendons. The figures given for relative fiber lengths are averages for fibers measured on several different muscles and for numerous fibers within a muscle. It was not possible to measure a given number of fibers within each muscle as some of the latter are difficult to measure. Moreover, it was not always possible to determine where fibers terminated and where their thin, tendinous ends began. In terms of the functional analysis of whole muscles given below, the measurements represent reasonable indexes to fiber length and as such will permit a number of useful functional comparisons between different muscles and between muscles in different species of birds.

No significant difference was found between relative fiber lengths of fixed and fresh material. Some shrinkage certainly takes place with fixation, but this is probably rather uniform throughout the muscle. Moreover, such shrinkage would be very difficult to detect unless measurements were made on birds of equal size.

Because of the flaccid and opaque nature of fresh material, measurements on preserved material are easier and probably more accurate.

The third heading, fiber histology, includes data on the percentage of twitch and tonus fibers in the muscle. Twitch (=fibrillenstruktur) and tonus (=felderstruktur) fibers are most easily differentiated with the use of the electron microscope (Hess, 1960, 1970; Peachey and Huxley, 1962; Page, 1965). These fibers are much more difficult to identify in light microscopy, but this is the technique most likely to be used by vertebrate morphologists who are studying problems of locomotion. Twitch fibers have a well-developed sarcotubular system, which tends to separate the fibrils and thus results in a punctate or fibrillar pattern in cross section. Tonus fibers lack a well-developed sarcotubular system, and thus when fixed, the "fibrils" coalesce together into irregular clumps (see Gray, 1958; Hess, 1961; Peachey and Huxley, 1962; Krüger, 1952; and Bock and Hikida, 1968, for a discussion of the morphological characteristics of twitch and tonus fibers). Because variations in fixation frequently make it difficult to differentiate twitch and tonus fibers, other techniques can also be employed for identification. The two fiber types possess different nerve endings, which can be demonstrated using cholinesterase staining of the nerve end-plates (Hess, 1960; 1961). However, the cholinesterase technique is too laborious to use as an efficient method for studying whole bone-muscle systems. A more promising approach resorts to different histochemical tests on sectioned whole muscle. Engel and Irwin (1967), studying amphibian muscle, have found high ATPase activity in twitch fibers and low activity in tonus fibers. Unpublished work suggests these relationships may also be true for avian muscle (R. S. Hikida, personal commun.).

For each muscle the fibers within a variable number of fasciculi, sampled throughout the muscle where possible, were scored. In almost all cases the percentages are based on fibers counted from muscles of two or three different birds. It was not possible to give accurate percentages for most of the muscles mainly because the process of fixation did not clearly differentiate the two fiber types. In these cases the most accurate statement I think possible will be made. Because of the problems of fixation, unambiguous recognition of twitch-tonus fibers using light micro-

scopy is still not resolved; hence, all estimates will have to be considered as tentative. Much more work needs to be done on the factors influencing variation of the percentages between muscles of a single species. On the other hand, although still preliminary, the data allow much

more meaningful conclusions about the functional analyses of these muscles and offer new avenues for future comparative research on studies of gross anatomy.

Unless noted otherwise, the muscle terminology is that of Hudson (1937).

DESCRIPTION OF THE MUSCLES

M. ILIOTIBIALIS

GENERAL DESCRIPTION: This broad, but very thin muscle is two-joint, passing over the hip and knee joints. It arises anteriorly by a thin aponeurosis from the anterior iliac crest (the aponeurosis begins posteriorly at the posterior edge of the hip joint). At the junction of the anterior and posterior iliac crests, the aponeurosis passes medially onto the pelvic shield. Posteriorly, the muscle arises fleshy, and sometimes slightly aponeurotically, from the anterior three-fourths of the posterior iliac crest. The aponeurosis of insertion is shared with M. femorotibialis and forms the patellar ligament. The latter inserts onto the head of the tibiotarsus at the base of the outer cnemial crest and portions of the tibiotarsus medial to the inner cnemial crest.

FIBER ARRANGEMENT: The muscle is fan-shaped and the aponeurosis of insertion extends distally up the middle of the muscle. Hence, the fibers in the middle are shorter (about 0.35 as long) than those anteriorly or posteriorly. Both the anterior and posterior fibers are very long (35 to 40 mm.), but the latter slightly more so than the former. The line of action of the anterior fibers lies nearly parallel to the tendinous fibers of the aponeurosis of insertion. The posterior fibers meet the aponeurosis at 30 to 40 degrees, but some of the posteriormost fibers approach 60 degrees.

FIBER HISTOLOGY: The iliotibialis is a mixed muscle, but twitch fibers are much more common than tonus fibers and comprise about 90 per cent (or more) of the fibers. Tonus fibers seem to be slightly more frequent in the posterior part of the muscle, but this will have to be checked.

M. SARTORIUS

GENERAL DESCRIPTION: The sartorius is a thin, straplike muscle passing over the hip and knee joints. The superficial fibers arise aponeurotically from the anterior iliac crest, median dorsal

ridge, and from the connective tissue covering the first free rib. The deeper fibers arise fleshy (or slightly aponeurotic) from the ventroanterior edge of the ilium. The tendon of insertion is narrow and flat. It attaches to the medial side of the patella and contributes to the medialmost portion of the patellar ligament; hence, it attaches to the anteromedial edge of the head of the tibiotarsus.

FIBER ARRANGEMENT: The fibers are parallel throughout the length of the muscle and converge only near the point of insertion. The anterior fibers tend to be longer than the posterior ones, but the difference is not much more than 10 per cent. Fiber length is difficult to measure because the dorsal portion of the muscle curves strongly over the ribs.

FIBER HISTOLOGY: The sartorius is a mixed muscle with twitch fibers comprising between 80 to 90 per cent of the fibers.

M. AMBIENS

GENERAL DESCRIPTION: The ambiens is essentially a two-joint muscle arising by means of a narrow, flat tendon from the ventral border of the iliopubic junction immediately ventral to the acetabulum. The long, thin tendon passes across the anterior surface of the knee joint within the patellar ligament (fig. 9). It emerges lateral to the head of the fibula and becomes confluent with aponeurosis 5 (fig. 18).

FIBER ARRANGEMENT: The tendon of origin extends over the medial surface of the muscle as an aponeurosis, and the tendon of insertion does likewise over the lateral surface. The fibers run unipinnately between these aponeuroses. The angle of pinnation is very small, and hence the fibers are nearly parallel. The fibers are extremely difficult to measure, but they seem to vary from 0.25 to 0.45 the length of the muscle (23 to 24 mm.).

FIBER HISTOLOGY: The ambiens is a mixed

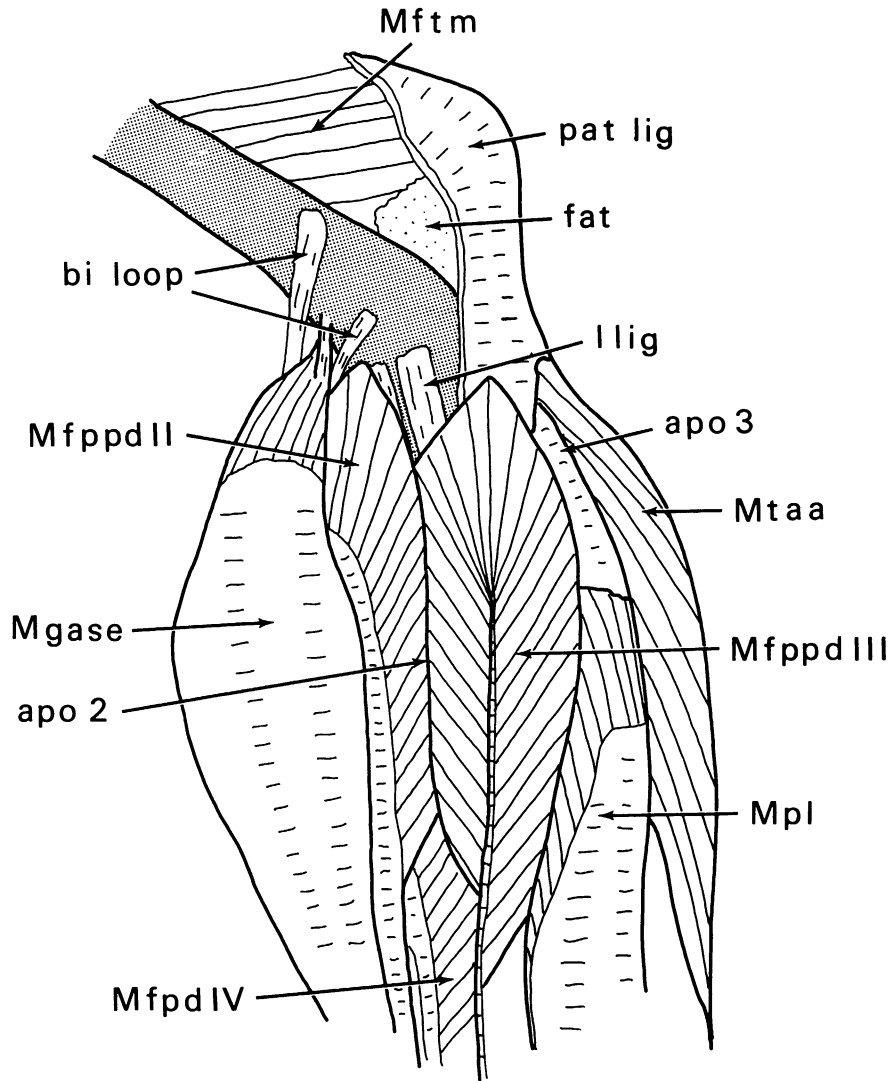


FIG. 17. View of lateral side of leg of *Columba livia* showing superficial muscles.

Abbreviations: apo 2, aponeurosis 2; apo 3, aponeurosis 3; bi loop, biceps loop; fat, fat pad; l lig, lateral ligament; M pl, M. peroneus longus; M fpdIV, M. flexor perforatus digiti IV; M fppdII, M. flexor perforatus et perforans digiti II; M fppdIII, M. flexor perforatus et perforans digiti III; M ftm, M. femorotibialis medius; M gase, M. gastrocnemius externus; M taa, M. tibialis anterior, anterior slip; pat lig, patellar ligament.

muscle, but twitch fibers appear to be slightly more common (about 60 per cent).

M. FEMORITIBIALIS

GENERAL DESCRIPTION: This is a large one-joint muscle passing over the knee joint, and it can be divided into four parts: (a) the externus portion arises fleshy from the entire lateral side of the femur and, distal to the insertion of

M. ischiofemoralis, from the posterior side of the femur; the lateral origin extends distally to the level of the external condyle. (b) The medius portion (figs. 4, 17) arises aponeurotically from the trochanter and trochanteric ridge and fleshy from the anterior and anteromedial surface of the femur beginning distal to the neck and extending fleshy down the shaft to the condyles. A raphe is found along the anterolateral edge of

the femoral shaft, and this central raphe serves as the division of the medius and externus portions. (c) The posticus portion is separate from the externus. The posticus arises from the posterior side of the femur beginning at the level of insertion of *M. piriformis*. Distally, the origin is situated more laterally and adjacent to that of externus. The origin extends distally to the external condyle. Some fibers arise fleshy, but others are aponeurotic. (d) The internus portion arises fleshy from the posterior and (principally) posteromedial surface of the femur beginning at the level of insertion of *M. iliacus* and continuing distally to the level of the internal condyle. The origin extends more anteriorly near the distal end of the femur.

The tendons of insertion of externus and medius are confluent and are formed by strong aponeuroses extending over the surfaces of the muscles. This common tendon contains the patella and forms the patellar ligament inserting onto the anterior edge of the head of the tibiotarsus. The tendon of insertion of posticus is by an aponeurosis over the outer (medial) surface of the muscle. The tendon forms the most lateroposterior part of the patellar ligament (but is posterior to the patella) and is confluent with the tendon of externus. The tendon of internus is separated from that of medius and inserts onto the head of the tibiotarsus medially to the inner cnemial crest; it does not form part of the patellar ligament.

FIBER ARRANGEMENT: (a) Externus—the fibers arise from the femur and insert onto the aponeurosis of insertion. Anteriorly, the fibers arise from the central raphe separating externus and medius. The fibers are thus unipinnate with a small angle of pinnation. The externus is about 35 mm. long, and the fibers average about 0.25 of that length laterally to about 0.36 medially near the central raphe. (b) Medius—most of the fibers of this unipinnate slip arise on the externus-mediis raphe; far fewer fibers arise directly from the femur. All insert onto the aponeurosis of insertion. The medius is about 40 mm. long, and the fibers average around 0.27 to 0.31 that length. (c) Posticus—the medial surface of the muscle is covered by an aponeurosis of origin which attaches to the femur. The aponeurosis of insertion covers the lateral surface of the slip. Anteriorly, the fibers arise from the femur and insert onto the aponeurosis of insertion; medially the fibers arise from the femur and aponeurosis

of origin and insert onto the aponeurosis of insertion. The fibers are about 0.20 the length of the muscle (about 25 mm.). (d) Internus—the fibers run unipinnately from the shaft of the femur to the aponeurosis of insertion on the outer (medial) surface of the muscle. The fibers are approximately 0.22 to 0.25 the length of the muscle (32 to 33 mm.).

The angle of pinnation varies greatly within each part. Typically it is about 40 to 45 degrees distally and approaches zero degrees proximally.

FIBER HISTOLOGY: The femorotibialis is a mixed muscle. Because of variations in fixation, it was not possible to take accurate counts of the fiber types. Twitch fibers seem to be much more common than tonus fibers.

M. BICEPS FEMORIS

GENERAL DESCRIPTION: The *M. biceps femoris* is a large, fan-shaped, two-joint muscle passing over the hip and knee joints. It has a fleshy origin from the anterior three-fourths of the posterior iliac crest and from the area immediately ventral to the crest and an aponeurotic origin from the posterior part of the anterior iliac crest and from the aponeurosis covering *M. iliopsoas* posterior. The muscle inserts by means of a strong, round tendon to the posterior side of the fibula slightly proximal to the fibular crest (fig. 18).

FIBER ARRANGEMENT: The tendon of insertion runs proximally up the posterior edge of the muscle for about one-third its length. Hence, most of the fibers insert onto the anterior side of the tendon, which results in an asymmetrical bipinnate muscle. All the fibers are very long, with the anterior fibers being longer (0.90 the length of the muscle, 40 to 45 mm.) than the posterior and central fibers (0.55 to 0.75).

FIBER HISTOLOGY: This muscle is composed of a very high percentage of twitch fibers (over 80 per cent).

M. ILIOTROCHANTERICUS POSTERIOR

GENERAL DESCRIPTION: This is a one-joint muscle passing over the hip. It has a large origin from the anterior part of the ilium, bordered dorsally by the anterior iliac crest. The insertion is by a strong tendon to the lateral side of the proximal end of the femur a few millimeters posterior to the trochanteric ridge (fig. 4).

FIBER ARRANGEMENT: This fan-shaped muscle is a good example of a bipinnate arrangement.

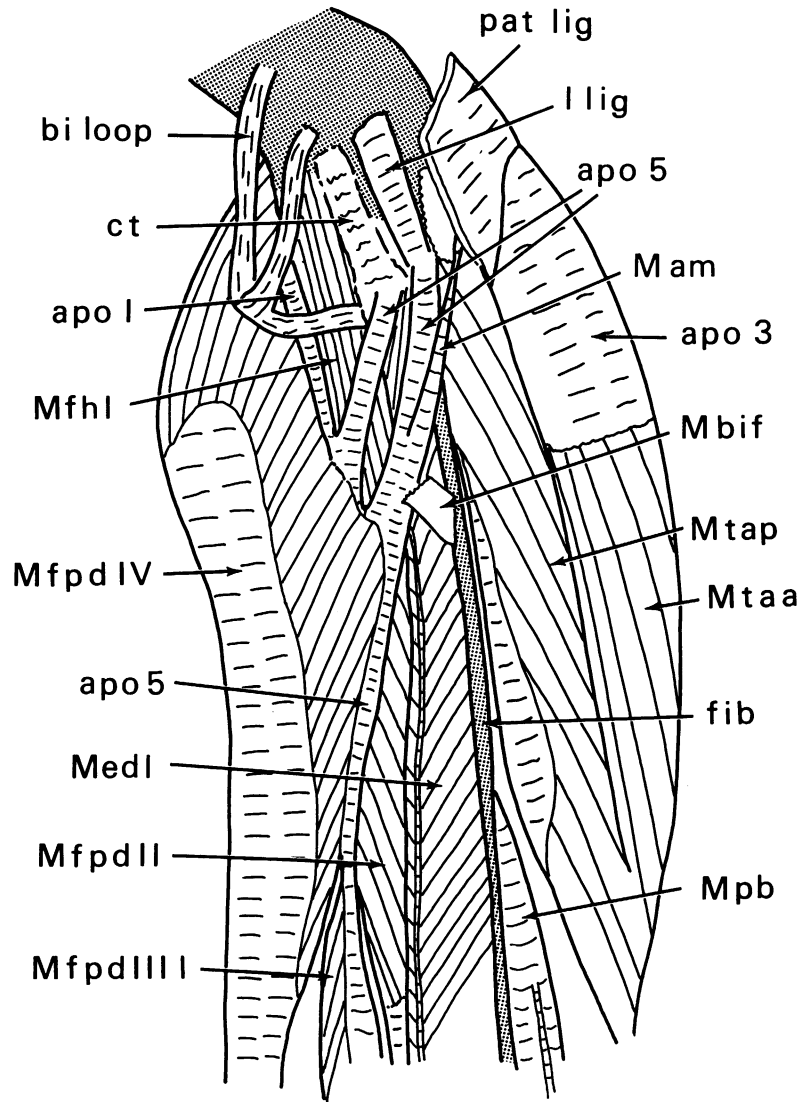


FIG. 18. View of lateral side of leg of *Columba livia* with superficial muscles removed.

Abbreviations: apo 1, aponeurosis 1; apo 3, aponeurosis 3; apo 5, aponeurosis 5; bi loop, biceps loop; ct, connective tissue associated with joint capsule and aponeurosis 2; fib, fibula; l lig, lateral ligament; M am, M. ambiens; M bif, M. biceps femoris; M edl, M. extensor digitorum longus; M fhl, M. flexor hallucis longus; M fpdII, M. flexor perforatus digiti II; M fpdIII, M. flexor perforatus digiti III, lateral slip; M fpdIV, M. flexor perforatus digiti IV; M pb, M. peroneus brevis; M taa, M. tibialis anterior, anterior slip; M tap, M. tibialis anterior, posterior slip; pat lig, patellar ligament.

A thin aponeurosis covers the outer surface of the muscle and contributes to the tendon of insertion. Another flat aponeurosis passes through the middle of the muscle (extends proximally about one-half to three-fourths the length of the

muscle) and is oriented in a plane parallel to the superficial aponeurosis; the superficial and central aponeuroses are continuous at the tendon of insertion. Most of the deep fibers arise fleshy from the ilium, but a few arise from the apo-

neurosis covering the outer surface of the M. iliотrochantericus anterior; the deep fibers insert onto the central aponeurosis. The superficial fibers arise from the outer aponeurosis and insert onto the central aponeurosis. Most of the deep fibers are about 0.28 to 0.31 the length of the muscle (26 to 32 mm.), whereas the superficial fibers usually are somewhat longer (about 0.38 to 0.45, occasionally longer). The length of the fibers varies greatly with position. Because of the tough aponeurosis covering the surface of the muscle, accurate measurements of the angle of pinnation are difficult to make.

FIBER HISTOLOGY: Most of the fibers of this muscle are twitch, and in some sections the percentage is over 90 per cent. However, several sections had an increased percentage of tonus fibers (about 50 per cent) in the fasciculi. These tonus fibers are apparently localized, and detailed studies of the entire muscle will be necessary before an accurate count can be given.

M. ILIOTROCHANTERICUS ANTERIOR

GENERAL DESCRIPTION: A one-joint muscle over the hip joint, this muscle arises from the ventralmost edge of the anterior end of the ilium ventral to the origin of M. iliотrochantericus medius. The insertion is by a short tendon to the anterolateral side of the shaft of the femur just distal to the insertion of M. iliотrochantericus medius.

FIBER ARRANGEMENT: The aponeurosis of origin covers the lateral surface of the muscle and extends distally about one-half the length of the muscle (about 20 mm.). The aponeurosis of insertion covers the medial surface of the muscle. The fibers run unipinnately between the two aponeuroses. The medial portion of the muscle is somewhat shorter than the lateral portion (about 14 to 16 mm. compared with 20 mm.). Laterally, the fibers are about 0.70 to 0.80 the length of the muscle, whereas medially the fibers have a value of 0.79 to 0.86. This suggests the fibers may remain about the same size absolutely, but there is an indication (in one specimen) that they are shorter medially with a relative value of 0.75 the length of the medial portion of the muscle.

FIBER HISTOLOGY: The muscle is composed of 80 to 90 per cent twitch fibers.

M. ILIOTROCHANTERICUS MEDIUS

GENERAL DESCRIPTION: This very small muscle takes its fleshy origin from the ventral-

most edge of the ilium beginning anterior to the acetabulum and extending to the origin of M. iliотrochantericus anterior. It inserts by a relatively strong tendon to the anterolateral side of the proximal end of the femur just distal to the insertion of M. iliотrochantericus posterior. Like the preceding two muscles, this is a one-joint muscle of the hip.

FIBER ARRANGEMENT: The tendon of insertion covers the distal one-half of the deep surface of the muscle. The muscle is unipinnate, but the fibers insert onto the aponeurosis at an acute angle. Most of the fibers are about 0.70 to 0.80 the length of the muscle (10–12 mm.), but some of the fibers are occasionally longer (0.87).

FIBER HISTOLOGY: Twitch and tonus fibers are both common, with twitch perhaps occurring a little more frequently (60 to 70 per cent).

M. ILIACUS

GENERAL DESCRIPTION: The iliacus is a very small one-joint muscle of the hip. It arises fleshy from the ventralmost edge of the ilium immediately below and medial to the origin of M. iliотrochantericus medius and just anterior to the hip joint. The insertion is fleshy to the medial side of the proximal end of the femur just anterior to the proximalmost portion of the origin of M. femoritibialis internus.

FIBER ARRANGEMENT: This is a parallel fibered muscle with fibers running the length of the muscle (16–17 mm.). There is slight variation in the length of the muscle, because it is not of constant width.

FIBER HISTOLOGY: Adequate histological material was not available to estimate fiber type frequencies. However, the iliacus is a mixed muscle with twitch fibers apparently more numerous.

M. SEMITENDINOSUS

GENERAL DESCRIPTION: This muscle, in conjunction with the M. accessory semitendinosus, is a one-joint muscle over the hip joint. It arises fleshy from the posterior portion of the posterior iliac crest and from the ilium below the crest. The most posterior and superficial fibers arise by a thin fascia that originates among the connective tissue at the base of the tail; the deeper fibers arise from the ilium. Near the middle of the femur, the muscle is divided into two parts by an anteroposteriorly oriented raphe; the most distal part is the M. accessory semitendinosus.

This latter muscle then has a fleshy insertion to the lateral part of the popliteal area of the femur. The raphe is confluent with the tendon of insertion of *M. semimembranosus* and with the aponeurosis covering *M. gastrocnemius medius*.

