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THE EVOLUTION OF THE KNEE JOINT *

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The knee joint is the largest joint in the body and the most vulnerable one. It is more complex than most joints. The semilunar cartilages, the cruciate ligaments, the large synovial membrane, and the overlying patella are all structures designed for protection and stability, and yet each of these is a frequent source of knee pathology.

In order to learn more of the function of these various structures found in the human knee joint and to discover, if possible, their origin, the knees of a series of animals were dissected and studied. Animals were selected according to their phylogenetic development in the main line of ascent from amphibians to primates.

Before describing the details of the knee joints of these animals, it would seem helpful to review briefly the history of the locomotor system. This will show us how environmental changes made necessary the many modifications and adaptations of these joints and will lead us to a better understanding of the relationship between present-day environment, morphology, and pathology.

Originally all animals, including vertebrates, lived exclusively in the water and moved by sending waves of contraction along the muscular segments of their bodies. Fins were projections of the skin or body wall and functioned in maintaining balance and steering the tapered bodies.

As water became shallower in some areas, certain fishes adapted themselves to swamp life, breathing air and using fins as paddles and then as limbs to crawl along the muddy banks. In search of food they climbed higher and higher, and after many millions of years gradually developed limbs like turtles and lizards that raised their bellies off the ground. The higher they climbed, the longer their limbs grew and the more complicated became their joints. Eventually they learned how to run along the ground very swiftly and to climb trees and to swing from branch to branch. Swamps, jungles, forests, deserts, prairies, mesas, mountains, and climatic changes necessitated modifications and adaptations of limb and body. As nature worked out some marked improvement, this device would be bequeathed to many diversified descendants. Thus the bodies of the more recently evolved animals came to have many structures—most of them of utmost importance, some of doubtful value—inherited through the will of bountiful nature from myriads of ancestors who fought a life-and-death struggle to acquire them.

The simplest present-day vertebrate having a knee joint is the amphibian, of which the *salamander* is a good example. This animal has a long

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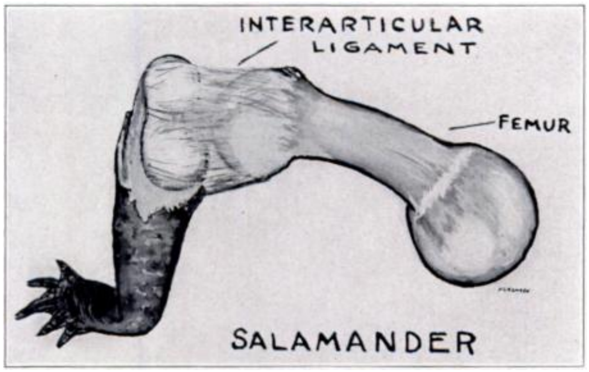

FIG. 1

reptilian body with very small limbs. The knee joint consists of the round condyles of the femur and the single tibiofibula with a simple thin interarticular membrane which is probably a synovial lining. No menisci nor cruciate ligaments are to be made out. There is no patella, the extensor muscles ending in a ligament which passes over the joint to insert in the shin bone.

The *frog* has very long hind limbs capable of considerable activity. The knee joint is not unlike that of the salamander just described except that the interarticular membrane when stretched out presents two crescentic thickenings suggestive of menisci. There is no cartilage in this membrane even where the thickenings occur. It is rather remarkable that this is the first indication of the morphology which in the more highly developed animals will shape the semilunar cartilages. No patella is present.

The reptilia show considerable advance in the development of the limbs and especially of the knee joint. The *alligator* which was dissected has two bones,—a tibia and a fibula. The condyles of the femur are more pronounced, so as to give a pulley-shaped appearance. The upper end of the fibula is enlarged and prolonged, so as to articulate with the lateral tuberosity of the femur. Definite cartilaginous menisci are present and seem to arise from the transverse ligaments of the joint. The lateral meniscus has a secondary cartilaginous ring which is attached to

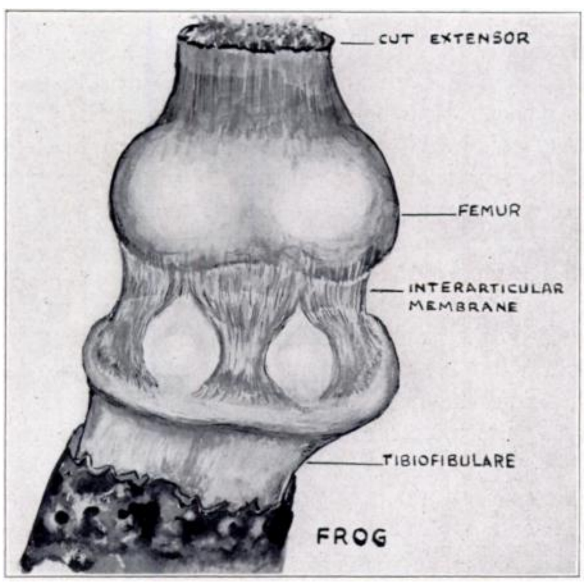

FIG. 2