FIBER ARRANGEMENT: This straplike muscle is composed of parallel fibers in both parts. Because of the shape of the muscle the anterior fibers are somewhat shorter (0.80 to 0.90) than the length of the posterior fibers (30 to 37 mm.). The posterior fibers of the accessory semitendi-

nosus tend to be shorter (0.80 to 0.90) than the anterior fibers (about 15 to 18 mm.).

FIBER HISTOLOGY: The most that can be said about this muscle is that it has mixed fiber types. The material available was not sufficient to determine frequencies of the fibers.

M. SEMIMEMBRANOSUS

GENERAL DESCRIPTION: The semimembranosus is a thin, narrow two-joint muscle passing over the hip and knee joints. It arises fleshy from

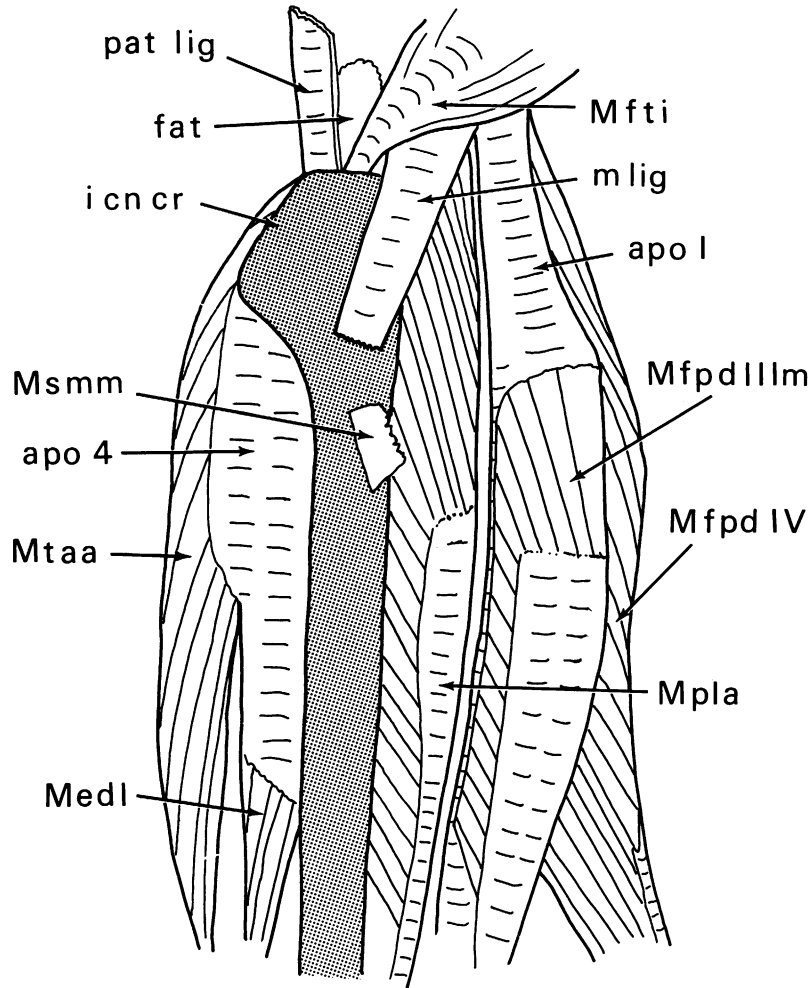


FIG. 19. View of medial side of leg of *Columba livia* with superficial muscles removed.

Abbreviations: apo 1, aponeurosis 1; apo 4, aponeurosis 4; fat, fat pad; i cn cr, inner cnemial crest; M edl, *M. extensor digitorum longus*; M fpdIV, *M. flexor perforatus digiti IV*; M fpdIII m, *M. flexor perforatus digiti III*, medial slip; M fti, *M. femorotibialis internus*; m lig, medial ligament; M pla, *M. plantaris*; M smm, *M. semimembranosus*; M taa, *M. tibialis anterior*, anterior slip; pat lig, patellar ligament.

the most posterior portion of the ischium including the posteroventral edge. It inserts by a broad, thin tendon to the medial side of the tibiotarsal shaft just distal to the attachment of the medial ligament (fig. 19). There is a rather strong fibrous connection between the lateral surface of the tendon of insertion, the central raphe of the *M. semitendinosus*, and a tendinous slip from the tendon of insertion of *M. gastrocnemius medius*.

FIBER ARRANGEMENT: This muscle is composed of long, parallel fibers. The tendon of insertion does not form an aponeurosis, the fibers all appearing to end at about the same place to form the tendon. All the fibers run very nearly the length of the muscle (30 to 35 mm.).

FIBER HISTOLOGY: This is a mixed muscle with the twitch fibers perhaps being slightly more frequent.

M. PIRIFORMIS

GENERAL DESCRIPTION: The piriformis is composed of two slips forming a one-joint muscle over the hip joint. The posterior slip (=pars caudofemoralis) arises by a thin tendon from the ventral side of the pygostyle. The anterior slip (=pars iliofemoralis) originates fleshy from the posteriormost part of the ilium (posterior to the ilioischiatric fenestra) just below the posterior iliac crest. The two slips have a common tendon of insertion to the posteromedial side of the femur slightly less than one-half the distance distally down the bone.

FIBER ARRANGEMENT: On the posterior slip, the aponeurosis of origin extends over the lateral surface of the muscle for about one-third its length, whereas the aponeurosis of insertion covers the medial surface for about one-half the muscle length. The fibers then run unipinnately between the two aponeuroses. It is very difficult to accurately measure the length of the posterior slip (approximately 45 to 55 mm.) and the muscle fibers themselves (0.65 to 0.75), because the slip is long and folded. The angle of pinnation is so small that the fibers are essentially parallel. The anterior slip is much shorter (about 21 to 25 mm.) than the posterior slip. The parallel fibers run very nearly 100 per cent of the length of the muscle, but there is some slight variation in absolute length as the muscle is not of uniform width. The fibers of the anterior slip pull at about a 30 degree angle to the line of action of the posterior slip.

FIBER HISTOLOGY: This is a mixed muscle, but the available material did not permit the determination of the fiber type frequencies.

M. ISCHIOFEMORALIS

GENERAL DESCRIPTION: The ischiofemoralis is a short, but relatively large one-joint muscle over the hip joint. It has a predominately fleshy origin from the ventral part of the ilium below the origin of the anterior slip of the *M. piriformis* and from the surface of the ischium posterior to the ilioischiatric fenestra. The most ventral part of the origin is by a thin aponeurosis. It also arises partly from the membrane covering the ilio-ischiatic fenestra. The insertion is by a strong, narrow tendon to the outer side of the proximal end of the femur adjacent and proximal to the origin of *M. femorotibialis externus*.

FIBER ARRANGEMENT: A thin aponeurosis of insertion covers the entire lateral surface of the muscle, and the fibers insert unipinnately onto it. The fibers are short and average about 0.20 to 0.30 the length of the muscle (about 23 to 24 mm.), hence a large number of fibers are present.

FIBER HISTOLOGY: The ischiofemoralis is a mixed muscle, and although the two fiber types appear to be present in about equal numbers, variation in the patterns of fixation requires further verification.

M. ADDUCTOR SUPERFICIALIS

(*M. adductor longus et brevis* of Hudson, 1937)

GENERAL DESCRIPTION: This large, flat, one-joint muscle has its origin by a short (but broad) tendon from the ventral edge of the ilium beginning anteriorly at a position even with the posterior edge of the ilio-ischiatic fenestra and extending posteriorly almost to the level of the termination of the posterior iliac crest. The posterior part of the origin lies deep (medial) to the anterior portion of the origin of *M. semimembranosus*. The deep fibers have their origin from the aponeurosis of origin of *M. adductor profundus*. The muscle inserts fleshy onto the posteromedial side of the distal half of the femur.

FIBER ARRANGEMENT: The muscle has long parallel fibers. Anteriorly, the fibers of *M. adductor superficialis* run in a more anteroventral direction than those of *M. adductor profundus*, which run more ventrally. Posteriorly, the fiber directions of the two muscles are the same, and the fibers intermingle. Because of the shape of

the muscle the length of the fibers varies greatly, the anterior fibers being about 17 mm. and the central and posterior fibers being about 27 to 30 mm.

FIBER HISTOLOGY: This muscle contains a high percentage of tonus fibers (apparently over 90 per cent).

M. ADDUCTOR PROFUNDUS

(*M. adductor longus et brevis* of Hudson, 1937)

GENERAL DESCRIPTION: This is a large, flat, one-joint muscle over the hip. It arises by a broad, thin tendon (aponeurosis) from the ventral edge of the ischium beginning anteriorly at the obturator foramen and extending posteriorly to the level of the end of the posterior iliac crest. The anterior part of the muscle inserts onto the distal half of the posterior surface of the shaft of the femur by a broad aponeurosis. In the popliteal area medial to the insertion of *M. accessory semitendinosus* the insertion is mostly fleshy, but there are present occasional thin, short tendons for some of the fibers. The more posterior fibers insert onto the aponeurosis covering the *M. gastrocnemius medius*, and some of the fibers insert onto the posterior part of the joint capsule.

FIBER ARRANGEMENT: Anteriorly, the aponeurosis of insertion covers the lateral surface of the muscle, and the fibers insert unipinnately upon it; the tendon of origin extends over the proximal end of the medial surface of the muscle as a very thin aponeurosis. Anteriorly, the fibers are so very nearly parallel that an angle of pinnation cannot be measured. Posteriorly, the fibers run almost the length of the muscle, there being no aponeurosis on the medial surface of the muscle. Because the muscle is trapezoid in shape, the anteriormost fibers are the shortest (about 14 mm.), whereas the posterior fibers are the longest (about 31 mm.).

FIBER HISTOLOGY: This muscle is composed of a high percentage of tonus fibers (over 90 per cent).

M. OBTURATOR

GENERAL DESCRIPTION: The obturator has three main parts in the pigeon, and all are one-joint over the hip. *Externus*—the *externus* arises fleshy from the pubis ventral to the obturator foramen. This part of the muscle inserts onto the tendon of the *internus* portion; the more ventral fibers insert by tendinous

threads to the femur. *Internus*—the *internus* arises from the inside of the pelvis. Dorsally, it arises from the excavation of the ventralmost portion of the ischium and ventrally from the pubis beginning anteriorly at the obturator foramen and extending posteriorly to the junction of the ischium and pubis. Fibers also arise from the membrane covering the ischiopubic fenestra. The strong tendon of the *internus* passes through the obturator foramen and inserts onto the posterolateral side of the head of the femur anterior to the very indistinct obturator ridge (fig. 4). *Anticus* (see Holmes, 1963, p. 424)—the *anticus* takes its origin from the pelvis between the anterior edge of the obturator foramen and the capsule of the hip joint. It inserts onto the head of the femur in the area of the obturator ridge and posterior to the tendon of the *internus*.

FIBER ARRANGEMENT: *Externus*—the fibers have a parallel arrangement. They are about 5 to 7 mm. long, the smallest being situated anteriorly. Few fibers are involved, and they intermingle with those of the *internus* portion. *Internus*—this portion is bipinnate, the dorsal and ventral fibers converging onto a central tendon. Most of the fibers average about 0.20 to 0.23 the length of the muscle (34 to 36 mm.), but some of the most posterior fibers are longer (0.28). The anteriormost fibers insert onto the central tendon at about a 23- to 27-degree angle; posteriorly the angle is smaller (about 16 to 19 degrees). *Anticus*—the fibers are short and parallel; they average about 5 to 6 mm.

FIBER HISTOLOGY: Adequate histological material was not available to determine the percentages of the fiber types. Both twitch and tonus fibers appear about equally frequent, but it is possible that tonus fibers may be predominant.

M. GASTROCNEMIUS

GENERAL DESCRIPTION: The *gastrocnemius* is composed of three separate slips. *Medius*—the *medius* portion is a two-joint muscle and arises from the distomedial part of the popliteal area. The more lateral part arises fleshy, whereas some of the posterior and medial fibers arise by thin tendons. The anteriormost fibers arise from the joint capsule. *Internus*—this portion has its origin from the medial surface of the inner cnemial crest beginning at the anterior edge of the medial ligament. Anteriorly some of the fibers arise from aponeurosis 4; posteriorly some of the fibers

arise from the joint capsule. The internus is a one-joint muscle of the intertarsal joint. Externus—the externus is a two-joint muscle that arises by a strong tendon from the posterolateral side of the femur at the base of the external condyle (fig. 17).

Distally, the tendons of all three parts form a common tendon of insertion. The externus and internus extend distally to about the same level (internus slightly longer). The medius slip is very short, being slightly less than one-half as long as the other two. The large common tendon crosses the posterior side of the intertarsal joint within a broad, superficial canal in the tibial cartilage and inserts along the posterior surface of the hypotarsus (fig. 14).

FIBER ARRANGEMENT: Medius—the tendon of insertion continues over the anterior (deep) surface of the muscle as an aponeurosis. The fibers insert onto this aponeurosis in a unipinnate manner. The fibers are usually about 0.47 to 0.55 the length of the muscle (17 to 18 mm.), although some may be relatively longer (0.66). Internus—the tendon of origin forms an aponeurosis over the deep surface of the muscle, and the tendon of insertion forms one over the outer surface of the muscle. The fibers thus run unipinnately between the aponeuroses. the fibers of the internus are the longest absolutely and average about 0.30 to 0.36 the length of the muscle (about 44 to 45 mm.). Externus—the fibers run unipinnately from a deep aponeurosis of origin to an outer aponeurosis of insertion. The fibers are shorter than those of the internus and average approximately 0.17 to 0.20 the length of the muscle (42 to 45 mm.).

The angle of pinnation is small, being less than 20 degrees. The angles of most of the fibers of these subdivisions are probably between 10 and 15 degrees.

FIBER HISTOLOGY: Adequate material was not available to make accurate determination of the percentages of the fiber types. All three parts appear to have large numbers of tonus fibers, but the externus appears to have a greater proportion of twitch fibers. The internus and medius seemingly have only a few twitch fibers. These results are the same as reported by Krüger and Günther (1958).

APONEUROSES OF ORIGIN OF THE FLEXOR MUSCLES

Most of the flexor muscles, and several of the

extensors, arising on the tibiotarsus and femur are intimately associated with one another through a series of aponeuroses of origin. In an effort to dispense with lengthy descriptions of the origins of these muscles, I will describe the aponeuroses here. Several of these are confluent with each other, and therefore cannot be defined sharply. I do not believe this argues against the usefulness of this approach. By describing aponeuroses the fiber arrangement of the muscles is naturally emphasized, and considerably more data are realized than simply the origin of the muscle. Zusi (1962) and Zusi and Storer (1969) have successfully adopted this approach in their analyses of the jaw muscles of some nonpasseriform birds.

Aponeurosis 1: arises from the middle of the popliteal area of the femur. Laterally, the aponeurosis is continuous with aponeurosis 5 (fig. 18). Anteriorly, aponeurosis 1 forms the medial surface of origin for *M. flexor hallucis longus*. More posteriorly, it forms the medial surface of origin of the medial portion of *M. flexor perforatus digiti IV* (figs. 18, 19). Proximally, the aponeurosis forms the lateral surface of origin for the medial slip of *M. flexor perforatus digiti III* and distally it forms the medial surface of origin for *M. flexor perforatus digiti II*.

It is interesting to note that all of the perforatus flexors (with the exception of the lateral slip of *M. flexor perforatus digiti III*) arise from aponeurosis 1.

Aponeurosis 2: arises from the connective tissue of the knee joint capsule and is attached posterior to the lateral ligament (fig. 17). The aponeurosis is only associated with two muscles, and it forms the anterior surface of *M. flexor perforatus et perforans digiti II* and the posterior surface of *M. flexor perforatus et perforans digiti III*.

All of the perforatus et perforans muscles arise (at least in part) from aponeurosis 2.

Aponeurosis 3: arises proximally from the outer cnemial crest (figs. 17, 18). Near this attachment the aponeurosis forms the anterior surface of *M. flexor perforatus et perforans digiti III* and the lateral surface of *M. tibialis anterior*. Distally, the aponeurosis becomes free of *M. tibialis anterior* and forms the medial surface of *M. peroneus longus*. In this region the aponeurosis also attaches to the fibula and thus becomes confluent with the aponeurotic covering of *M. peroneus brevis*.

Aponeurosis 4: arises from the inner cnemial crest (fig. 19). It forms the entire medial surface of *M. extensor digitorum longus* and the medial surface of the proximal portion of *M. tibialis anterior*. The aponeurosis attaches along the anteromedial side of the tibiotarsus.

Aponeurosis 5: originates as two separate, parallel tendinous slips from the knee joint capsule at the distal end of the lateral ligament (fig. 18). Where these tendinous slips merge, the aponeurosis broadens medially and becomes contiguous with aponeurosis 1. The tendon of *M. ambiens* joins aponeurosis 5 near the origin of the latter. Proximally, the lateral fibers of *M. flexor perforatus digiti IV* arise from the posterior surface of aponeurosis 5. Distally, the aponeurosis forms the anterior surface of origin for the lateral slip of *N. flexor perforatus digiti III*.

M. FLEXOR PERFORATUS ET PERFORANS DIGITI II

GENERAL DESCRIPTION: This is a small, flat, multi-joint muscle. It arises mostly by way of aponeurosis 2 from the joint capsule posterior to the lateral ligament (fig. 17). The tendon of insertion is broad and flat proximally but narrows distally. It crosses to the medial side of the leg, passes across the intertarsal joint, and comes to occupy the most medioposterior canal of the hypotarsus. Proximally, on the posterior side of the tarsometatarsus, the tendon occupies a posterior position relative to the tendon of *M. flexor perforatus digiti II*, but these positions are reversed distally. *M. flexor perforatus et perforans digiti II* perforates the latter tendon somewhat proximal to the level of the tarsometatarsal joint and at the base of phalanx 1 is perforated itself by *M. flexor digitorum longus*. The tendon then passes distally and inserts onto the medial side of the proximal end of the subarticular cartilage of the first interphalangeal joint.

FIBER ARRANGEMENT: The tendon of insertion forms an aponeurosis over the superficial (posterolateral) side of the muscle. Most of the fibers arise from aponeurosis 2, which covers the deep (medial) and anterior sides of the muscle, and insert unipinnately onto the aponeurosis of insertion (fig. 17). Some of the proximal fibers arise fleshy from the femur and joint capsule posterior to the lateral ligament. The fibers average about 0.30 to 0.38 the length of the

muscle (24 to 26 mm.). The maximum angle of pinnation is about 10 to 15 degrees.

FIBER HISTOLOGY: This muscle is of mixed fiber type, but many of the fibers cannot be differentiated. It does appear that tonus fibers are more common, but this will have to be verified histochemically.

M. FLEXOR PERFORATUS ET PERFORANS DIGITI III

GENERAL DESCRIPTION: This is a multiple-joint muscle. It arises from the anterolateral side of the distal end of the tibiotarsus. Posteriorly, the origin is from the joint capsule in the region of the lateral ligament by way of aponeurosis 2; anteriorly, the origin is from the outer cnemial crest by way of aponeurosis 3 (fig. 17). The long, thin tendon of insertion passes posteromedially, and just proximal to the tibial cartilage it is in-sheathed by the tendon of *M. flexor perforatus digiti III*. The tendon occupies the medialmost part of this sheath. The tendon continues down the posterolateral side of the tarsometatarsus, and at the distal end the tendon passes from a position posterior to the tendon of *M. flexor perforatus digiti III*, first to a lateral, then to an anterior position. In this region the two *digiti III* tendons are connected by a small vinculum. At the level of the tarsometatarsal joint the tendon of *M. flexor perforatus et perforans digiti III*, along with that of *M. flexor digitorum longus*, perforates *M. flexor perforatus digiti III*. At the middle of phalanx 1, the tendon of *M. flexor perforatus et perforans digiti III* gives off a broad, slightly elastic slip, which is in turn perforated by *M. flexor digitorum longus*. The elastic slip inserts onto the proximal end of the subarticular cartilage of the first interphalangeal joint. At the level of this latter joint, the main portion of the tendon bifurcates, and the *M. flexor digitorum longus* passes through the bifurcation. The branches then insert onto the lateral and medial sides of the proximal end of the subarticular cartilage of the second interphalangeal joint.

FIBER ARRANGEMENT: Distally, the tendon of insertion enters the posterior side of the muscle and becomes flattened lateromedially. The fibers arise from aponeuroses 2 and 3 and insert bipinnately onto the tendon (fig. 17). The fibers vary from about 0.25 to 0.40 the length of the muscle (31 to 35 mm.), but the posterior fibers tend to average shorter than the anterior fibers. The angle of pinnation is about 20 to 25 degrees

but decreases slightly both distally and proximally.

FIBER HISTOLOGY: This is a mixed muscle, and tonus fibers seem to be much more common than twitch. However, like those of *M. flexor perforatus et perforans digiti II*, many of the fibers are poorly differentiated, and the relative amounts will have to be checked histochemically.

M. FLEXOR PERFORATUS DIGITI IV

GENERAL DESCRIPTION: The origin of this multi-joint muscle is from the popliteal fossa by means of aponeurosis 1 and from the joint capsule of the lateral side by way of aponeurosis 5 (fig. 18). The strong tendon of insertion is the most lateral of two tendons enclosed within the tendon of *M. flexor perforatus digiti III*. The tendon passes down the posterolateral side of the tarsometatarsus. As the tendon approaches the tarsometatarsal joint, it broadens and is held firmly against the bones by a strong tendon sheath. At the level of phalanx 1 small lateral and medial branches are given off which insert onto the proximal end of the subarticular cartilage and the adjacent joint capsule of the second interphalangeal joint. A short distance distal to these small branches the main tendon bifurcates at the first interphalangeal joint into two large subdivisions, through which the tendon of *M. flexor digitorum longus* passes. The lateral bifurcation again divides, the more lateral branch inserting onto the proximal end of the subarticular cartilage of the second interphalangeal joint, the more medial branch inserting onto the proximal end of the subarticular cartilage of the third interphalangeal joint. The medial bifurcation also has insertions to the proximal ends of the subarticular cartilage of the second and third interphalangeal joints.

FIBER ARRANGEMENT: The tendon of insertion extends over the posterolateral surface of the muscle as an aponeurosis. Most of the fibers arise medially from aponeurosis 1; proximolaterally, some of the fibers originate fleshy from the lateralmost part of the popliteal area and from the femur just distal to the external condyle; laterally, the fibers arise from the posterior surface of aponeurosis 5 (fig. 18). The fibers insert unipinnately onto the aponeurosis of insertion. The fibers average 0.20 to 0.26 the length of the muscle (40 to 42 mm.). The angle of pinnation is about 15 degrees.

FIBER HISTOLOGY: This is a mixed muscle. Tonus fibers are less common than in *M. flexor perforatus et perforans digiti II* and *M. flexor perforatus et perforans digiti III*, but many fibers are still difficult to differentiate.

M. FLEXOR PERFORATUS DIGITI III

GENERAL DESCRIPTION: This multiple-joint muscle has two widely separated slips. Medial slip—this arises from the popliteal fossa by means of aponeurosis 1 (fig. 19). Lateral slip—this arises from the joint capsule near the fibula by way of aponeurosis 5 (fig. 18). The tendon of insertion of the medial slip is about twice as large as that of the lateral slip. They join proximal to the tibial cartilage and broaden to form a sheath around the tendons of *M. flexor perforatus digiti IV* and *M. flexor perforatus et perforans digiti III*. A short distance distal to the intertarsal joint the tendon of *M. flexor perforatus digiti III* is joined by the tendon of *M. peroneus longus*. At the level of the tarsometatarsal joint the tendon comes to occupy a posterior position to *M. flexor perforatus et perforans digiti III* and is perforated by the latter (along with *M. flexor digitorum longus*); in this region a small vinculum connects these *digiti III* tendons. The tendon then bifurcates, and the branches insert onto the lateral and medial sides of the proximal end of the subarticular cartilage of the first interphalangeal joint and to the adjoining areas of phalanx 1.

FIBER ARRANGEMENT: Medial slip—the tendon of insertion covers the medial surface as an aponeurosis. The fibers run unipinnately from the medial surface of aponeurosis 1 to the aponeurosis of insertion (fig. 19). The medial slip has many more fibers than the lateral slip, and they average about 0.21 to 0.28 the length of the muscle (28 to 30 mm.). Lateral slip—the tendon of insertion forms an aponeurosis over the lateral surface of the muscle. The fibers arise from the lateral surface of the distalmost portion of aponeurosis 5 and insert onto the aponeurosis of insertion (fig. 18). The fibers are longer than those of the medial slip, averaging about 0.40 to 0.45 the length of the muscle (about 19 to 20 mm.). Within the lateral slip the fibers insert at an angle of less than 10 degrees and hence are nearly parallel; the fibers of the medial slip have an angle of pinnation of 20 to 30 degrees.

FIBER HISTOLOGY: This is a mixed muscle with both twitch and tonus fibers being about

equally common. Accurate counts were not possible.

M. FLEXOR PERFORATUS DIGITI II

GENERAL DESCRIPTION: This multi-joint muscle has its origin from the popliteal fossa by way of aponeurosis 1, and from the joint capsule near the lateral ligament by way of aponeurosis 5 (fig. 18). The tendon of insertion passes through the tibial cartilage immediately anterior to the canal for the flexors of digiti III and IV (fig. 12) and then occupies the medioposterior canal of the hypotarsus. Proximally, the tendon of M. flexor perforatus digiti II occupies an anterior position relative to M. flexor perforatus et perforans digiti II until the distal half of the tarsometatarsus where these relationships are reversed. Slightly proximal to the tarsometatarsal joint, the tendon broadens and is perforated by the tendons of M. flexor perforatus et perforans digiti II and M. flexor digitorum longus. The tendon then bifurcates, and the two branches insert onto the medial and lateral sides of the proximal end of the subarticular cartilage of the tarsometatarsal joint. At its insertion the tendon is also continuous with a strong tendon sheath around the subarticular cartilage; the sheath attaches to phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion enters the muscle on the lateral side and then occupies a central position. The medial fibers arise from the lateral surface of aponeurosis 1; the lateral fibers arise from the posterolateral portion of the proximal end of aponeurosis 5. The arrangement then is more or less bipinnate. The fibers average about 0.16 to 0.23 the length of the muscle (about 43 mm.) with the most medial and distal fibers tending to be the smallest. The angle of pinnation is very small and is certainly less than 15 degrees (most fibers may be less than 10 degrees).

FIBER HISTOLOGY: This is a mixed muscle, and the twitch and tonus fibers appear to be about equally frequent. The fiber types do not show unequivocal structural differentiation and need to be checked histochemically.

M. FLEXOR HALLUCIS LONGUS

GENERAL DESCRIPTION: This multi-joint muscle has its origin from the popliteal fossa by way of aponeurosis 1 (fig. 18). Distal to the hypotarsus, the tendon of insertion is situated on the lateral side of the tarsometatarsus. As it

passes distally the tendon crosses over to the medial side, and two-thirds the distance down the bone the tendon has a vinculum with the tendon of M. flexor digitorum longus. The tendon passes under the lateral process of metatarsal 1 and is held tight against the anterior side of the phalanx by a strong tendon sheath. Near the middle of the hallux three or four very small, elastic branches are given off. These join into a single branch which inserts onto the anterior side of the distal end of the hallux. The main branch of the tendon inserts on to the base of the claw.

FIBER ARRANGEMENT: The tendon of insertion forms an aponeurosis over the posterolateral surface of the muscle. The fibers arise from aponeurosis 1 and insert unipinnately onto the aponeurosis of insertion. Some of the more proximal fibers insert bipinnately, but few fibers are involved. The fibers average about 0.25 to 0.32 the length of the muscle (37–45 mm.). The fibers have a small angle of pinnation (about 10 degrees).

FIBER HISTOLOGY: This muscle contains both twitch and tonus fibers, the former seemingly being the most common. As in the preceding flexor muscles, many fibers are poorly differentiated, thus making an exact count impossible.

M. PLANTARIS

GENERAL DESCRIPTION: This is a one-joint muscle over the posterior side of the intertarsal joint. It arises fleshy from the posteromedial portion of the proximal end of the tibiotarsus (fig. 19). The origin is posterolateral to the medial ligament and distal to the knee joint and extends distally about one-third the length of the tibiotarsus. The muscle inserts by a long, thin tendon to the medial side of the proximal end of the tibial cartilage.

FIBER ARRANGEMENT: The tendon of insertion is formed from an aponeurosis over the posterior side of the muscle. The fibers insert unipinnately onto this aponeurosis (fig. 19). Most of the fibers average about 0.32 to 0.36 the length of the muscle (about 28 mm.), although some may be as small as 0.29. The angle of pinnation is between 15 and 20 degrees.

FIBER HISTOLOGY: Although the plantaris is a mixed muscle, tonus fibers are overwhelmingly the most common. Comparatively few twitch fibers are present.

M. FLEXOR DIGITORUM LONGUS

GENERAL DESCRIPTION: This multi-joint muscle arises from the posterior side of the tibiotarsus and extends distally from the origin of *M. popliteus* nearly to the tibial cartilage. The most lateral part of the origin is from the posterior surface of the fibula. Near the knee joint the origin is only from the posterolateral surface of the tibiotarsus. The tendon of insertion passes down the posterolateral surface of the tarsometatarsus. About two-thirds the distance down the bone the tendon has a vinculum with *M. flexor hallucis longus* and soon thereafter divides into three branches. The lateral branch goes to digit IV. At the distal end of phalanx 1 the lateral branch perforates the tendon of *M. flexor perforatus digiti IV*. At the level of phalanx 4 a thin, broad elastic slip is given off which inserts onto the posterior end of the subarticular cartilage and the surrounding connective tissue of the fourth interphalangeal joint. The main part of the tendon inserts onto the base of the claw. The central branch goes to digit III. At the level of phalanx 2 a thin, narrow elastic slip is given off and inserts onto the proximal end of the subarticular cartilage of the second interphalangeal joint. At the level of phalanx 3 a thin, broad elastic slip is given off, and it inserts onto the proximal end of the subarticular cartilage of the third interphalangeal joint and the distal end of phalanx 3. A very short distance distal to the preceding slip, an additional slip (not always present) is given off to insert onto the proximal end of the third interphalangeal subarticular cartilage. The main part of the tendon attaches to the base of the claw. The medial branch goes to digit II. At the level of phalanx 1 a thin, narrow elastic slip is given off to insert onto the lateral side of the first interphalangeal subarticular cartilage. At the level of phalanx 2 a thin, broad elastic slip is given off to insert onto the proximal end of the second interphalangeal subarticular cartilage and to the distal end of phalanx 2. The main portion of the tendon inserts onto the base of the claw.

FIBER ARRANGEMENT: This muscle has a bipinnate arrangement. The fibers average about 0.20 to 0.24 the length of the muscle (50 to 51 mm.). The angle of pinnation is about 30 degrees.

FIBER HISTOLOGY: This is a mixed muscle. Although an exact count was not possible, tonus fibers appear to be slightly more common.

M. POPLITEUS

GENERAL DESCRIPTION: This is a small one-joint muscle of the tibiotarsal-fibular joint. It arises from the posterior surface of the tibiotarsus just distal to the knee joint. The insertion is onto the posterior end and posteromedial side of the head of the fibula.

FIBER ARRANGEMENT: This muscle has a complex pinnate arrangement as there are several tendons of origin and insertion. Superficially the pattern is essentially bipinnate. Deeper, the arrangement is unipinnate with the fibers arising from the tibiotarsus and inserting onto an aponeurosis of insertion covering the distomedial surface of the muscle. The fibers vary from 0.33 to 0.50 the length of the muscle (8 to 9 mm.). The angle of pinnation is difficult to measure but is very small.

FIBER HISTOLOGY: The popliteus is a mixed muscle, twitch fibers perhaps being slightly more common. Because of the small size of the muscle, exact cross sections are difficult to obtain.

M. PERONEUS LONGUS

GENERAL DESCRIPTION: This is essentially a one-joint muscle of the intertarsal joint. It arises by aponeurosis 3 from the outer cnemial crest and from the fibula (fig. 17). A strong tendon of insertion is formed proximal to the intertarsal joint. At the level of the proximal end of the external condyle, the tendon divides into two branches. The posterior branch, which is considerably broader and thinner than the anterior branch, inserts onto the lateral side of the tibial cartilage. The anterior branch continues distally across the intertarsal joint, passes immediately posterior to the insertion of *M. peroneus brevis*, and soon thereafter becomes confluent with the tendon of *M. flexor perforatus digiti III*.

FIBER ARRANGEMENT: An aponeurosis of insertion is formed over the outer surface of the muscle. The fibers insert unipinnately onto this aponeurosis (fig. 17). The fibers are about 0.16 to 0.20 the length of the muscle (37 to 41 mm.). The maximum angle of pinnation is about 15 degrees.

FIBER HISTOLOGY: This is a mixed muscle with both fiber types being about equally common.

M. TIBIALIS ANTERIOR

GENERAL DESCRIPTION: The tibialis anterior is divided into posterior and anterior slips, the

former being a two-joint muscle and the latter a one-joint muscle. The posterior slip arises as a thick tendon from the anterodistal surface of the external condyle of the femur (fig. 7). The tendon passes between the head of the fibula and the outer cnemial crest. The anterior slip has its origin from the medial surface of aponeurosis 3, which arises from the outer cnemial crest, and from the lateral surface of aponeurosis 4, which arises from the inner cnemial crest (figs. 17 to 19). Some of the fibers arise fleshy from the shaft of the tibiotarsus. The anterior and posterior slips remain separated most of the length of the muscle but join near the distal end. The large tendon of insertion passes down the antero-medial surface of the tibiotarsus and at the base of the internal condyle is held against the bone by a strong ligament. The tendon crosses the intertarsal joint and inserts onto the proximal end of the tarsometatarsus in the anterior metatarsal groove.

FIBER ARRANGEMENT: The tendon of origin of the posterior slip covers the deep (posterior) surface as an aponeurosis (fig. 18). The tendon of insertion covers the anterior surface, and the fibers run unipinnately between these aponeuroses. The fibers of the posterior slip are about 0.29 to 0.35 the length of the muscle (48 to 51 mm.). Proximally, the anterior slip is bipinnate. Distally, the fibers of the anterior slip that attach to the lateral side of the central tendon are missing and are replaced by the fibers of the posterior slip. Hence, fibers insert bipinnately onto the central tendon throughout the length of the muscle. The fibers of the anterior slip are long both absolutely and relatively, averaging about 0.45 to 0.50 the length of the muscle (48 to 51 mm.). The angle of pinnation averages about 10 to 15 degrees but approaches zero degrees proximally.

FIBER HISTOLOGY: This mixed muscle has twitch fibers much more frequent than tonus fibers.

M. EXTENSOR DIGITORUM LONGUS

GENERAL DESCRIPTION: This is a multi-joint muscle. It has its origin from the proximal end of the tibiotarsus between the outer and inner cnemial crests and from the inner cnemial crest by way of aponeurosis 4 (fig. 19). The origin extends distally one-third to one-half the length of the tibiotarsus. A strong tendon of insertion is

formed and distally is held close to the shaft by a strong ligament. The tendon passes deep within the joint capsule and passes beneath the supratendinal bridge of the tibiotarsus. It emerges onto the anterior surface of the tarsometatarsus just mediad to the insertion of *M. tibialis anterior*. The tendon flattens and broadens, and about two-thirds the distance down the tarsometatarsus, the tendon divides into two main, flat branches connected by a thin connective tissue sheet (fig. 20). The main medial branch goes to digit II. As it passes over the tarsometatarsal joint it is incorporated into the joint capsule. Level with phalanx 1 this tendon bifurcates. The left bifurcation is incorporated into the joint capsule of the first interphalangeal joint and inserts onto the proximal end of phalanx 2. The lateral bifurcation continues distally and inserts onto the base of the claw. The main lateral branch divides at a level proximal to the tarsometatarsal joint, and the lateral subdivision goes to digit IV and the medial subdivision to digit III. The lateral subdivision bifurcates at the tarsometatarsal joint. The lateral bifurcation extends distally and inserts at the base of the claw; the medial bifurcation has a very flat, thin branch confluent with the capsule of the second intertarsal joint, and the tendon then inserts onto the proximal end of the last phalanx. The medial subdivision to digit III extends distally to insert onto the base of the claw. A thin tendinous slip is also given off at the tarsometatarsal joint, and it too inserts at the base of the claw. The connective tissue between the two main lateral and medial branches is organized so that a thin tendinous strand goes from the main medial branch to digit III. This strand becomes more distinct on the digit itself and runs on the anteromedial side to insert at the base of the claw. It is somewhat arbitrary as to what is to be called a tendon since the connective tissue has varying degrees of concentration.

FIBER ARRANGEMENT: Distally, the tendon of insertion lies along the lateral surface of the muscle, and in this region the arrangement is unipinnate. Proximally, the muscle has a bipinnate arrangement (fig. 18). The fibers on the medial side arise from aponeurosis 4, whereas the lateral fibers arise fleshy from the tibiotarsus. The fibers average 0.17 to 0.20 the length of the muscle (about 46 to 51 mm.). Distally, the angle of pinnation is about 10 degrees, but this

increases to 15 to 20 degrees proximally where the muscle is bipinnate.

FIBER HISTOLOGY: This is a mixed muscle. Twitch fibers do, however, seem to be slightly more common.

M. PERONEUS BREVIS

GENERAL DESCRIPTION: This is a one-joint muscle across the intertarsal joint. It arises by a strong aponeurosis from the tibiotarsus beginning slightly distal to the fibular crest and extending nearly to the base of the external condyle, and from the fibula (fig. 18). The tendon of insertion is round and strong and is held against the side of the tibiotarsus at the base of the external condyle by a tight ligament. The tendon crosses the anterolateral corner of the intertarsal joint and inserts onto the external ligamental prominence of the proximal end of the tarsometatarsus.

FIBER ARRANGEMENT: Proximally, the fibers are arranged in a radial pattern around a central tendon. Here, the fibers arise posteriorly from the fibula, laterally from the aponeurosis covering the side of the muscle, anteriorly from the aponeurosis that covers the muscle and attaches to the tibiotarsus, and medially (deep) from the surface of the tibiotarsus anterior to the fibula. At the distal end of the muscle, the central tendon lies more on the anterior surface of the muscle, so the fiber arrangement is unipinnate. The fibers are short absolutely (about 4 mm.) and are about 0.12 to 0.15 the length of the muscle (27 to 32 mm.). The angle of pinnation could not be measured.

FIBER HISTOLOGY: This is a mixed muscle. The two fiber types appear to be about equally common, although twitch fibers may occur at a slightly greater frequency.

M. EXTENSOR HALLUCIS LONGUS

GENERAL DESCRIPTION: This one-joint muscle has two separate origins and insertions. The proximal head arises from the medialmost part of the anterior side of the tarsometatarsus beginning just distal to the intertarsal joint and extending nearly to the level of metatarsal 1; the proximal head also arises from the anterior surface of the tarsometatarsus beginning at the level of and distal to the insertion of M. tibialis anterior and extending a very short distance down the bone (figs. 20 to 21). The insertion of M. tibialis anterior separates the two slips of the

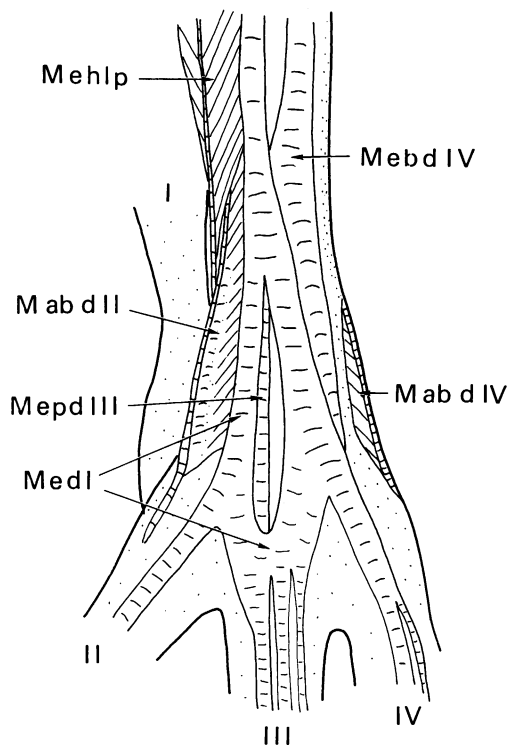


FIG. 20. Anterior view of muscles of tarsometatarsus of *Columba livia*.

Abbreviations: M ab d II, M. abductor digiti II; M ab d IV, M. abductor digiti IV; M eb d IV, M. extensor brevis digiti IV; M edl, M. extensor digitorum longus; M ehlp, M. extensor hallucis longus, proximal slip; M ep d III, M. extensor proprius digiti III.

proximal head. The insertion of the proximal head is by a strong tendon that extends down the posterior surface of the hallux and inserts onto the base of the claw (fig. 21). The distal head arises from the posteromedial side of the tarsometatarsus just proximal to metatarsal 1 (fig. 21). The medial (superficial) surface has a deep longitudinal groove in which are found portions of the proximal head. The tendon of insertion is small and crosses over the posterior side of the distal end of metatarsal 1 and inserts at the lateral edge of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion of the proximal head extends into the muscle, and the fibers insert bipinnately onto it (fig. 20). The tendon of insertion of the distal head extends up the most posterior part of the muscle, and the fibers insert unipinnately onto this tendon (fig. 21). Some of the fibers arise from

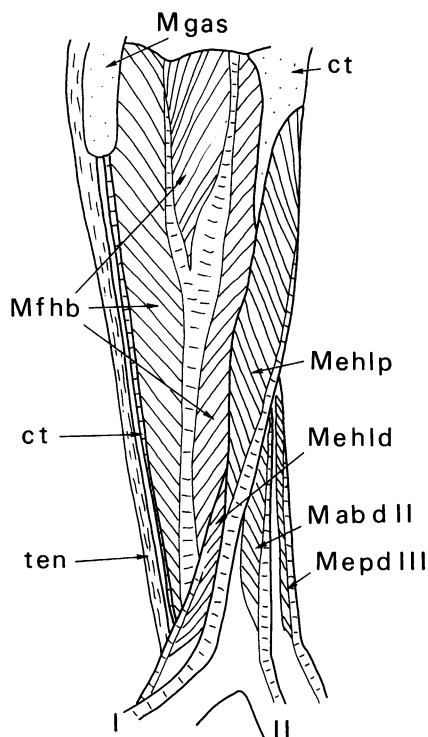


FIG. 21. Posteromedial view of muscles of tarsometatarsus of *Columba livia*.

Abbreviations: ct, connective tissue; M abd II, M. abductor digiti II; M ehld, M. extensor hallucis longus, distal slip; M epdIII, M. extensor proprius digiti III; M fhb, M. flexor hallucis brevis; M gas, M. gastrocnemius attachment to hypotarsus; ten, flexor tendons.

the aponeurosis covering the medial surface of M. flexor hallucis brevis. The fibers of the proximal head are absolutely and relatively longer (about 0.41 to 0.55 the length of the muscle, 17 to 18 mm.) than those of the distal head (about 0.30 to 0.40) which is about 20 mm. The proximal head has an angle of pinnation of about 15 to 20 degrees, whereas the fibers of the distal head insert at about a 20-degree angle.

FIBER HISTOLOGY: This appears to be a nearly pure twitch muscle; very few unequivocal tonus fibers were observed.

M. ABDUCTOR DIGITI II

GENERAL DESCRIPTION: This one-joint muscle has its origin from the distomedial end of the anterior surface of the tarsometatarsus beginning a short distance proximal to the medial distal foramen and extending proximally about two-

thirds the length of the tarsometatarsus (figs. 20, 21). The muscle narrows proximally. Distomedially, some of the fibers arise from the medial surface of metatarsal 1. The strong tendon of insertion runs along the medial edge of the trochlea and inserts onto the posteromedial edge of the proximal end of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion extends over the anteromedial surface of the muscle as an aponeurosis. The fibers insert more or less unipinnately (more bipinnately where the tendon of insertion is narrow) to the tendon of insertion (figs. 20, 21). The very short fibers average about 0.11 to 0.16 the length of the muscle (about 19 mm.). The angle of pinnation is difficult to measure but seems to vary from less than 10 degrees to as much as 20–30 degrees.

FIBER HISTOLOGY: This is a mixed muscle, but twitch fibers are about twice as common as tonus fibers.

M. EXTENSOR PROPRIUS DIGITI III

GENERAL DESCRIPTION: This one-joint muscle has its origin from the middle of the anterior surface of the tarsometatarsus beginning proximally at the level of insertion of M. tibialis anterior and extending distally nearly to the base of the middle trochlea (figs. 20, 21). A strong tendon of insertion is formed which inserts onto the dorsal edge of the proximal end of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion extends over the anterior surface of the muscle. The fibers insert more or less bipinnately (depending on the width of the aponeurosis) onto the central tendon. The fibers average about 0.12 to 0.18 the length of the muscle (about 28 mm.). The angle of pinnation is from 20 to 25 degrees.

FIBER HISTOLOGY: This is a mixed muscle with twitch fibers being slightly more common than tonus fibers.

M. EXTENSOR BREVIS DIGITI IV

GENERAL DESCRIPTION: This narrow muscle arises from the lateral edge of the anterior surface of the tarsometatarsus beginning at the level of the insertion of M. tibialis anterior and extending to the external distal foramen (fig. 20). The tendon of insertion passes into the external distal foramen and emerges on the posterior side. It runs along the medial face of the trochlea and inserts onto the posteromedial edge of the proximal end of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion extends into the muscle and becomes slightly broader proximally. The fibers are arranged more or less radially around the tendon. The deepest fibers arise from the surface of the tarsometatarsus, whereas all others arise from an aponeurosis on the surface of the muscle. The fibers are very short and average about 0.08 to 0.09 the length of the muscle (24 to 26 mm.). The angle of pinnation could not be measured.

FIBER HISTOLOGY: This appears to be a mixed muscle, but the available material is so poor that a more definite statement cannot be given.

M. LUMBRICALIS

GENERAL DESCRIPTION: This muscle occupies the distal end of the posterior side of the tarsometatarsus. It arises from the lateral and anterior surfaces of the tendon of *M. flexor digitorum longus* extending distally from the vinculum with *M. flexor hallucis longus*. The more proximal fibers insert onto the proximal end of the subarticular cartilage of the tarsometatarsal joint of digit IV, whereas the more distal fibers insert onto the subarticular cartilage of the tarsometatarsal joint of digit III.

FIBER ARRANGEMENT: The fibers are essentially parallel and have a fleshy origin and insertion. The proximal fibers going to digit IV are longer (about 14 to 15 mm.) than the distal fibers going to digit III (about 10 to 12 mm.).

FIBER HISTOLOGY: The lumbricalis is a mixed muscle, but twitch fibers are much more common (perhaps 70 per cent of the fibers).

M. ABDUCTOR DIGITI IV

GENERAL DESCRIPTION: This one-joint muscle arises from the lateral side of the tarsometatarsus beginning proximally at the level of the intertarsal joint (posterior to the insertion of *M. peroneus brevis*) and extending nearly to the base of the outer trochlea (fig. 20). The strong tendon of insertion passes down the lateral side of the outer trochlea and inserts onto the proximal end of the lateral side of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion extends over the lateral surface of the muscle but becomes aponeurotic only at the proximal end. The fibers insert unipinnately onto the tendon (fig. 20). The short fibers average about 0.11 to 0.14 the length of the muscle (about 28 mm.). The angle of pinnation is about 30 degrees.

FIBER HISTOLOGY: This muscle is composed

of both twitch and tonus fibers with the former being more common than the latter.

M. FLEXOR HALLUCIS BREVIS

GENERAL DESCRIPTION: This one-joint muscle has its origin on the posteromedial surface of the tarsometatarsus beginning proximally at the intertarsal joint and extending distally to the base of metatarsal 1 (fig. 21). The origin is from the medial side of the proximal end of the hypotarsus, from the medial surface of the hypotarsus, and from the shaft of the tarsometatarsus. The tendon of insertion occupies the medialmost position beneath the lateral process of metatarsal 1. It runs along the anterior surface of phalanx 1 and inserts at the proximal end of the latter.

FIBER ARRANGEMENT: The tendon of insertion continues over the posteromedial surface as a tough aponeurosis that narrows proximally. Proximally, the fibers insert bipinnately onto the aponeurosis, but more distally, where the aponeurosis is broad, the fibers tend toward a unipinnate arrangement. Anteriorly, the fibers arise from the shaft, laterally from the strong ligament attached distally to the hypotarsus, and medially from a ligamentous slip attached along the posteromedial side of the tarsometatarsus. The fibers average about 0.16 to 0.23 the length of the muscle (25 to 26 mm.). The angle of pinnation is between 30 and 40 degrees.

FIBER HISTOLOGY: This is a mixed muscle with both fiber types being about equally frequent.

M. ADDUCTOR DIGITI II

GENERAL DESCRIPTION: The adductor digiti II is the deepest muscle arising from the lateral side of the posterior surface of the tarsometatarsus. The origin extends distally to the base of the second (inner) trochlea. The tendon of insertion runs along the lateral face of the inner trochlea and inserts onto the lateroposterior side of the proximal end of phalanx 1.

FIBER ARRANGEMENT: The tendon of insertion extends over the posterior surface of the muscle. The fibers arise from the posterior surface of the tarsometatarsus and from the ligament extending distally from the hypotarsus, and they insert unipinnately onto the tendon. The fibers are short and average about 0.10 to 0.12 the length of the muscle (about 25 mm.). The angle of pinnation is about 15 to 20 degrees.

FIBER HISTOLOGY: No material of this muscle was examined.

FUNCTIONAL ANALYSIS OF THE HIND-LIMB MUSCLES

THIS SECTION will present a functional analysis of the muscles described in the previous section. The functional conclusions have been reached by using several different approaches. First, fresh material of each muscle was examined with emphasis placed upon analyses obtained by pulling on tendons of origin and insertion. This provided information about the direction and effect of the muscle force acting on the skeletal systems at the points of attachment, although the important question about magnitude of the force is still unanswered. It must be emphasized that the functional conclusions are based only on fresh material. Preserved muscle is stiff and non-compliant as are ligaments and joint capsules, and consequently many of the actions of the muscles are easily misinterpreted.

Second, the data on the frequencies of twitch and tonus fibers (see previous section) were also used in the analysis. Twitch fibers respond to a stimulation with a rapid development of tension to the maximum possible and, after stimulation ceases, loose tension rapidly. Tonus fibers, on the other hand, have a slow increase in tension with stimulation, and then after stimulation ceases, these fibers loose tension slowly (Kuffler and Vaughan Williams, 1953a, 1953b; Ginsborg, 1960; Peachey, 1961; Peachey and Huxley, 1962; Hess, 1970). Tonus fibers also fatigue much more slowly than do twitch fibers (Bock, personal commun.).

The physiological studies on twitch and tonus fibers cited above allow certain predictions to be made about the functional properties of given muscles. For example, we would not expect muscles that have a high percentage of tonus fibers to function mainly to move bones during rapid phases of locomotion. Likewise, those muscles with a high percentage of twitch fibers would not be functioning predominately as postural muscles in which slow, sustaining contractions are required.¹

¹In a recent paper Goldspink, Larson, and Davies (1970) provided some experimental support for several of the functional inferences I have made about fibrillenstruktur and felderstruktur fiber types (that is, twitch and tonus fibers). Goldspink and his co-workers compared the thermodynamic efficiency and physiological characteristics

Third, the data on the arrangement, length, number, and angle of pinnation of the muscle fibers were used to reach functional interpretations of the whole muscles. These interpretations have their basis in the findings of muscle physiologists, and much of this information has been available in the literature for many years (see, for example, the following summaries: Sandow, 1952; Wilkie, 1954; Davson, 1959; Bourne, 1960; H. E. Huxley, 1960; Abbott and Brady, 1964; and Gans and Bock, 1965).

I have attempted to place my results in perspective with those of other authors, but no effort has been made to survey all of the literature on the functions of avian hind-limb muscles. I have consulted the major papers (cited in the introduction) and have used these as the basis for any comparisons. For many of the muscles, my results do not differ. For others, there is substantial disagreement, and I have emphasized these differences in the discussion. However, my conclusions are derived from a study of only *Columba livia*, and because I have not examined fresh material of other species, my criticisms are intended to focus on the problems requiring additional study and not to pass as absolute refutation of previous work.

The information given in this section pertains, for the most part, to the kinds of movements that are produced by the muscles around joints. Later in the present paper I will discuss the co-ordination of the various muscles during the walking cycle and will attempt to construct activity sequences for the different locomotor movements.

Given in this section also are general comments on the relative numbers of fibers. This parameter is included here instead of in the section on description of muscles because the number of fibers is the best index available of

of the chick anterior latissimus dorsi (ALD), which is composed almost entirely of felderstruktur fibers, with the posterior latissimus dorsi (PLD), which is composed principally of fibrillenstruktur fibers. Compared to the PLD, the ALD had a rate of shortening 15 times slower, was able to sustain isometric tensions for longer periods of time (and was more efficient thermodynamically in doing so), and was more inefficient at performing isotonic work.

potential muscle force, except for actual experimental data. The discussions on the number of fibers are, at best, gross approximations and within the study are considered significant only when making relative comparisons among muscles which seem to have similar functional roles.

M. ILIOTIBIALIS

The major function of this muscle is slight extension and flexion and turning outward of the tibiotarsus (and hence the lower leg). The posterior fibers could contribute to retracting the femur as they have a moment arm around the hip joint of about 25 mm. The anterior fibers are nearly parallel with the femur and therefore have a short moment arm around the hip. It is doubtful that M. iliotibialis contributes much to abduction of the thigh as the lateromedial moment arm through the neck of the femur is short. Moreover, abduction is limited by joint structures. The muscle could resist adduction, however. The iliotibialis of *Columba* seems to be predominately a twitch muscle, which may cast some doubt on its serving as a stabilizer of the femur (Berger, 1952, p. 563), at least if long-term stabilization is involved.

M. SARTORIUS

The sartorius has long, parallel fibers, and most of these are twitch. Hence, the muscle probably functions to protract the femur (and tibiotarsus) rapidly over a great distance; the moment arm around the hip joint is about 20 mm. The sartorius is apparently more important in the beginning phases of femoral protraction rather than in the later phases and is the only muscle that can protract the femur quickly and through a great distance. Because of its insertion to the tibiotarsus the sartorius also contributes force to extend that element. However, in the early parts of the recovery phase of the walking cycle (see below) when the femur is protracted, the knee joint angle remains relatively constant and only extends at the terminal stages of the recovery phase. If the sartorius is responsible for protraction of the femur, then the muscle will probably be in the lower portion of the tension-length curve when the time for extension of the tibiotarsus is reached. Hence, little force would be available for this extension, and it would have to be accomplished by M. femorotibialis (or less likely, M. iliotibialis).

M. AMBIENS

Because this muscle contains very few fibers, the amount of tension developed is comparatively small. Perhaps the major action of this muscle mentioned by most authors is as an aid to flexion of the toes (e.g. Hudson, 1937; Fisher, 1946). However, I think the ambiens contributes little or nothing to toe flexion, because its association with the toe flexors is only by its insertion to an aponeurosis of origin (aponeurosis 5) and not to a tendon of insertion. The principal role is probably as an extensor of the tibiotarsus in the terminal stages of extension. In *Columba*, if the knee joint angle is less than about 130 degrees, the ambiens has no effect on extension. But when the angle is greater than 130 degrees, the muscle contributes force to extension. The ambiens may sometimes contribute to adduction of the thigh, but the muscle can develop very little force and the moment arm around the hip joint is very short.

M. FEMORITIBIALIS

The femorotibialis is unquestionably the chief extensor of the tibiotarsus, but because of its great subdivision, each part contributes differently to this process. The most medial fibers of the medius portion are only effective when the knee joint has already been extended somewhat. In a fully flexed position the patella is pulled distally a considerable distance over the femoral condyles. As the tibiotarsus extends, the patella moves proximally and the moment arm of these fibers increases. More anteriorly, the fibers are effective when the knee joint is in all positions, although the moment arm is slightly increased in the extended position. The externus can also extend the joint in all positions but is situated in a less favorable position than the medius. The internus does not extend the knee at all but rotates the tibiotarsus (and thus the whole leg) medially. The posticus functions to extend the knee only in the terminal stages; this part can also rotate the tibiotarsus laterally.

The medius and externus have large numbers of fibers. The internus is smaller but still has fairly large numbers of fibers. The posticus has far fewer fibers than the other subdivisions.

The fibers of externus and medius are the longest absolutely and support the suggestion that these parts of the muscle produce the first parts of tibiotarsal extension and hence probably shorten for the longest time. The posticus has

short fibers and thus probably contracts near the end of the extension phase. The fibers of the internus are also short, but long excursions are not necessary for rotational movements.

This muscle plays little role in propulsion and does not act "directly against the weight of the body" as emphasized by Miller (1937, p. 31).

M. BICEPS FEMORIS

The numerous fibers of the biceps femoris are long and parallel and are thus capable of high contractile velocities and/or movement over long excursions. Because it is not necessary for the tibiotarsus to be flexed over a great distance (see section on motion-picture analysis), I believe the main function of such a fiber arrangement is to develop high velocities. The biceps femoris is probably important in rapidly flexing the tibiotarsus immediately after lift-off in the recovery phase of walking. The high percentage of twitch fibers supports this conclusion. The biceps femoris may also resist the torques placed on the knee joint by the posterior slip of tibialis anterior (see below).

M. ILIOTROCHANTERICUS POSTERIOR

Almost all authors who have studied this muscle have believed that it protracts the femur and rotates it inward (e.g., Miller, 1937, p. 23; Fisher, 1946, pp. 659, 698; Berger, 1952, p. 562). In *Columba*, however, this muscle has the opposite action because it inserts slightly dorsal to the axis of protraction-retraction that runs through the head of the femur. Hence, the moment arm for retracting the femur is about 1 to 2 mm. The muscle rotates the femur forward around the longitudinal axis of the bone as was also observed by the above workers. The iliotrochantericus posterior may protract the femur in some birds, but this must be checked carefully using fresh material. Some workers in the past have probably been misled by inferring the function of this muscle from preserved specimens.

As the muscle retracts the femur, it contributes passively to the extension of the tibiotarsus. As the femur is being retracted and rotated, it is also moving over the proximal surface of the tibiotarsus; the configuration of the joint probably brings about tibiotarsal extension. This action can take place when all other muscles running from the pelvis and femur to the tibiotarsus are removed.

The high proportion of twitch fibers indicates

that this muscle takes an active part in the locomotor cycle. The rotation of the femur undoubtedly plays a major role. But I also think the iliotrochantericus posterior is one of the most important shock-absorbers in the hind limb (discussed in more detail below). As the femur protracts, as it would in landing, the muscle is stretched and thereby reduces the shock as it resists this stretching.

M. ILIOTROCHANTERICUS MEDIUS

The tendon of insertion of this muscle is distal to that of *M. iliotrochantericus posterior* and has a moment arm for protraction of 1 to 2 mm. However, because exceedingly few fibers are present, this muscle almost assuredly does not protract the femur. Instead, it may contribute slight force to bringing about mediad rotation.

M. ILIACUS

This muscle tends to protract the femur, but because little force is generated and because the moment arm is very short (about 5 mm.), the protraction is no doubt ineffectual. Perhaps more important is the role of the iliacus in lateral rotation of the femur, but again the muscle is probably not very effective.

M. SEMITENDINOSUS

The function of this muscle is not readily apparent. It seems to function as a retractor of the femur because of its interconnections with the accessory semitendinosus, and also it probably functions to flex the tibiotarsus because of its connections to *M. semimembranosus* and *M. gastrocnemius medius*. The main part of the semitendinosus and the accessory semitendinosus would place equal (the number of fibers in each is nearly the same) and opposite forces on the raphe. Because the fibers of the main part of the muscle are longer than the accessory portion, the former would remain in the higher parts of the tension-length curve for a longer period of time, thus the raphe would move in a postero-dorsal direction and the femur would retract.

The fibers of the main portion are long and thus could contract quickly, and in flexing the tibiotarsus, speed is probably more important than the degree of excursion.

Unfortunately, data are not available on the frequency of the two fiber types. It is interesting to note that the accessory semitendinosus occurs mainly in terrestrial forms and is absent in most

swimming birds (George and Berger, 1966, p. 403), and so the muscle may play an important role in posture.

Rather large numbers of fibers are present.

M. SEMIMEMBRANOSUS

If the femur is held stationary, then the semimembranosus has a moment arm around the knee joint of about 20 mm. The muscle is thin and has fewer fibers than the semitendinosus, and the long, parallel fibers indicate that the muscle is capable of high contractile velocities and/or lengthy excursions. On the other hand, the fact that many of the fibers may be tonus indicates a somewhat different role. It can be postulated that the semimembranosus also functions to resist the extension of the tibiotarsus, caused by contraction of *M. sartorius*, *M. iliotibialis*, and *M. femorotibialis*, as the leg (femur) is brought forward in the recovery phase. The torque produced by the semimembranosus probably could easily counteract those produced by the extensor muscles that have very short moment arms (see also discussion of *M. tibialis anterior* below). The semimembranosus probably does not contribute as much to rapid flexion of the tibiotarsus immediately after lift-off as does the biceps femoris but begins to act soon thereafter.

M. PIRIFORMIS

The main function of this muscle is probably to move the tail to the side. The fibers of the posterior slip are very long and thus are perfectly suitable for producing the fast and lengthy excursions that are necessary for controlling the action of the tail. Except for the small anterior slip, it is doubtful that the piriformis contributes much force to femoral retraction.

The anterior slip might be important in contributing to retraction of the femur during positions of posture. Unfortunately, data on frequency of fiber types are too incomplete to shed any light on this.

It is interesting to note that the piriformis is an example of a two-joint muscle in which the two attachments (femur and pygostyle) are movable, but the middle bone (pelvis) is stationary relative to the end bones. This mechanical construction further suggests that the femur is the stationary element and that the muscle is functioning to move the tail.

M. ISCHIOFEMORALIS

This muscle has a large number of short fibers; hence, a large amount of force can be generated, but only over a short excursion. Because the muscle inserts on the lateral side of the femoral shaft, it undoubtedly is most important in bringing about lateral rotation ("toeing out") of the femur relative to the body. The moment arm for retraction around the hip is about 7 to 8 mm., and Fisher (1946, p. 666) thought this was too short for effective retraction. However, the muscle has a large number of fibers, and the distance the femur must move is not significant. Twitch and tonus fibers are about equally common. This would suggest that the muscle plays some role in posture and possibly in contributing to retraction.

M. ADDUCTOR SUPERFICIALIS

The moment arm of the anterior fibers is about 9 to 10 mm., that of the posterior fibers about 28 mm. The adductor superficialis is composed of many fibers. Almost all authors have considered the main role of this muscle to be retraction of the femur, although some (Miller, 1937; Fisher, 1946) have also emphasized its role in maintaining posture. Because a very high percentage of the fibers are of the tonus type, I think it can be reasonably postulated that the main function of this muscle is to resist protraction of the femur during standing or landing. It is doubtful whether this muscle contributes much to femoral retraction.

M. ADDUCTOR PROFUNDUS

As in the preceding muscle, most of the fibers are tonus. Hence, this muscle also functions to resist femoral protraction during positions of posture. The moment arm of the anterior fibers is 8 to 9 mm., that of the posterior fibers 25 to 26 mm. The adductor profundus has large numbers of fibers and thus can generate large amounts of force.

M. OBTURATOR

The obturator acts to rotate the femur laterally (backward and inward). The internus portion has a large number of fibers and thus can develop rather considerable amounts of force. The moment arm for rotation is only a few millimeters long and is difficult to measure. The externus and anticus portions are so small as to be almost certainly unimportant.

M. GASTROCNEMIUS

The external and internal heads of this muscle are very different in gross and histological structure and presumably also in physiology. Because the externus originates from the femur and inserts onto the tarsometatarsus, some torques are probably present which would tend to flex the knee joint. However, until an exact analysis can be made of the force the tarsometatarsus is placing on the distal end of the tibiotarsus (see Bock, 1968), it will be impossible to say whether the externus actually does contribute to this flexion. In any case, the moment arm of such a force would probably be very small. The externus is predominately a twitch muscle and has a large number of fibers. I suggest that this part of the muscle functions mainly to extend the tarsometatarsus. On the other hand, the internus, which has a large number of fibers, and the medius, which has few fibers, are predominately tonus muscles, and therefore they probably are functioning to resist flexion and maintain posture. I suspect they are contributing little force (compared with the externus) during rapid extension of the tarsometatarsus during walking. During landing, the externus is possibly the portion of the muscle that absorbs most of the shock and acts as a break to tarsometatarsal flexion.

M. FLEXOR PERFORATUS ET PERFORANS DIGITI II

This muscle clearly functions in flexing the second digit, but other roles seem equally, if not more, important. When tension is developed in the muscle, the first effect is to extend the intertarsal joint. Only after some resistance is met, either from the joint structures or from flexor muscles such as the tibialis anterior, does the second toe begin to flex. Hence this muscle may contribute to extending the joint in the terminal stages of the walking cycle. More important than toe flexion, the muscle undoubtedly aids in maintaining posture, and the fact that the muscle is apparently composed of a large proportion of tonus fibers supports this conclusion. The tonus fibers would also enable toe flexion to be maintained during long periods of perching. I cannot support Owre's (1967, p. 87) contention that this muscle flexes the knee joint. The origin is from an aponeurosis associated with the knee joint capsule, and the moment arm would be virtually zero. Moreover, only a moderate number of fibers are present, thus the amount of force generated is rather low.

M. FLEXOR PERFORATUS ET PERFORANS DIGITI III

This muscle has much the same roles as does the preceding muscle except that it flexes the third digit. The flexor perforatus et perforans digiti III has a greater number of fibers and so develops a greater amount of force. The apparently high percentage of tonus fibers suggests that posture is the most important role of this muscle. There is a greater influence on tarsometatarsal extension when the intertarsal joint is nearer the fully flexed position, but this is probably the result of less resistance from the joint structures.

M. FLEXOR PERFORATUS DIGITI IV

This muscle has a very large number of fibers and is one of the largest flexor muscles. It flexes the fourth digit and extends the tarsometatarsus. The percentage of twitch fibers seems higher than in the preceding two muscles, and in addition to the fairly long fibers, which indicate a rapid contractile velocity, this would seem to indicate that this muscle may play an important role in rapid extension of the tarsometatarsus during the terminal stages of the walking cycle.

M. FLEXOR PERFORATUS DIGITI III

The medial slip of this muscle has a fairly large number of fibers, but the lateral slip is decidedly smaller. Like the other flexors, this muscle extends the tarsometatarsus, and when resistance is met from joint structures or intertarsal extensors, it flexes digit III.

M. FLEXOR PERFORATUS DIGITI II

A fairly large number of fibers are present. This muscle extends the tarsometatarsus and, when resistance is met, it flexes digit II.

M. FLEXOR HALLUCIS LONGUS

The flexor hallucis longus first extends the tarsometatarsus until resistance is met. Because of the presence of a vinculum with *M. flexor digitorum longus*, this muscle flexes all the digits and is about equally efficient for each digit. Twitch fibers seem to be more frequent than tonus; therefore, this muscle may be most important in providing rapid flexion movements of the toes rather than sustained grasping. A moderate number of fibers are present.

M. PLANTARIS

The role of this muscle has not been generally

agreed upon by previous workers. Hudson (1937, p. 37) and Miller (1937, p. 37) thought that the plantaris extends the tarsometatarsus by way of the connection between that bone and the tibial cartilage, but they listed no other possible roles. Fisher (1946, p. 688) also acknowledged possible weak extension of the tarsometatarsus, but he was of the opinion that the main function of this muscle is "to move the tibial cartilage proximally into the optimum position for the action of the tendons of the tarsal extensors and toe flexors. Thus it aids in preventing the crushing of the tendons (Gadow, 1891, p. 186) when the tarsus is extended." Owre (1967, p. 94) stated that the plantaris pulls the tibial cartilage proximally, "presumably when the tarsometatarsus is extended," but he did not consider the significance of this action.

The histological structure of the plantaris indicates that the vast majority of the fibers are tonus, and this fact provides a basis for determining the function of the muscle. Because slow, sustained contractures are apparently characteristic of the plantaris, it is doubtful whether the muscle could play a role in extending the tarsometatarsus during the walking cycle. Likewise, the role of the muscle per se is not to pull the tibial cartilage proximally so that the cartilage is in the optimal position for the flexor tendons, but rather to pull the cartilage in order to help maintain posture. When the intertarsal joint is extended, the tibial cartilage is pushed proximally by the fat pad and other connective tissue between the cartilage and hypotarsus. It is difficult to envision any time when the flexor tendons could be "crushed." During flexion of the intertarsal joint the tendons are pulled taut passively and during extension the tendons would be taut because of contraction. Furthermore, the tendons are situated in protective canals or grooves within the cartilage. In any case, only a moderate number of fibers are present, thus the amount of force generated is limited.

M. FLEXOR DIGITORUM LONGUS

This muscle probably works in close association with *M. flexor hallucis longus*. The flexor digitorum longus extends the tarsometatarsus and flexes digits II, III, and IV. The muscle has little effect on digit I, because the vinculum passes distally from the tendon of *M. flexor hallucis longus* to that of *M. flexor digitorum*

longus. Hence, the anterior toes can be flexed independently of the hallux but not vice versa (the statement of Fisher, 1946, p. 682, that the function of this muscle is the same as that of *M. flexor hallucis longus* needs to be verified on fresh specimens of cathartid vultures). The flexor digitorum longus appears to be much more effective in flexing the toes than does *M. flexor hallucis longus*. The flexor digitorum longus has a large number of fibers, the majority of which are apparently tonus. The muscle therefore certainly contributes some force to maintaining posture.

M. POPLITEUS

The role of the popliteus has been discussed by various authors, but they have not offered convincing explanations of its function. This stems from a failure to include in their studies an analysis of knee joint structure and function. Some authors have stated that the only role of the muscle is to pull the fibula medially (Hudson, 1937, p. 51; Owre, 1967, p. 91). Miller (1937, p. 35) added that the popliteus is apparently "a brace against the action of other muscles attaching to the fibula that might cause the fibula to be pulled from its position beside the tibia." It is questionable whether the popliteus functions in this manner. The head of the fibula is attached to the tibiotarsus by several ligaments and these would be sufficient (and more efficient) in protecting the fibula against disruption (which almost certainly would not be the result of muscle forces anyway). Fisher (1946, p. 683) further mentioned that the muscle "may serve to hold the caput fibulae in the fibular groove of the femur when the tibia is rotated inward and forward as the bird 'toes in.' " Because the complex ligamental system of the knee joint seems to be sufficient for maintaining the relative positions of the articular surfaces, it is doubtful that the popliteus is important in this process.

The popliteus has very few fibers and thus develops little force. From my examination of fresh specimens I have found that the popliteus seems to have little effect in pulling the fibula posteromedially. Moreover, this action probably is not necessary, because as the joint is flexed, the fibula is pulled posteriorly by the combined action of the ligaments and the forces distributed across the joint surfaces. The popliteus has both twitch and tonus fibers, and it may be that the muscle is important in resisting and controlling

the forward velocity of the fibula as the joint is extending. This, in turn, may have some effect on controlling knee joint extension itself. Yet, the muscle is so small that even this role can be reasonably doubted. No clear explanation can be given at this time.

M. PERONEUS LONGUS

The main function of this muscle is to extend the tarsometatarsus by means of the interconnections of the tibial cartilage and the hypotarsus. All previous workers have noted the joining of the anterior tendon to that of *M. flexor perforatus digiti III* and have assumed this implies a role in flexion of the third digit. Because of the posterior connections with the tibial cartilage, the thin anterior tendon is not pulled proximally far enough to cause much toe flexion. This muscle brings about almost no lateral swing as this is resisted by joint structures on the medial side. Miller (1937, p. 37) believed that the peroneus longus would counteract the toeing-in produced by the gastrocnemius. However, the peroneus longus itself causes a slight medial rotation and turning inward of the toes.

That there are many fibers, of which about half appear to be tonus, indicates this muscle plays a role in maintaining posture.

M. TIBIALIS ANTERIOR

The numerous, long twitch fibers found in this muscle clearly indicate that the tibialis anterior functions to flex the tarsometatarsus very rapidly and through a wide arc of joint movement. In nonaquatic birds the large force that is generated is needed only to develop the necessary torque for high angular velocities. I question the correctness of Miller's statement (1937, p. 32) that the posterior slip functions merely as a counteracting force for those toe flexors that arise from the femur. As I have argued above, these flexors probably contribute little to knee joint flexion, and, moreover, they could be easily "balanced" by any one of the large extensors. Upon superficial examination, it would seem that the posterior slip would contribute significant force for knee joint extension. There are at least two arguments against this view (held by Miller, 1937; Fisher, 1946; and Owre, 1967, p. 86; the latter author stated that this slip flexed the tibiotarsus, but this is surely a typographical error). First, the moment arm is so small that little torque could be developed.

Second, and most important, the time during the locomotor cycle when the tibialis anterior must be functioning to flex the tarsometatarsus is the exact time when the knee joint must be flexed and not extended. I suggest, then, that the posterior slip has evolved to enable the addition of muscle fibers (therefore, more force generated) which maintain a minimum length. If these fibers had been added to the anterior slip instead, problems of space would have required the fibers to become shorter. This would have greatly reduced the contractile velocity and excursion, and hence, the effectiveness of the muscle. When extension torques are placed on the knee joint by the posterior slip, these can easily be counteracted by the numerous flexors of the tibiotarsus (this may be one of the functions of the biceps femoris and semimembranosus).

M. EXTENSOR DIGITORUM LONGUS

The extensor digitorum longus has a moderate number of fibers that are fairly long, but do not have to shorten much to extend the digits significantly. The muscle also flexes the tarsometatarsus slightly, and the opposition of the toe flexors is not necessary for this action as stated by Miller (1937, p. 37). Indeed, if the toe flexors were contracting, they would easily counteract any forces of the extensor digitorum longus that were causing flexion of the tarsometatarsus.

M. PERONEUS BREVIS

There is considerable difference of opinion as to the function of this muscle. Hudson (1937, p. 34), Fisher (1946, p. 684), and Owre (1967, p. 92) all listed abduction of the tarsometatarsus. Fisher and Owre and also Miller (1937, p. 35) included tarsometatarsal extension as a role of this muscle.

I doubt whether the peroneus brevis is important in causing abduction, because this latter movement is all but prevented by the joint structures. 'Tarsometatarsal extension may be possible in rare cases where the tendon of insertion apparently has a connection to the tibial cartilage (Fisher, 1946, p. 684). But in the vast majority of birds the peroneus brevis probably does not extend the tarsometatarsus but instead flexes it. The functional conclusions of previous workers seem to have been based on study of preserved material, and the conclusions need to be re-evaluated using fresh specimens.

The peroneus brevis has very short fibers, and

so its contribution to tarsometatarsal flexion (or extension, as the case may be) is certainly minimal. More important in *Columba* is the role of causing medial rotation (toeing-in) of the tarsometatarsus. Very little shortening is necessary to effect this action; medial rotation is ultimately limited by the joint structures. Miller (1937, p. 35) thought that the peroneus brevis might counteract rotational forces of the gastrocnemius. At least in *Columba* this is doubtful as the gastrocnemius does not cause such rotational movements.

The peroneus brevis could possibly operate to counteract the forces of tarsometatarsal extension created by the toe flexors and thereby aid the latter muscles in toe flexion.

M. EXTENSOR HALLUCIS LONGUS

This muscle has a fairly large number of fibers, the distal head being approximately one-third to one-half as large as the proximal head. The muscle acts to extend the hallux. It is interesting to note the apparently low number of tonus fibers, which indicates that the muscle does not maintain the hallux in an extended position for very long periods of time.

M. ABDUCTOR DIGITI II

In *Columba* the abductor digiti II seems to have a variety of roles, all of which suggest that it is important in the fine control of the second digit. There are few fibers, and thus little force is developed. The muscle can flex phalanx I if the phalanx is already in the flexed position. Likewise, the muscle also appears to contribute to extension, if the phalanx is in the extended position. These movements take place because

the tendon can slide over the surface of the trochlea with movement of the phalanx. Extension movements appear stronger than those of abduction or flexion. The large proportion of twitch fibers would facilitate rapid and fine control of the movements.

M. EXTENSOR PROPRIUS DIGITI III

A moderate number of fibers are present. The muscle extends the first phalanx of digit III.

M. EXTENSOR BREVIS DIGITI IV

This is a small muscle but there is a considerable number of fibers as the latter are very short. The extensor brevis digiti IV moves the digit slightly mediad. Very little, if any, extension takes place as the mechanical advantage of the muscle is poor.

M. LUMBRICALIS

Because the lumbricalis has few fibers, only weak flexion of digits III and IV is possible. It is difficult to see the advantage in pulling the sub-articular cartilages proximally, as they move that direction with any flexion of the toes.

M. ABDUCTOR DIGITI IV

This muscle pulls phalanx I laterally and also perhaps extends the phalanx slightly.

M. FLEXOR HALLUCIS BREVIS

A fairly large number of fibers are present which contribute to flexing the hallux.

M. ADDUCTOR DIGITI II

A moderate number of fibers are present. The muscle pulls digit II laterally.

ANALYSIS OF THE LOCOMOTOR PATTERNS

IN FUNCTIONAL STUDIES of vertebrate locomotion the importance of having an accurate description of the different locomotor patterns cannot be overemphasized. Without such a description, a reasonably precise explanation of the morphological factors producing the patterns is almost impossible. The absence of a detailed analysis of locomotor patterns has seriously limited the functional explanations of the avian hind-limb bone-muscle system. Unfortunately, the problems cannot be resolved merely by making unaided visual observations or even by photography at conventional speeds. Instead, owing to the minute details that must be recorded, the various kinds of information that must be collected about the locomotor cycle, and the speed of the individual events, it is almost mandatory that high-speed motion picture analysis be employed (see Materials and Methods). With this technique numerous measurements, such as angular displacements and angular velocities of the joints, can be made and eventually correlated with the morphological and physiological data gathered from a study of the muscles to produce a reasonably rigorous functional interpretation of the locomotor cycle.

THE WALKING CYCLE

Although analyses were made of 14 walks of differing speeds, for convenience I will describe and compare only three representing slow, moderate, and fast gaits. These three walks will be sufficient to demonstrate the patterns of movement of the several limb elements. The locomotor cycle will be defined as beginning when the right foot touches the ground and ending when the foot again touches the ground.

THE SLOW WALK

Figure 22 illustrates a walk of slow speed (133 frames long) of *Columba livia*. Only the movements of the femur, tibiotarsus, and tarsometatarsus are shown. The movements of the foot are omitted for the present (but see below) as they greatly complicate the figure. Except for the last two diagrams (frames 120 and 133), all are 10 frames apart, or, at 250 frames per second, 1/25 of a second apart.

Table 1 gives the measurements of the joint

angles, angular displacements, and angular velocities of each element throughout the cycle.

Soon after the foot strikes the ground, there is a tendency for the hip joint angle (measured anteriorly) to increase slightly. Near the end of the propulsion phase which takes place between frames 30 and 86, and during the recovery phase (frames 86–133), the femur protracts and the angle decreases as the lower part of the leg is brought forward. The elements of the hip joint exhibit far less motion relative to one another than do the elements of any other joint. In the walking cycle of figure 22 the femur circumscribes an arc of only 18 degrees. This arc in 13 other locomotor cycles of different speeds varied from 15 to 46 degrees with an average of 28 degrees, but no correlation exists between the amount of the arc and the speed of the gait. Because the femur does not show large angular displacements, the average angular velocity is low. The greatest angular velocity was measured at 200 degrees/second or at about 3.5 radians/second.

The knee joint is nearly in the fully extended position when the foot strikes the ground. As the leg begins to support the weight of the bird, the knee joint flexes sharply (frames 0–10). The force for this flexion can be attributed to the effect of gravity rather than actual contraction of the muscles; only with lift-off is the joint actively flexed by the muscles. Before lift-off, knee joint flexion proceeds rather gradually (frames 10–80), but with lift-off (frames 80–90) a higher angular velocity of flexion is observed (650 degrees/second or about 11.4 radians/second). This marked increase in flexion results from the onset of flexor muscle activity which was not present (or at least the muscles were not contracting) previous to this point. As the tibiotarsus is extended, just before the leg again touches the ground, high angular velocities are noted. The greatest angular velocity was recorded between frames 110 and 120 and was measured at 875 degrees/second or approximately 15.3 radians/second. The knee joint pictured in figure 22 exhibited a total arc of movement of 97 degrees. In 13 additional locomotor cycles the knee joint had an arc of movement from 85 to 107 degrees with an average of 95 degrees. As in the hip joint no correlation was

TABLE 1
LEG JOINTS DURING SLOW WALK^a

Frame	Hip Joint			Knee Joint			Intertarsal Joint		
	Angle ^b	Angular Displacement ^c	Angular Velocities ^d	Angle	Angular Displacement	Angular Velocities	Angle	Angular Displacement	Angular Velocities
0	66	—	—	144	—	—	153	—	—
	—	0	0	—	-18	-450 (-7.9)	—	-20	-500 (-8.7)
10	66	—	—	126	—	—	133	—	—
	—	+1	+25 (+0.44)	—	-13	-325 (-5.7)	—	-7	-175 (-3.1)
20	67	—	—	113	—	—	126	—	—
	—	0	0	—	-13	-325 (-5.7)	—	-8	-200 (-3.5)
30	67	—	—	100	—	—	118	—	—
	—	-5	-125 (-2.2)	—	-13	-325 (-5.7)	—	+5	+125 (+2.2)
40	62	—	—	87	—	—	123	—	—
	—	+3	+75 (+1.3)	—	-5	-125 (-2.2)	—	+5	+125 (+2.2)
50	65	—	—	82	—	—	128	—	—
	—	+8	+200 (+3.5)	—	+3	+75 (+1.3)	—	+18	+450 (+7.9)
60	73	—	—	85	—	—	146	—	—
	—	+5	+125 (+2.2)	—	-8	-200 (-3.5)	—	+10	+250 (+4.4)
70	78	—	—	77	—	—	156	—	—
	—	+2	+50 (+0.88)	—	-2	-50 (-0.88)	—	+9	+225 (+3.9)
80	80	—	—	75	—	—	165	—	—
	—	-6	-150 (-2.6)	—	-26	-650 (-11.4)	—	-34	-850 (-14.8)
90	74	—	—	49	—	—	131	—	—
	—	+1	+25 (+0.44)	—	-2	-50 (-0.88)	—	-40	-1000 (-17.5)
100	75	—	—	47	—	—	91	—	—
	—	-8	-200 (-3.5)	—	+18	+450 (+7.9)	—	-17	-425 (-7.4)
110	67	—	—	65	—	—	74	—	—
	—	-5	-125 (-2.2)	—	+35	+875 (+15.3)	—	+12	+300 (+5.2)
120	62	—	—	100	—	—	86	—	—
	—	+8	+200 (+3.5)	—	+34	+850 (+14.8)	—	+57	+1425 (+25)
133	70	—	—	134	—	—	143	—	—

^aSee figure 22.

^bJoint angle (to nearest degree).

^cAngular displacement (to nearest degree); minus (-), decrease in joint angle; plus (+), increase in joint angle.

^dAngular velocity; degrees/second (radians/second).

observed between the speed of the gait and the arc of movement.

In contrast to the knee joint, the intertarsal joint is subjected to more sustained, and more continuously changing, high angular velocities. When the foot touches the ground, the joint is somewhat less than fully extended. The large forces of impact cause a rapid flexion of the joint, but this movement lasts a short time (frames 0-30). Then, during the propulsion phase (frames 30-80), the joint is actively and rapidly extended until, at lift-off, the intertarsal joint has nearly attained the fully extended position. Immediately after lift-off the intertarsal joint is rapidly flexed to about 70-90 degrees and is maintained more or less constant at this angle as the lower leg is advanced forward (frames 90-120). The

joint is then rapidly extended before the foot again touches the ground (frames 110-133). In figure 22 the intertarsal joint circumscribes an arc of about 91 degrees. Arcs in 13 other cycles ranged from 88 to 110 degrees and averaged 96 degrees. As seen in table 1 the intertarsal joint maintains higher angular velocities throughout the cycle than does the knee joint. For example, during the flexion phase after lift-off (frames 90-100) the joint attains a velocity of -1000 degrees/second or about -17.5 radians/second, and during the final extension phase the joint reaches a velocity of 1425 degrees/second or 25 radians/second.

Figure 23 summarizes the above data by graphically illustrating the flexion-extension phases of the three joints during the slow walking

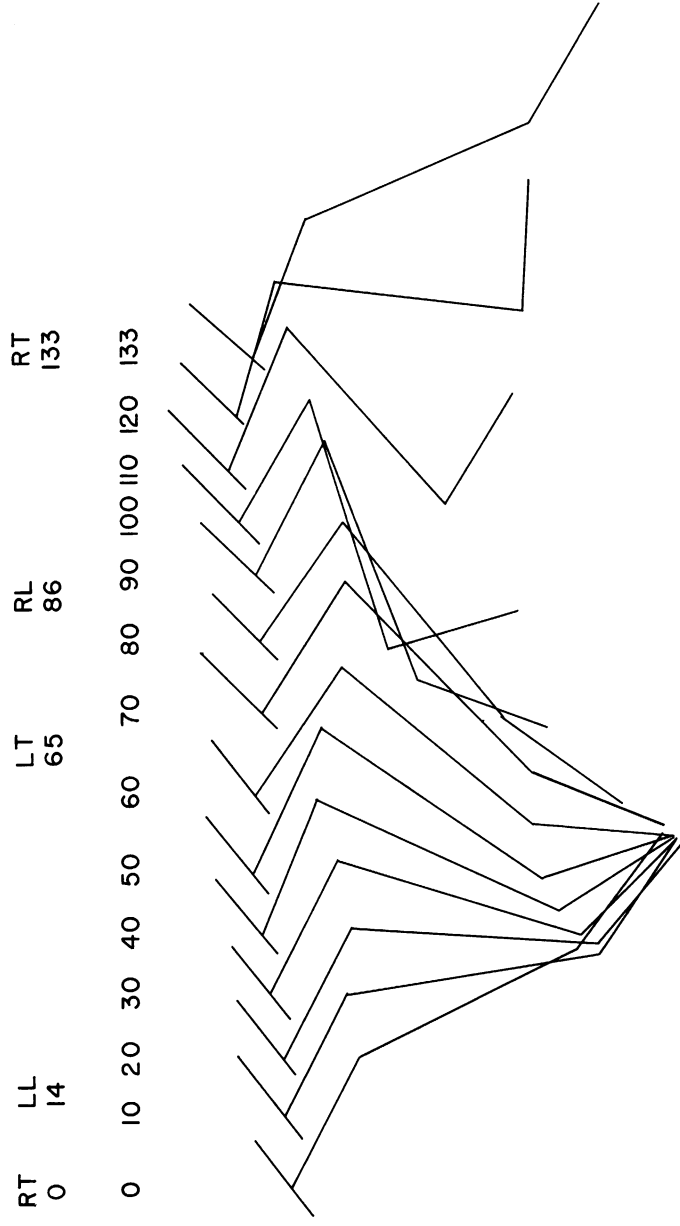


FIG. 22. Stick diagram showing a slow walk (133 frames long) in *Columba livia* taken at a speed of 250 frames per second. Only the pelvic axis, femur, tibia, and tarsometatarsus are shown.
Abbreviations: LL, left foot leaving ground; LT, left foot touching ground; RL, right foot leaving ground; RT, right foot touching ground.

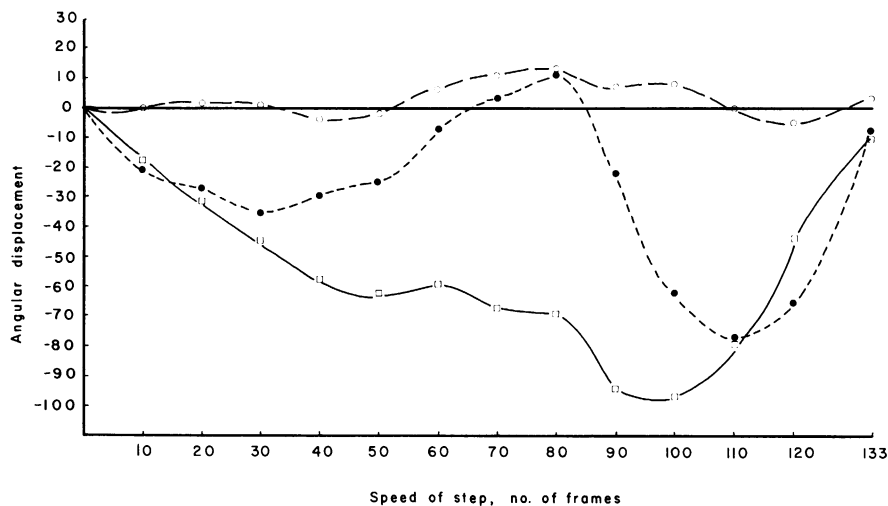


FIG. 23. Angular displacement of hind-limb joints in *Columba livia* plotted against speed of step of a slow walk (see fig. 22). Hip joint, open circles, base line equals 66 degrees; knee joint, open squares, base line equals 144 degrees; intertarsal joint, dark circles, base line equals 153 degrees.

cycle of figure 22. A change of the coordinates in a positive direction along the y-axis indicates retraction of the femur and extension of the knee and intertarsal joints; change in a negative direction along the y-axis indicates protraction of the femur and flexion of the knee and intertarsal joints. The slopes of the curves are proportional to the angular velocity. The hip joint clearly shows the least amount of angular displacement. Nevertheless, two fairly well-marked phases are noticeable. From frame 40 near the beginning of the cycle to frame 80 shortly before the lift-off, the femur has a retraction phase, but at the onset of lift-off the femur is protracted and the leg is brought forward. Movement at the knee joint can also be divided into two well-defined phases, a gradual flexion phase and a rapid extension phase. Figure 23 illustrates the decided break between the passive and active portions of the flexion phase (but see also below). Frames 0–80 show a relatively smooth slope, but between frames 80 and 90 the steepness of the slope increases markedly. The intertarsal joint shows more complicated movement with two flexion peaks (frames 30 and 110) and two extension peaks (frames 80 and 133). The slopes of the curves, i.e., the angular velocities, are accordingly greater than those of the knee joint.

THE MODERATE WALK

Figure 24 shows a stick-diagram of a decidedly faster walk (96 frames long) than that of figure 22. The joint angles, angular displacements, and angular velocities are given in table 2, and a graph of the angular displacements is pictured in figure 25. Examination of tables 1 and 2 demonstrates that, as might be expected, the angular velocities of the joints in the slow walk are generally lower than those of the moderate gait.

The hip joint of the moderate walk exhibits the same two-phased pattern that is seen in the slow walk, that is, retraction (frames 10–40) followed by protraction (frames 40–96) as the leg is brought forward. Interestingly, the relative timing of the two phases does not seem proportionate. The retraction phase is shifted slightly more to the left in the moderate gait, which means that in this cycle the retraction phase is starting relatively sooner and the protraction phase is lasting relatively longer.

The patterns of the knee and intertarsal joints in figures 23 and 25, are in general, very similar. Of particular importance are the differences in the angular velocities shown by the two joints at various phases of the cycle and the differences in the relative onset of some patterns in the two cycles.

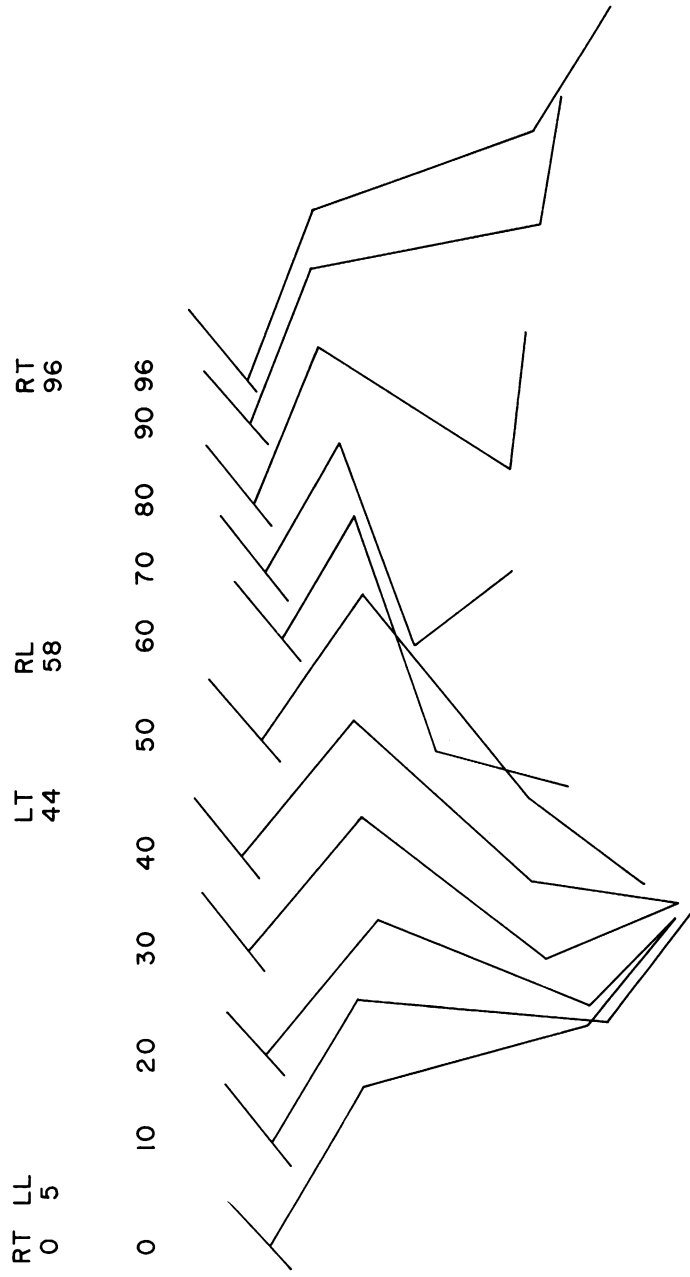


FIG. 24. Stick diagram of *Columba livia* showing a walk of moderate gait (96 frames long) taken at a speed of 250 frames/second. Only the pelvic axis, femur, tibiotarsus, and tarsometatarsus are shown.
 Abbreviations: LL, left foot touching ground; LT, left foot leaving ground; RL, right foot touching ground; RT, right foot leaving ground.

TABLE 2
LEG JOINTS DURING WALK OF MODERATE GAIT^a

Frame	Hip Joint			Knee Joint			Intertarsal Joint		
	Angle ^b	Angular Displacement ^c	Angular Velocity ^d	Angle	Angular Displacement	Angular Velocity	Angle	Angular Displacement	Angular Velocity
0	74	—	—	136	—	—	144	—	—
	—	-3	-75 (-1.3)	—	-19	-475 (-8.3)	—	-21	-525 (-9.2)
10	71	—	—	117	—	—	123	—	—
	—	+12	+300 (+5.2)	—	-9	-225 (-3.9)	—	-10	-250 (-4.4)
20	83	—	—	108	—	—	113	—	—
	—	-4	-100 (-1.75)	—	-15	-375 (-6.5)	—	+7	+175 (+3.1)
30	79	—	—	93	—	—	120	—	—
	—	+1	+25 (+0.44)	—	-5	-125 (-2.2)	—	+26	+650 (+11.4)
40	80	—	—	88	—	—	146	—	—
	—	-3	-75 (-1.3)	—	-13	-325 (-5.7)	—	+20	+500 (+8.7)
50	77	—	—	75	—	—	166	—	—
	—	-6	-150 (-2.6)	—	-25	-625 (-11)	—	-42	-1050 (-18.4)
60	71	—	—	50	—	—	124	—	—
	—	-1	-25 (-0.44)	—	+1	+25 (+0.44)	—	-51	-1275 (-2.2)
70	70	—	—	51	—	—	73	—	—
	—	-8	-200 (-3.5)	—	+30	+750 (+13)	—	-8	-200 (-3.5)
80	62	—	—	81	—	—	65	—	—
	—	+2	+50 (+0.88)	—	+41	+1025 (+18)	—	+45	+1125 (+19.6)
90	64	—	—	122	—	—	110	—	—
	—	-2	-50 (-0.88)	—	+9	+225 (+3.9)	—	+31	+775 (+13.5)
96	62	—	—	131	—	—	141	—	—

^a See Fig. 24.

^b Joint angle (to nearest degree).

^c Angular displacement (to nearest degree); minus (-), decrease in joint angle; plus (+), increase in joint angle.

^d Angular velocity; degrees/second (radians/second).

A comparison of the knee joint patterns of figures 23 and 25 shows that the slope of the flexion phase is somewhat less steep in the slow walking animal, but that the slopes of the extension phases are more nearly the same. This can be interpreted to mean that as the bird increases its forward speed, the knee joint component of this increase may be relatively greater in the flexion phase than in the extension phase. But the differences are not striking and will have to be verified with future work. The extension phase of the moderate walk takes place relatively sooner than that of the slow walk (see also fig. 29). Thus, although the extension phase of the moderate walk is faster absolutely and develops greater angular velocities than the same phase of the slow walk, the extension phase of the moderate walk is about 10 per cent longer with respect to the time of a single step.

The two patterns of the intertarsal joint in figures 23 and 25 have different angular veloci-

ties in the different phases. The slope of the first extension (propulsion) phase (frames 20-50 in fig. 25) is decidedly steeper in the moderate gait pigeon than the slow-walking bird. On the other hand, the slopes of the flexion phase (frames 50-80) and the final extension phase (frames 80-96) are only slightly greater in the moderate gait animal. Hence, this seems to indicate that the contribution of the intertarsal joint to the increase of speed is relatively greater in the propulsion phase than in the final extension phase. Like the knee joint, several phases of the moderate walk appear to occur relatively sooner in the cycle than they do in the slow-walking bird. For example, figure 30 shows that the flexion (lift-off) phase and the final extension phase occur 5 to 10 per cent sooner in the moderate walk.

THE FAST WALK

Figure 26 shows a stick-diagram of a running pigeon whose step is completed in 70 frames.

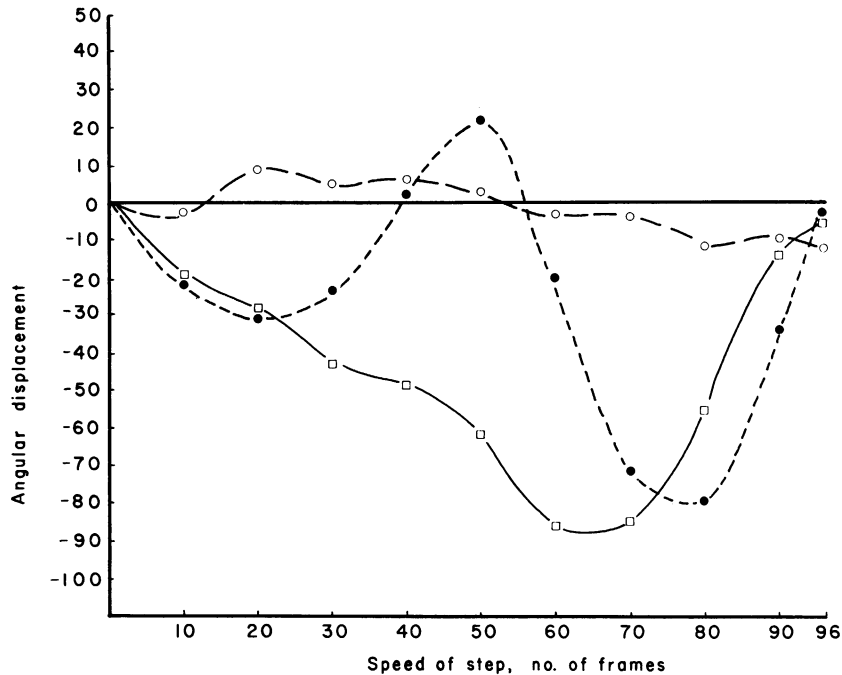


FIG. 25. Angular displacement of hind-limb joints of *Columba livia* plotted against speed of step in a walk of moderate gait (see fig. 24). Hip joint, open circles, base line equals 74 degrees; knee joint, open squares, base line equals 136 degrees; intertarsal joint, dark circles, base line equals 144 degrees.

The joint angles, angular displacements, and angular velocities are given in table 3, and the angular displacements are plotted graphically in figure 27. The data of table 3 demonstrate quite clearly that all three joints of the fast walk undergo very much higher angular velocities. In the hip joint the peak angular velocity is 3.5 radians/second higher than in the moderate walk and 5.2 radians/second higher than in the slow walk. The peak velocity of the knee joint is 9.0 radians/second higher than in the moderate walk and 11.7 radians/second higher than in the slow walk. The intertarsal joint shows the greatest differences with its peak angular velocity in the run being 16 radians/second faster than in the moderate walk and 13 radians/second faster than in the slow walk (the higher velocity recorded during the slow walk in table 1 was averaged over 13 frames instead of the normal 10, thus the difference between the run and slow walk is less than what would be expected). The incredibly large angular velocities some joints are subjected to are seen in the final extension phase of the intertarsal joint where the joint attains a velocity of 2175 degrees/second or 38 radians/second.

Moreover, because the running cycle is shorter, the changes from negative to positive and vice versa are more abrupt and the angular accelerations are much greater (the angular accelerations are represented by the slopes of figs. 28–30).

In general, the pattern of each joint is the same in the run as in the two walks, but the different elements show less oscillation in the run (compare fig. 27 with figs. 23 and 25). This damping of the oscillation in the run has two readily apparent explanations. First, the cycle is so short that oscillations are not so evident when every 10 frames are pictured (but compare figs. 28, 29, and 30 in which the cycle is drawn in terms of the per cent of step, that is, every seven frames in the run). Second, the movements of the elements are more forceful and faster and because of this are less likely to oscillate.

A comparison of figure 27 with figures 23 and 25 suggests several conclusions about the motion at the hip joint. The retraction phase during a run (frames 0–40 in fig. 27) occupies a relatively greater part of the whole step and has its onset shifted to the very beginning of the cycle. At the

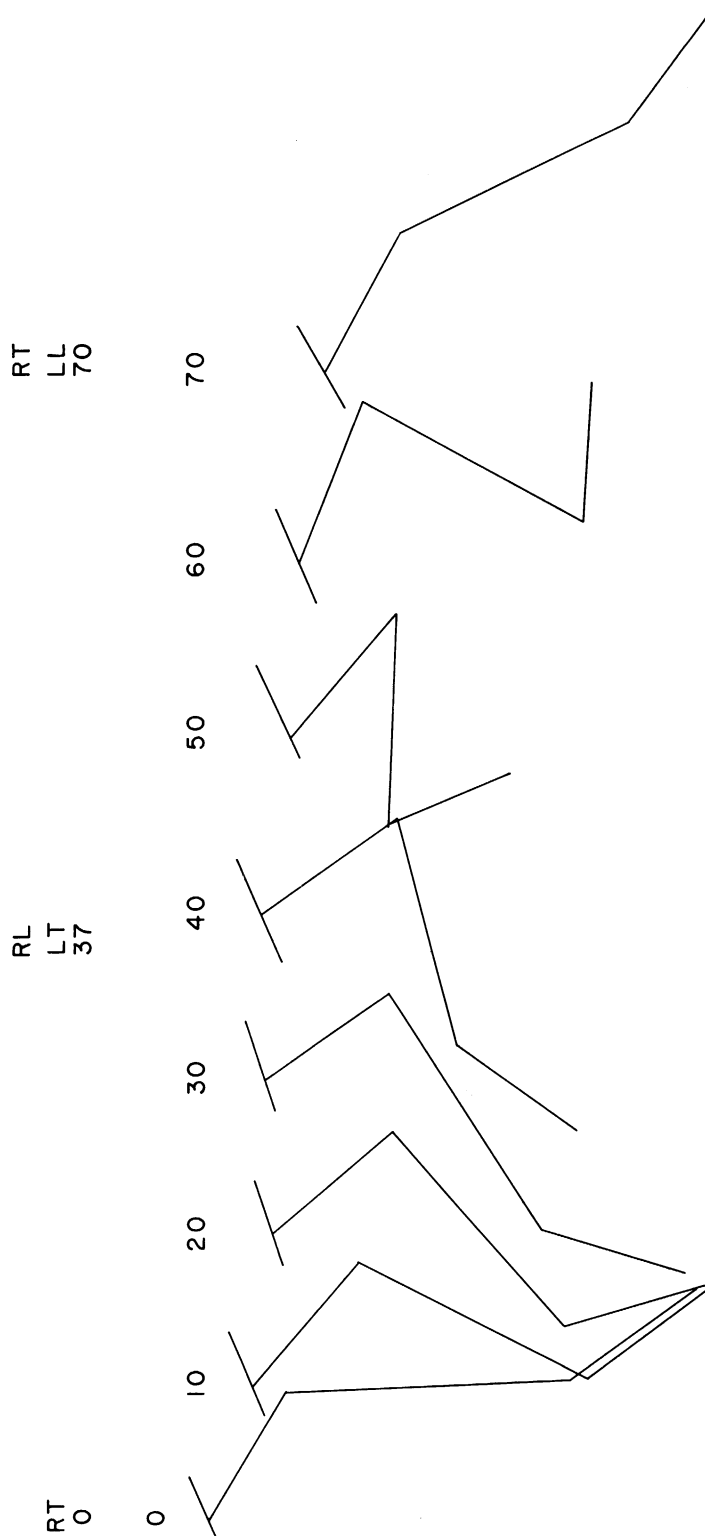


FIG. 26. Stick diagram showing a run (70 frames long) of *Columba livia* taken at 250 frames per second. Only the pelvic axis, femur, tibia, and tarsometatarsus are shown.

Abbreviations: LL, left foot leaving ground; LT, left foot touching ground; RL, right foot leaving ground; RT, right foot touching ground.

TABLE 3
LEG JOINTS DURING RUN^a

Frame	Angle ^b	Hip Joint		Angle	Knee Joint		Angle	Intertarsal Joint	
		Angular Displacement ^c	Angular Velocity ^d		Angular Displacement	Angular Velocity		Angular Displacement	Angular Velocity
0	55	—	—	123	—	—	146	—	—
	—	+9	+225 (+3.9)	—	-19	-475 (-8.3)	—	-30	-750 (-13)
10	64	—	—	104	—	—	116	—	—
	—	+5	+125 (+2.2)	—	-13	-325 (-5.7)	—	-1	-25 (-0.44)
20	69	—	—	91	—	—	115	—	—
	—	+5	+125 (+2.2)	—	-3	-75 (-1.3)	—	+24	+600 (+10.5)
30	74	—	—	88	—	—	139	—	—
	—	+5	+125 (+2.2)	—	-19	-475 (-8.3)	—	+1	+25 (+0.44)
40	79	—	—	69	—	—	140	—	—
	—	-3	-75 (-1.3)	—	-31	-775 (-13.5)	—	-76	-1800 (-31)
50	66	—	—	38	—	—	64	—	—
	—	-20	-500 (-8.7)	—	+45	+1125 (+19.7)	—	+1	+25 (+0.44)
60	46	—	—	83	—	—	65	—	—
	—	+14	+350 (+6.1)	—	+61	+1525 (+27)	—	+87	+2175 (+38)
70	60	—	—	144	—	—	152	—	—

^a See Fig. 26.

^b Joint angle (to nearest degree).

^c Angular displacement (to nearest degree); minus (-), decrease in joint angle; plus (+), increase in joint angle.

^d Angular velocity; degrees/second (radians/second).

same time, the protraction phase is relatively shorter in the run.

The knee joints of all three cycles are similar, and all three change from flexion to extension at about the same relative position in the cycle. No noticeable differences are apparent between the onset of the phases in the run and moderate walk, but both of these differ from the slow walk as explained above (see also fig. 29). In figure 27 the passive part of the flexion phase is approximately frames 0-30, whereas the active part of the phase takes place between frames 30 and 50.

The patterns of the intertarsal joint are relatively similar in the three cycles, but there are some differences in the onset of the various phases. In both the run and moderate walk the propulsion phase reaches its peak slightly in advance of the peak in the slow walk (fig. 30), although the slope of this extension is steeper in the run than in the moderate walk. The flexion phase following lift-off occurs sooner in the run, and the peak occurs at 60 per cent of the step instead of 70 per cent as in the moderate and slow walks. It follows that the final extension phase begins sooner in the run than in the moderate or slow walks.

THE FOOT-FALL PATTERNS

A well-known characteristic of locomotor cycles in terrestrial vertebrates is that the amount of time the individual limbs are in contact with the ground during a step is inversely proportional to the speed of the gait. This is true also for the walking cycles of the pigeon as reflected in the amount of overlap of the right and left feet (fig. 31). Figure 31A shows the foot-fall pattern of the moderate walk of figure 24. The right and left feet overlap for about 20 per cent of the step and each foot is on the ground about 60 per cent of the step. The slow walk of figure 22 is pictured in figure 31B. The overlap has increased to 26 or 27 per cent and the amount of time on the ground to 63 or 64 per cent. Figure 31C shows the run of figure 26, and in this case the overlap has dropped to about zero and the time on the ground is about 50 per cent for each foot. The per cent of overlap for 11 other cycles and the three just discussed are plotted in figure 32. As expected, there is a direct relationship between the amount of overlap and the length of time for a stride. It should be pointed out that it is possible to have pigeons running faster than 70 frames/second, but that the over-

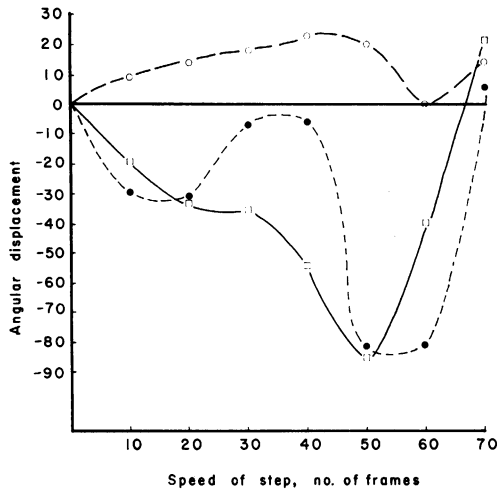


FIG. 27. Angular displacement of hind-limb joints in *Columba livia* plotted against speed of step of a running gait (see fig. 26). Hip joints, open circles, base line equals 55 degrees; knee joint, open squares, base line equals 123 degrees; intertarsal joint, dark circles, base line equals 146 degrees.

lap is still zero. It is also possible during a given step for both legs to be off the ground at the same time, although this would occur only rarely under natural conditions.

MOVEMENTS OF THE FOOT

Figure 33 illustrates the movements of the tarsometatarsus and foot during a walking cycle 101 frames long. Drawings for frames 10 and 20 have been omitted as they would have greatly complicated the figure; no information is lost as there is little movement during this time period, and furthermore, the movements of the tarsometatarsus can be observed in figures 22, 24, and 26.

Because this study was concerned mainly with the movements of the leg elements proximal to the foot, the photographic techniques were not ideal for recording the detailed movements of the toes. As mentioned above, the speed of the camera (250 frames/second) was not fast enough to completely stop the action of the toes. Also, the distance between the bird and the camera, although adequate to record general leg movements, was too great to allow the resolution necessary for detailed study of the toes. Nevertheless, the techniques employed permit a broad outline of the joints in the foot. This is important

because many of the muscles causing these movements are also responsible for motions at other joints as well.

As the foot makes contact with the ground, the hallux and foretoes touch at very nearly the same time. With the foot on the ground the forward momentum of the bird flexes the tarsometatarsal-phalangeal joints (frames 0–50). At lift-off the foretoes are the last part of the foot to leave the ground, and soon after lift-off (frame 60) the foretoes and hallux are in the extended position. As the intertarsal joint is flexed (frame 70), the foretoes are also flexed, but this is certainly the result of the tightening of the flexor tendons over the posterior side of the intertarsal joint. The toes are then extended as the leg prepares to touch the ground again. Throughout the cycle the hallux maintains a relatively constant angle to the axis of the tarsometatarsus, but it does seem to extend slightly as the foot is placed on the ground. This extension of the hallux probably does not have as large a “passive component” of extension as occurs in the foretoes. Instead, the hallux is probably actively extended by muscles.

LANDING

The general features of landing in the domestic pigeon have been described by Fisher (1956a, 1959), and I will treat only those aspects that will be used in a later discussion of muscle function.

When a pigeon prepares to land, the knee and intertarsal joints are extended; the extension of the intertarsal joint automatically extends the toes. The knee and intertarsal joints are extended only slightly more than at the completion of a walking cycle. Because the pigeons in my experiments had their wings immobilized, the degree of extension in the joints is undoubtedly greater than what is observed under natural conditions. As the feet approach the ground, the second and fourth toes are abducted and all the toes are actively extended. Fisher (1956a, p. 90) found that the two legs are extended uniformly in only about 25 per cent of the landings. My observations substantiate this; the trailing leg usually extends faster than the leading leg, so that both touch the ground at approximately the same time. It is not uncommon, however, for one foot to touch before the other, as Fisher observed.

On landing, the joints of the experimental birds show a characteristic pattern with respect

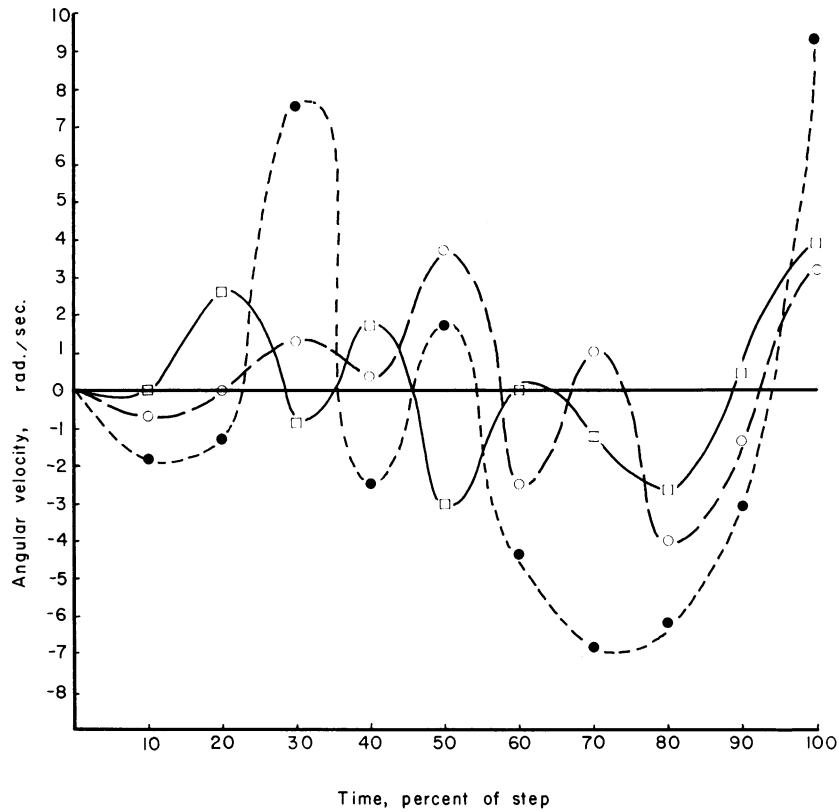


FIG. 28. Angular velocity (radians per second) of hip joint (femur) in moderate, slow, and running gaits of *Columba livia* plotted against time (per cent of step). Moderate gait, open squares, see fig. 22; slow gait, open circles, see fig. 24; running gait, dark circles, see fig. 26.

to flexion. The intertarsal joint exhibits the greatest amount of flexion, and the joint angle frequently decreases to less than 90 degrees, especially when the bird is off balance. The knee joint also flexes upon landing but not to the degree that the intertarsal joint does. Finally, the femur apparently shows the least amount of movement, but yet it may be protracted under some conditions until it is nearly parallel with the long axis of the pelvis.

REMARKS

It is difficult, if not impossible, to compare the above results with those of other workers as none of the latter has utilized high-speed cinematography. Several authors have constructed stick-diagrams based on visual observations, still photographs, or conventional motion-picture photography. For example, Stolpe's (1932)

diagrams of unnamed walking and swimming birds were apparently based on visual observations and still photographs and as such are not necessarily an accurate representation of what occurs in life. Similarly, Miller (1937) used visual observations and photographs to draw the walking sequence of the goose *Branta canadensis*. Sigmund (1959) photographed three species of rails at 24 to 64 frames/second and constructed diagrams from which he showed the arcs circumscribed by each of the elements. Unfortunately, Sigmund did not mention how the movements of the knee and hip joints (which are not visible on his illustrations) were measured. The most important point, which must be stressed, is that all previous functional studies of the avian hind limb have been based on inadequate data concerning the actual movements of living organisms. It is critical to know when during a walking cycle particular elements are reaching their

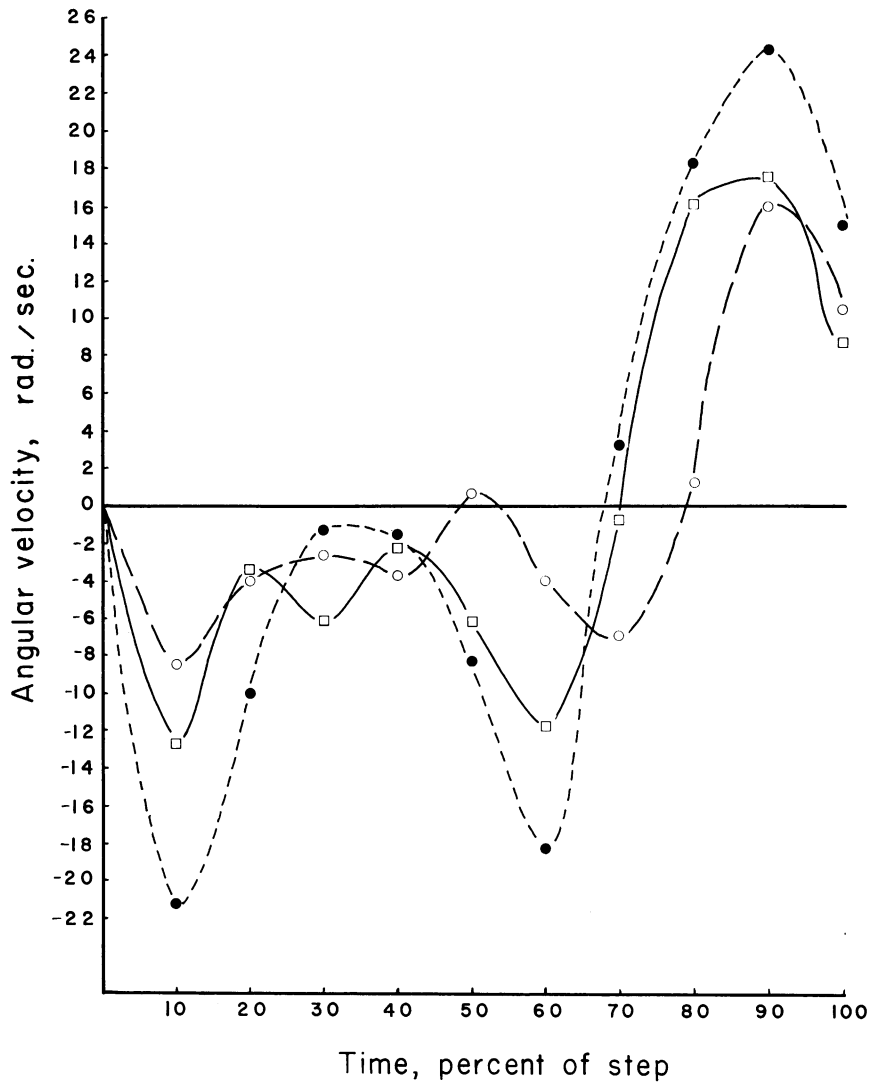


FIG. 29. Angular velocity (radians per second) of knee joint (tibiotarsus) in moderate, slow, and running gaits of *Columba livia* plotted against time (per cent of step). Moderate gait, open squares, see fig. 22; slow gait, open squares, see fig. 24; running gait, dark circles, see fig. 26.

peak angular velocity. A knowledge of the curves of the angular velocities will permit numerous statements about the onset, peak activity, and termination of muscle activity. In some cases it may even be possible to identify precisely the period of contraction.

The above data suggest that high-speed cinematography can provide information as to how an animal increases its speed. Do certain skeletal elements increase their velocity relatively faster

than do other elements? If differential rate changes can be identified by cinematography, then this information is likely to help identify the morphological factors responsible for the observed changes.

In summary, once a worker has a reasonable understanding of the locomotor patterns, he can begin to construct a morphological—but more importantly, a functional—interpretation of these patterns. Thus, the functional morphologist

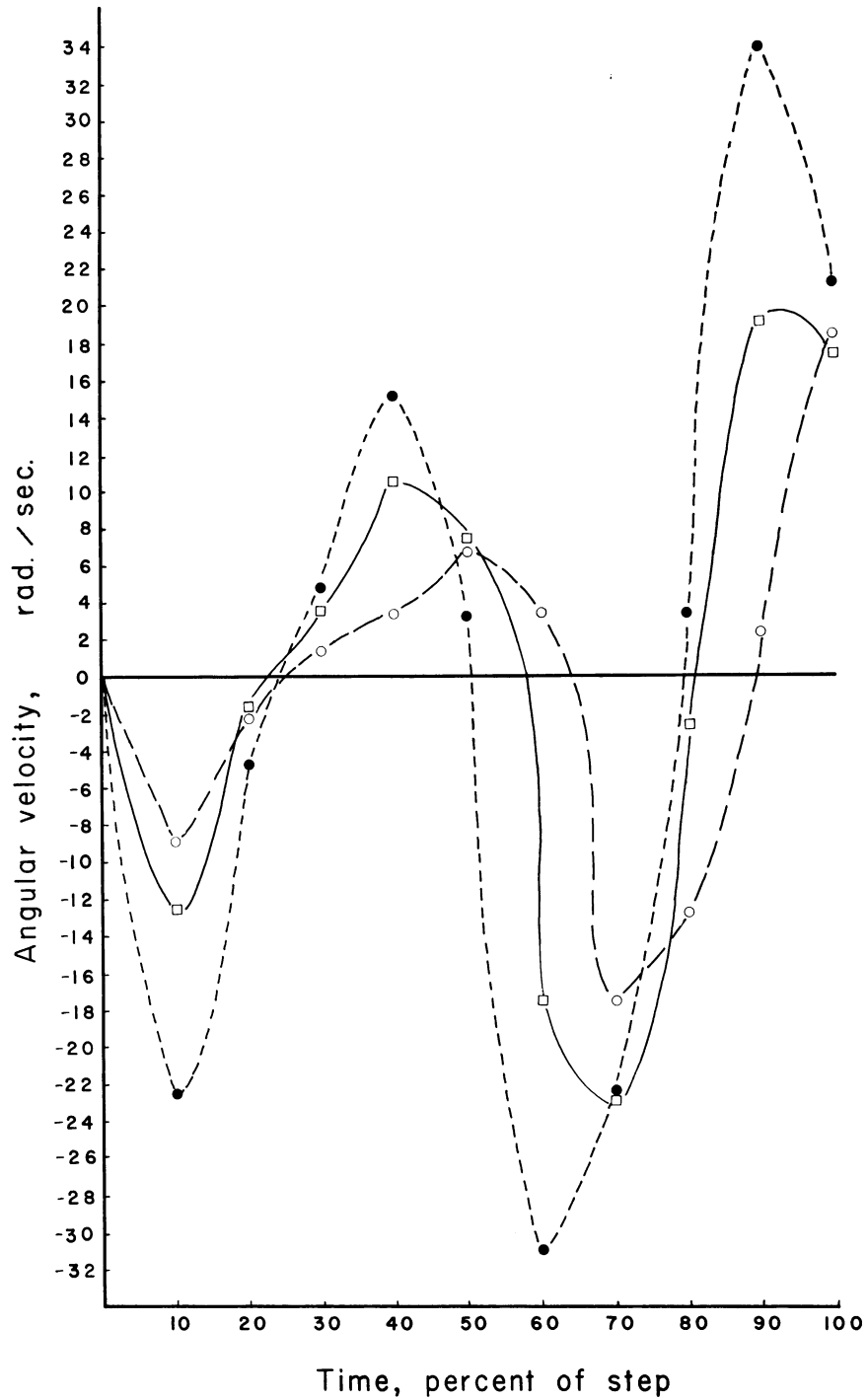


FIG. 30. Angular velocity (radians per second) of intertarsal joint (tarsometatarsus) in moderate, slow, and running gaits of *Columba livia* plotted against time (per cent of step). Moderate gait, open squares, see fig. 22; slow gait, open circles, see fig. 24; running gait, dark circles, see fig. 26.

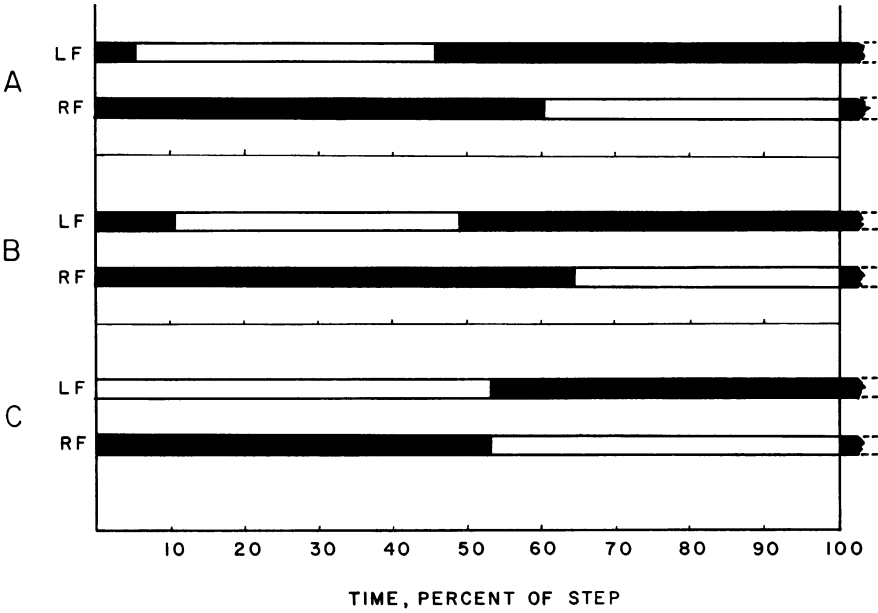


FIG. 31. Foot-fall pattern of right (RF) and left (LF) feet of moderate walk (A), slow walk (B), and run (C) in *Columba livia*. Dark bar indicates foot in contact with ground; open bar indicates foot not in contact with ground.

can combine the results of high-speed cinematography with data on joint structure and function, the fiber arrangement of the muscles, fiber length, angle of pinnation, relative fiber

number, and considerations of muscle physiology and biomechanics to arrive at more exact interpretations of muscle function and the locomotion process itself.

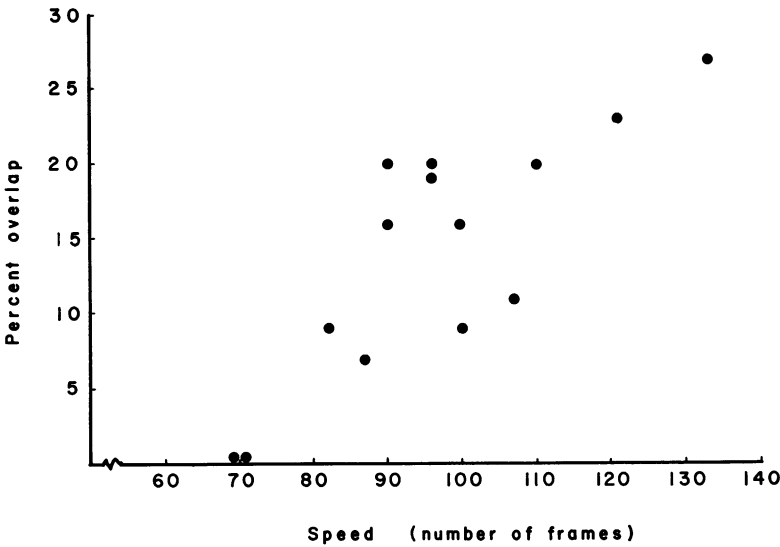


FIG. 32. Percentage of overlap relative to time of step of right and left feet plotted against speed of gait (expressed as number of frames taken at 250 frames per second) in *Columba livia*.

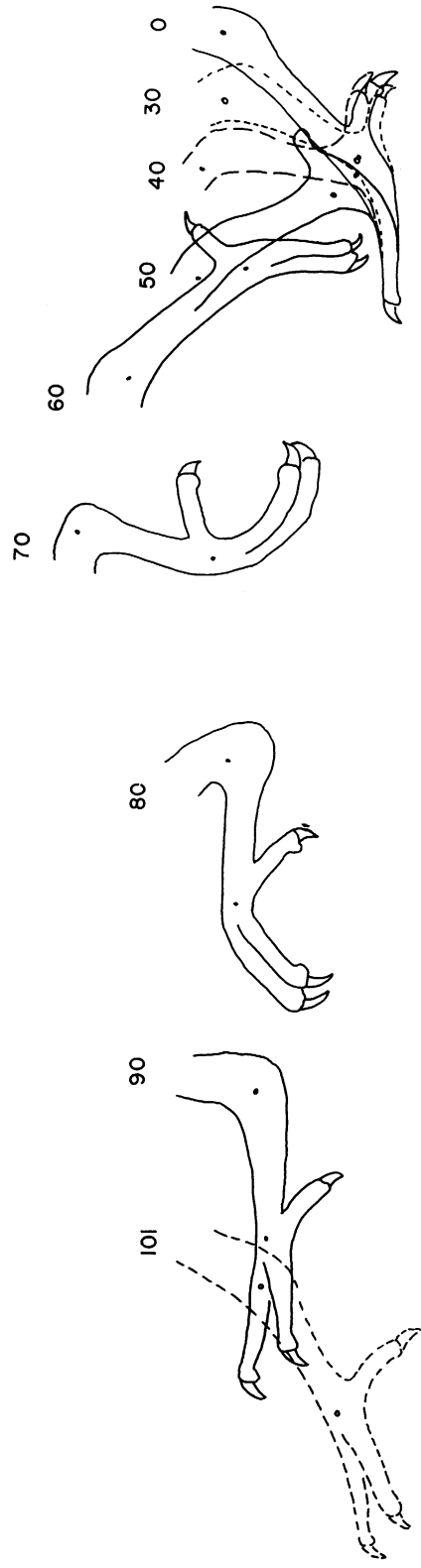


FIG. 33. Diagram of walk 101 frames long (taken at 250 frames per second) in *Columba livia*, to show movements of tarsometatarsus and the toes.

DISCUSSION

COORDINATION AND ACTIVITY SEQUENCES OF THE HIND-LIMB MUSCULATURE

VERTEBRATE LOCOMOTION is clearly a case in which the whole is more than the sum of its parts. That is, a knowledge of the kinds of movements produced around joints by each muscle is not to be equated with having acquired an understanding of the mechanism of locomotion. The function of a muscle may not be inferred from knowing only the points of origin and insertion. In addition to those parameters mentioned earlier, the amount of tension developed and the load placed on the muscle are important in determining the function of the muscle at a particular time. Likewise, a study of locomotion is just as dependent on a knowledge of the activity sequences of the muscles as on knowing the movements produced by those muscles. The fact that a muscle is capable of producing a given effect on a bone and that casual observation would suggest the muscle could be contracting (shortening) at a particular phase in the locomotor cycle is no confirmation that the muscle functions only during this phase of the cycle. This is particularly obvious with muscles whose main function is to resist movement. Hence, an integral part of the investigation of vertebrate locomotion is the determination of the activity sequences of each muscle (that is, the time period when a muscle is developing tension) and the kinds of movement produced in each phase of the cycle.

As far as I am aware, no activity sequence has been determined for any vertebrate other than for human beings. A vast literature on the electromyography of human walking has provided a rather accurate picture of the activity of many muscles during the locomotor cycle. Data are available for some of the muscles in a few mammals, but analyses of the majority of muscles with respect to locomotion studies apparently have never been undertaken. The activity sequences presented below for the pigeon are based on my functional analysis of the muscles and on the results of high-speed cinematography. A major purpose for constructing these sequences, aside from providing a better understanding of the process of locomotion,

is to furnish a better basis for future experimental work using the technique of electromyography. The sequences that I have constructed are, I believe, the best available determination other than actual electrical measurement of the muscles themselves. Consequently, the results presented here will have to serve as hypotheses on which to conduct further experiments.

Two activity sequences are described and discussed. The first is for the moderate walk pictured in figure 24 and graphed in figure 25. Each 10 frames are considered to represent a separate stage in the cycle (see table 4), and the analysis will proceed stage by stage. In table 4 the activity sequence of each muscle is identified as being either an active shortening (Sh) or holding (H) of the bony elements. During a "holding" phase, a muscle is resisting those forces causing the point of insertion to move away from the point of origin. Hence, it is possible that a muscle may be stretching during a "holding" phase. The second activity sequence will be for a standing pigeon, emphasizing the postural muscles.

ACTIVITY SEQUENCE OF THE WALKING CYCLE

STAGE 1: During stage 1 of figure 24 the leg is responding mainly to the impact of the step and then to the additional weight that is placed on the leg as the opposite leg leaves the ground. The force of gravity acts to cause rotational moments at each joint. The femur has moments placed on it by the tibiotarsus which tend to cause protraction. The tarsometatarsus places a moment upon the tibiotarsus which contributes to flexion of the knee joint. And, the reaction of the foot against the tarsometatarsus flexes the latter bone at the intertarsal joint. All these turning moments must be resisted by intra-articular structures or by the muscles, and consequently it is not surprising that most of the muscles functioning at this time have a high percentage of tonus fibers.

Sudden protraction movements of the femur are resisted mainly by M. iliotrochantericus

[illegible]

posterior, *M. adductor superficialis*, and *M. adductor profundus*. Other muscles, which probably aid in this action, are the anterior slip of *M. piriformis* and *M. ischiofemoralis*. The moments flexing the tibiotarsus must be resisted by muscle forces that also do not cause protraction of the femur. Hence, the only muscle that can do this is the femorotibialis. A large amount of force is probably not necessary to resist knee joint flexion, as the joint continues to flex in the succeeding stages. Some initial resistance would be expected in order to preserve the balance of the bird and to insure smoothness in the walking cycle, however. Flexion of the intertarsal joint, on the other hand, must be more strongly resisted because the joint must be forcefully extended during the propulsion part of the cycle that begins in stage 3. This flexion is probably counteracted by three main groups of muscles: the gastrocnemius and the plantaris, the toe flexors, and the peroneus longus.

STAGE 2: In stage 2 the femur is being actively retracted. The knee and intertarsal joints are continuing the same types of motion as in stage 1, except that the rate of flexion of the intertarsal joint is somewhat less.

The same muscles controlling femoral motion in stage 1 are probably active in stage 2. With active retraction, it seems reasonable to assume that the twitch component of these muscles is playing a more prominent role than if the requirement were solely for resistance of protraction. Undoubtedly, the tonus muscles, such as the two adductors, continue to resist protraction. The knee joint would still only require the femorotibialis to maintain a smooth flexion. The muscles around the intertarsal joint are functioning so that by the end of stage 2, flexion at this joint has ceased.

STAGE 3: The femur continues to remain retracted, and the knee joint continues its gradual flexion. The intertarsal joint, in contrast, is beginning its propulsion phase and is being actively extended.

The muscle activity for the hip and knee joints probably has not changed appreciably. Two points are important to make about the propulsion phase of the intertarsal joint. First, the joint has to be extended rapidly to enable the development of rather large amounts of forward momentum. Second, this extension has to be accomplished against large resistant forces, namely, the weight of the animal. At the time of

propulsion all the weight is being supported on this one leg, and the muscles have to work against this. The gastrocnemius is the major extensor muscle of the tarsometatarsus. The *M. gastrocnemius internus* and *medius* have a large percentage of tonus fibers, and this fact may raise some doubts as to their active participation in the extension process. It might be postulated that the tonus portions of the *internus* and *medius* are functioning to resist flexion in stages 1 and 2 and that in stage 3 the twitch component results in shortening of the muscle, which in turn results in extension. This does not imply that the tonus component plays no role in active extension, but only that its role is less than the twitch component. The *M. gastrocnemius externus* muscle is predominately twitch and certainly is important in extension.

If the *internus* and *medius* portions contribute little to extension, then it is essential that other muscles support the action of the gastrocnemius *externus*. The toe flexors probably function like the different parts of the gastrocnemius. The tonus portion of the flexors is most likely important in stages 1 and 2, and the twitch component may be predominant in stage 3 during extension of the intertarsal joint. Stage 3 of figure 24 is approximately equivalent to frames 30–40 of figure 33. In the latter figure it is seen that the toes progressively support the weight of the bird. This weight should be sufficient to counteract any flexion moments on the toes produced by the toe flexors. Thus, more of this force could be used to extend the intertarsal joint.

STAGE 4: This stage does not differ significantly from the previous one. The velocity of extension of the intertarsal joint is increasing, thus indicating that more of the flexor muscles are being activated or at least more fibers appear to be.

STAGE 5: Again, few changes are apparent from the preceding stages. The femur is beginning to protract, and the rate of flexion of the knee joint has increased slightly. Also, extension of the intertarsal joint is reaching its peak.

This part of the protraction of the femur could be accomplished by relaxation of the muscles that have previously been resisting this movement. It is not apparent in figure 25 just when this relaxation takes place, but it would be in stage 4 or 5. Active protraction can take place only after the leg has been lifted from the

ground. The increased flexion of the knee could also be accomplished by relaxation of the femoritibialis. Near the end of stage 5 most of the muscles contributing to intertarsal joint extension are probably approaching the lower portions of the tension-length curve, and the amount of force produced is rapidly dropping.

STAGE 6: The early parts of this stage see the continuation of femoral protraction and knee joint flexion. In the later parts of the stage the leg is lifted from the ground, which is accomplished mainly by knee joint flexion. Soon after knee joint flexion there follows a quick flexing of the intertarsal joint.

The action of three muscles is responsible for knee joint flexion. Most important is the biceps femoris. The contraction of this muscle begins at lift-off, but the muscle may not remain active once the tibiotarsus is pulled to its dorsalmost position. The semitendinosus and *M. semimembranosus* (see below) also may contribute to lifting the tibiotarsus dorsad.

At the end of stage 6, soon after lift-off, the intertarsal joint is flexed rapidly by the tibialis anterior. The long fibers of this muscle enable high excursion velocities to be attained.

STAGE 7: Protraction of the femur is continuing. Because the beginning of stage 7 is only a few frames after lift-off, flexion of the knee is in its early phases. Rapid flexion of the intertarsal joint is also continuing.

With lift-off the sartorius should become active in protracting the knee joint. The iliotibialis probably plays little role in this movement as the moment arm of the anterior fibers is very small. At the same time the sartorius is contracting, the semimembranosus, which apparently has significant numbers of tonus fibers, is resisting tibiotarsal extension as the leg is brought forward. This means that all of the shortening of the sartorius can be used for protraction of the knee joint.

STAGE 8: The femur shows an increased rate of protraction. The knee joint begins to extend in order to bring the lower leg forward. Flexion of the intertarsal joint ceases and extension is beginning at the end of stage 8.

The sartorius is apparently the only muscle that can protract the femur. The iliotrochantericus anterior and medius and the iliacus may assist in protraction, but they probably would contribute little force. The femoritibialis is now functioning to rapidly extend the tibiotarsus.

The medius and externus portions of the femoritibialis are probably the only part working during the early portion of stage 8, but the posticus becomes active toward the end of the stage. The tibialis anterior is apparently approaching the low part of the length-tension curve or is ceasing activity altogether, and flexion of the intertarsal joint is coming to an end.

STAGE 9: In this stage femoral protraction ceases and the femur even retracts slightly. Rapid extension of the knee is continuing, and extension of the intertarsal joint is beginning.

The muscles controlling the movements of the hip and knee joints in the previous stages are undoubtedly still operative in stage 9. The gastrocnemius is contracting and thus extending the tarsometatarsus. The externus portion of this muscle would probably be sufficient to accomplish this action as there is essentially no resistance to the tarsometatarsus. Motion-picture analysis (see fig. 33) suggests that the toe flexors are not active, and for the reasons presented earlier, the internus and medius portions of the gastrocnemius are doubtful participants.

STAGE 10: With respect to the hip, knee, and intertarsal joints, there does not appear to be much change from stage 9.

As the foot is placed on the ground, several groups of muscles become active (whether these muscles begin to function in stage 9 is unknown). The resulting actions are extension of the hallux and foretoes and abduction of digits II and IV. The extension movements are accomplished principally by the extensor digitorum longus and extensor hallucis longus. The extensor proprius digiti III probably aids in extending digit III, but the extensor brevis digiti IV appears to be rather insignificant in this movement. The abductors of digits II and IV function at this time to spread the toes.

The above discussion attempts to postulate the time sequences within a step in which the muscles are most likely to be active. It seems reasonable to assume that many of these muscles will begin their activity prior to the starting points I have indicated, because a certain amount of time will be needed to initiate the build-up of muscle tension. The movement during this period could be opposed by the antagonists. In fact, the major source of error in table 4 is probably the inaccuracy of recognizing when a muscle is functioning not as a prime mover but when the muscle is opposing the

action of another muscle in order to make the movement smooth and continuous. Experiments on the electrical activity of these muscles will be necessary before many of the above problems are solved.

ACTIVITY SEQUENCE OF THE STANDING PIGEON

The process of standing involves the use of muscles that can maintain sustained contractures against continuing stresses. It also involves the functioning of the complex ligamental apparatus at the knee joint, an aspect of posture in birds which has not been described before.

When a bird stands, the force of gravity causes certain moments around the joints (the foot will be considered as stationary). These moments bring about protraction of the femur and flexion at the knee and intertarsal joints. For the bird to maintain a standing position, these movements must be counteracted.

The sustained contraction of the tonus component of muscles is the main factor in preventing protraction at the hip joint and flexion at the intertarsal joint. The position of the femur is controlled by the action of the adductor superficialis and adductor profundus. These are large muscles and are composed predominately of tonus fibers. The tonus portions of the ischiofemoralis, the anterior slip of *M. piriformis*, *M. ilirotrochantericus anterior*, and *M. ilirotrochantericus medius* would also contribute to maintaining posture.

Flexion of the intertarsal joint is counteracted by the gastrocnemius medius and internus and by the tonus component of *M. gastrocnemius externus*. The tonus fibers of the toe flexors also play a major role in resisting this flexion, and variations in the amount of force produced by these muscles would regulate the degree of flexion of the joint.

Flexion of the knee would first appear to be resisted by the action of the large extensor muscle, *M. femoritibialis*. Histological examination reveals that this muscle is apparently a twitch muscle with few tonus fibers however. This observation correlates well with the functions suggested earlier, that is, with a rapid extension of the tibiotarsus at the end of the step.

No other muscles serve to prevent knee joint flexion without also protracting the femur. Thus, other explanations for the maintenance of posture at the knee joint must be sought. In the standing position the knee joint forms an angle of about 90 degrees. As long as both protraction of the femur and flexion of the intertarsal joint are prevented, flexion at the knee joint cannot take place while the bird is standing. The important problem is the resisting of forces that would tend to disrupt the joint. This resistance is accomplished in several ways. First, the joint surfaces are such that it is difficult for the condyles of the femur to move forward or backward; instead, only rotational movements are permitted. Second, the anterior cruciate ligament prevents forward translation of the tibiotarsus relative to the femur. Likewise, the posterior cruciate ligament halts posterior translation of the tibiotarsus relative to the femur. Finally, the other ligaments, joint capsule, and the tendons surrounding the joint would also prevent disruption. Changes in the angle of the knee joint during standing are brought about by changes in the tension developed by the muscles holding the femur and intertarsal joint.

The divisions of the femoritibialis probably function during standing to help maintain stability and to provide additional control to the movements at the knee joint. Unlike the muscles at the other joints, however, the femoritibialis is not functioning strictly as a holding muscle against flexion of the tibiotarsus.

The maintenance of stability at the knee joint is an important factor during posture. In addition to the intra-articular structures mentioned above, some of the toe flexors also possibly assist in preserving stability. The forces transmitted across the knee joint are, in general, a function of the weight of the bird, and these forces tend to push the femur and tibiotarsus together. The toe flexors which have their origin from the popliteal area of the femur have their line of action nearly parallel to the tibiotarsus and consequently increase substantially the forces pushing these two bones together. The toe flexors arising from the tibiotarsus would clearly not increase this transarticular force.

ONE-JOINT AND MULTI-JOINT MUSCLES

A study of the avian hind limb provides an excellent opportunity to evaluate some of the

functional properties of one- and multi-joint muscles. The relationship between the functional

characteristics of a muscle and the number of joints the muscle crosses has intrigued morphologists for decades. Recently, Bock (1968) has reviewed the early literature and has attempted a clarification of the concepts surrounding the mechanics of these muscles. My treatment of this subject will be organized, in part, around several specific points mentioned by Bock in his discussion (pp. 32-39).

1. The most obvious property of multi-joint muscles is their effect on bones other than the ones to which they are attached. Bock has stressed (p. 36) that the consequences of a multi-joint muscle cannot be determined solely from a knowledge of the morphological configuration of the bone-muscle system. He was referring principally to the necessity of having information about the magnitude and direction of the forces between the different bony elements, the magnitude of the inertia forces under dynamic conditions, the magnitude of the gravitational forces, and so forth.

Another factor complicating the consequences of multi-joint muscles is the effect of other muscles, including antagonists, in the bone-muscle system. I believe this to be the most important factor influencing the prediction of the mechanical results of multi-joint muscles. For example, the sartorius arises on the anterior end of the pelvis and inserts onto the tibiotarsus. This morphological system would suggest that the muscle extends the tibiotarsus and that this would produce a reaction force between the tibiotarsus and femur which would result in the protraction of the latter bone. It is impossible, however, to ascertain the relative influences the sartorius has on tibiotarsal extension and femoral protraction without considerable knowledge of the functional characteristics of almost all the muscles inserting onto the femur and tibiotarsus. Thus, although it may be possible to analyze multi-joint muscles in order to gain some additional information about possible influences these muscles have on the central bones, such mechanical analyses will probably be of limited value with respect to the living animal unless all other relevant muscles are included in the study. The bone-muscle systems of living animals are, in general, too complex to enable analysis of isolated parts of these systems, and the neuromuscular controls over these systems are probably too subtle to be characterized graphically.

2. Bock (1968) has emphasized that two-joint

muscles exercise less independent control over the bones than do one-joint muscles. Thus, the question is raised whether one- and multi-joint muscles might not have different roles with respect to functioning primarily as movers or as holding muscles.

For movements around the hip and knee joints, the suggestion is that whereas both one- and two-joint muscles function as movers of the bones, most of the muscles that resist motion are one-joint. This is clearly to be expected at the hip, and most of the muscles moving the femur are also one-joint. There are few muscles that resist movement at the knee. The femorotibialis is a one-joint muscle (the popliteus is also one-joint, but its action is across the tibiotarsal-fibular joint). The other major muscles resisting extension movements at the knee joint are the semimembranosus and biceps femoris which are two-joint muscles.

Any correlation between one- and multi-joint muscles and their possible roles breaks down when considering the intertarsal joint. The major movers of the tarsometatarsus are the peroneus muscles (one-joint muscles), the tibialis anterior (principally one-joint, but with a two-joint slip), the gastrocnemius (both one- and two-joint), and the toe flexors (multi-joint muscles). Also, the toe flexors and the gastrocnemius are the major holding muscles around the intertarsal joint.

In the vertebrate leg, and in any other bone-muscle system which I can imagine, I believe there is little evidence leading to the conclusion that one-joint muscles are less important than two-joint muscles are in moving bones. Because many two-joint (or multi-joint) muscles can work against each other, any particular muscle can have several functional properties. And indeed, the histological, and thus presumably the physiological, data indicate muscles are moving bones and resisting movement regardless of whether they are one- or multi-joint.

3. Bock (1968, p. 39) made the statement that longer muscles shorten with greater speed than do shorter muscles, and as multi-joint muscles are longer, they have an advantage with respect to speed. Bock was referring to the length of the muscle fibers rather than strictly the length of the muscles themselves (Bock, personal communication.), and he has raised a question for which, as far as I know, a quantitative answer has not been given. My data can provide a direct

answer to this problem. First, there is no correlation between the length of the muscle (contractile portion only) and the length of the muscle fibers. When these measurements are plotted against each other, the points are scattered and with no correlation. Second, there does not appear to be any relationship between the length of the fibers and the fact that a muscle is one- or multi-joint. The two-joint muscles of the hip and knee are all long fibered, but the multi-joint toe flexors have very short fibers. The one-joint adductors of the hip have relatively long fibers. The tibialis anterior, a part of which is one-joint, has very long fibers. My conclusion is that the length of the muscle fibers is determined by functional requirements (long excursions or high contractile speed), and any correlation with the length of the muscle or with one- or multi-joint muscles is probably fortuitous.

4. Bock also suggested (p. 38) that two-joint muscles in general have longer moment arms, thus resulting in either greater torque or equal torques for less muscle force. (Bock's analysis was restricted to muscles having a direct pull from the origin to insertion and did not consider muscles with long tendons passing over many joints). A larger torque would impart a greater angular acceleration on the bone. Thus, a possible correlation of moment arm length and one- or multiple-joint muscles could be of great significance in animals and deserves careful consideration.

Most of the two-joint muscles over the hip and knee joints have long moment arms, whereas the one-joint muscles of the hip and knee have shorter moment arms. This apparent correlation may only be a result of these muscles being situated within the proximal part of the leg,

however. Distally, all the muscles have short moment arms for obvious reasons. Furthermore, there are even exceptions in the proximal part of the leg. The adductors are one-joint but, portions of these muscles have rather long moment arms. Some two-joint muscles, such as *M. ilio-tibialis*, have short moment arms.

As a generalization, there is little evidence to support a relationship between moment arm length and one- and two-joint muscles in a complex bone-muscle system. Too many other factors such as geometry of the leg and functional requirements of the muscles obscure the relationship. If one considers a part of the system in which a one-joint muscle is next to a two-joint muscle, then the former would probably have a shorter moment arm.

5. Two-joint muscles can perform a unique function when they serve as an analogue of a ligament (see Bock, 1968, p. 39). By holding the end bone stationary, they permit the movement of the central bone by another two-joint muscle. In the avian hind limb the semimembranosus (and possibly the biceps femoris) apparently functions to prevent tibiotarsal extension by the sartorius as the latter muscle protracts the femur. In this case the same action would be accomplished if the semimembranosus were replaced by a ligament, but the muscle possesses some obvious functional properties that a ligament does not have.

The act of holding distal elements stationary while other muscles move the central bone may be one of the most important roles of two-joint muscles. It certainly seems to be common among the two-joint muscles passing over the hip and knee joints in birds.

STRUCTURE AND FUNCTION OF JOINTS

The foregoing studies on the hind-limb joints of *Columba* form a foundation for a brief discussion of some current ideas regarding the structure and function of vertebrate joints. The general literature on vertebrate joints has been summarized by Barnett, Davies, and MacConaill (1961). My remarks are confined to those aspects of joint structure about which my studies can yield the most information.

1. Joint capsule: The capsule plays two important roles in the proper functioning of the

joint. First, it encloses the joint and thus serves as a container for the synovial fluid. And second, the capsule is important in resisting stresses across the joint and thereby limiting movement. Although my studies provide less direct information about the first role, the importance of the second is easy to demonstrate.

Portions of the capsule of all three joints are thickened and are important in limiting motion. The capsule of the hip joint may occasionally function to limit protraction of the femur during

periods of standing, thereby contributing to the maintenance of posture. The capsule of the knee and intertarsal joints is so constructed as to resist lateromedial swings, translations, and rotations that would tend to disrupt the joint. And in these two joints the capsule, along with other structures, sets a limit to the amount of extension.

It is important to note that in the normal functioning of the joints the capsule may not regularly limit motion, but rather this limitation may be brought about after stretching of the muscles has taken place. The capsule becomes particularly critical when the muscles fail to respond properly. Further experimental work is necessary before the role of the capsule and other articular structures is fully understood, however. Smith (1956) has produced experimental data on the contribution that these structures make to the postural mechanism of the human knee joint, and similar experiments must be made on nonhuman vertebrates.

2. Joint ligaments: In birds, few joint structures have received as little attention as the ligaments. The ligaments certainly function in much the same way as does the capsule in preventing disruptive movements. Of more interest is their role in flexion and extension of the knee joint. Experimental work should be able to verify my earlier suggestion that the ligaments, because of differential changes in tension, can actually contribute force to flex or extend the joint. Smith (1954) has determined that the anterior cruciate ligament of the rabbit can extend as much as 20 per cent of its length under stress. To my knowledge no stress-strain measurements have been made on avian ligaments, and if they stretch as much as 20 per cent, their presumed functional roles would be greatly affected. Because the cruciate ligaments of birds are apparently important in posture, and hence are subject to continuing tensile forces, a study of their mechanical properties is especially pertinent.

3. Menisci: The structure and function of menisci and other fibrocartilages have received considerable attention from human anatomists but little from workers studying nonhuman vertebrates (see Barnett, Davies, and MacConaill, 1961, pp. 54-73). Perhaps the oldest idea about the possible function of these structures is that they make the joint surfaces of an articulation more congruent. This in turn would

(a) increase stability, (b) distribute weight more evenly across the joint, and (c) facilitate rotational movements. MacConaill (1932) proposed that menisci function to "bring about the formation of wedge-shaped films of synovia in relation to the weight transmitting parts of joints in movement," and he even went so far as to state that menisci increase the incongruence of the joint surfaces rather than decrease it. In later publications (1950, 1966) MacConaill has maintained this idea about the function of menisci and has at the same time tended to de-emphasize other possible functions. Recently, Barnett (1954b) has examined the function of the fibrocartilages in a variety of vertebrate joints. He found that there was a direct correlation between the presence of fibrocartilages and the ability of the joint surfaces to slide past one another. Those joints lacking fibrocartilages did not exhibit sliding. He concluded that "it was the necessity for a sliding movement, to co-exist with flexion and extension, that resulted in the evolution of fibrocartilages." Barnett was of the opinion that fibrocartilages could aid in lubrication of the joint, especially in joints with large radii of curvature and/or where high velocities of movement are attained.

A study of the avian knee and intertarsal joints provides some evidence about the possible functions of the fibrocartilages in nonhuman vertebrates. First, it is obvious from a morphological examination that the menisci increase the congruence of the joints. If any of the menisci are removed, the joint surfaces are less closely apposed to one another. This fact would seem to support the contention that the weight would be more evenly distributed across the joints. The menisci are also contributing rather substantially to the maintenance of joint stability. If any of the menisci are damaged or their attachments to articular surfaces or to ligaments are cut, instability of the joint is noticeably increased, that is, the kinds and amounts of the movements are abnormally exaggerated. As the joints are flexed or extended, the condyles of the femur and tibiotarsus cause a movement of the menisci across the surface of the tibiotarsus and tarsometatarsus, respectively (see section on joint structure and function). Because the menisci are attached to other structures, either directly or through ligaments and connective tissue, they will provide some resistance to the rotation of the bony elements. Admittedly the resistance

will be slight at first, but near the limits of extension the resistance may be great enough to help determine the position of this limitation. In addition to possible control of the rotational movements, the menisci also resist translational (sliding) movements in either an anteroposterior or lateromedial direction. In general, then, the major function of the menisci is to provide for smooth functioning of the articular surfaces and to maintain the stability of the articulation.

Barnett, Davies, and MacConaill (1961, pp. 201–202) objected to the notion that fibrocartilages prevent joint incongruity by arguing that organisms should have evolved congruent surfaces directly rather than having accomplished this by the evolution of fibrocartilages. Furthermore, they go on to point out that fibrocartilages are absent from those joints capable only of translation or of rotation. They then argue, following Barnett (1954b) mentioned above, that fibrocartilages are necessary in joints showing both translation and rotation, and that “if translation is one of the movements taking place at a joint close congruity between the male and female surfaces is mechanically impossible. A ball must have a flat table upon which to slide.” On the other hand, congruency of the joint surfaces and the ability to show translation are not irreconcilable. Fibrocartilages can make joints congruent to enable stable rotational movements, and indeed stable rotation is essentially impossible without the congruency

provided by the fibrocartilages. At the same time, because the fibrocartilages themselves can move, the surfaces can exhibit translatory movements relative to one another despite their congruency.

MacConaill's (1932) suggestion that the menisci facilitate the flow of synovial fluid is difficult to evaluate. In his papers and in Barnett, Davies, and MacConaill (1961, p. 203) MacConaill postulated that the menisci serve as a wedge which maintains a thin convergent layer of synovial fluid between the moving surfaces. MacConaill further postulated that the wedge-shaped meniscus maintains thin layers of synovial fluid both above and below the meniscus. A detailed criticism of the “hydrodynamic lubrication theory” of MacConaill is beyond the scope of the present paper (see Charnley, 1959; Dintenfass, 1963; and McCutchen, 1967 for a discussion of vertebrate joint lubrication), but my observations indicate that the menisci are pressed very tightly against the distal joint surface by the proximal element. The menisci appear to be constructed, in fact, so as to grade as smoothly as possible into the distal surface. The separation between the meniscus and the underlying surface would undoubtedly be much greater than the thickness of the fluid film necessary for hydrodynamic lubrication. MacConaill never stated how great the separation must be, but in avian joints it probably is very small, if present at all.

CONCLUSIONS

MOST PREVIOUS STUDIES of the hind limb of birds have been based on a comparative approach. In general, earlier workers have restricted themselves to the descriptive morphology of the muscles and to discerning the patterns of difference among the forms being studied. In some cases the results of this work have been used to reach taxonomic decisions about the groups, but their findings have also served as the basis for comparing adaptations for locomotion among the species.

The present study has involved only a single species and, because of this, it cannot provide data bearing directly on taxonomic problems or on aspects of comparative hind-limb adaptations. However, in the long run single-species studies should provide a sounder framework on which future taxonomic and comparative functional investigations can be undertaken, and it is the application of single-species studies that I want to discuss now.

With respect to systematic questions, single-species studies should be able to provide a substantial amount of new information. As an example, anatomists have used the presence and absence of certain hind-limb muscles to construct "leg muscle formulae," which in turn have been taken to be important taxonomic characters. Unfortunately, no anatomist has attempted to explain the significance of these formulae, nor have they explained the presence or absence of muscles on a functional basis. Thus, questions of convergence or multiple-origins of characters have been ignored. Because single-species studies concentrate on the functional analysis of muscles, they should permit systematists to evaluate more critically the leg muscle formulae.

One possible goal of a comparative-systematic

study is to interpret the observable morphological differences in terms of function. After this has been accomplished, it may then be possible to explain the morphological-functional patterns by postulating the selection forces that could direct these changes. For example, almost all genera of birds, particularly nonpasseriforms, show differences in the form of the hind-limb bones, and these differences are found principally in the shapes of the articular surfaces. With an understanding of the functional anatomy of the joints, we can begin to explain (rather than merely describe) various patterns with respect to probable selection forces. The results of these studies can in turn be applied to the analysis of fossil populations. Avian fossils usually consist of the ends of bones, and it is the form of the articular surfaces and associated features to which paleontologists turn for useful systematic characters. The fossil record of several groups of birds is becoming increasingly well-known, and in certain cases (e.g., the Gruiformes) probable phyletic lineages can be constructed. Hence, functional-morphological studies in Recent forms can be used to interpret the morphological changes observed within these lineages. Following the argument presented above, a reasonable explanation of the adaptive radiation in these birds may be possible. The success of the foregoing is greatly dependent upon the completion of single-species studies which provide detailed observations about joint structure and function.

In conclusion then, once numerous single-species investigations have been completed, comparisons between organisms will certainly be more fruitful than in the past, and new avenues of research will become apparent. Those workers interested in evolutionary problems will find single-species studies particularly rewarding.

SUMMARY

THE PRESENT PAPER presents the results of a study on the functional morphology of hind-limb locomotion in the Domestic Pigeon, *Columba livia*.

The structure and function of the hind-limb joints is discussed first. The major morphological features of the joint are examined using techniques of microscopic and gross anatomy, and these results are correlated with the kinds and amounts of movement permitted at each joint.

Next, a detailed description of the hind-limb muscles is presented. Included in the descriptions are data on origins and insertions, the arrangement of the fibers in relation to aponeuroses of origin and insertion, the relative length of the fibers, the angle of pinnation, and information about the histological composition of twitch (fibrillenstruktur) and tonus (felderstruktur) fibers within the muscle.

The data in the section on muscle description

are then used in conjunction with some basic principles of muscle physiology to arrive at more well-founded conclusions as to the functions of the different muscles.

A high-speed motion picture analysis of hind-limb locomotion in the pigeon is then given. Three different gaits (moderate walk, slow walk, and a run) are studied and compared with respect to angular displacements and angular velocities. The important aspects of landing are briefly considered.

Finally, the results of the functional analysis of the muscles are combined with those of the motion picture analysis to enable the construction of an activity sequence of the muscles during a walk. Information such as when muscles are active during a step and the kinds of motion observed is considered. Certain features of one-joint and multi-joint muscles and of vertebrate joint structure and function are discussed.

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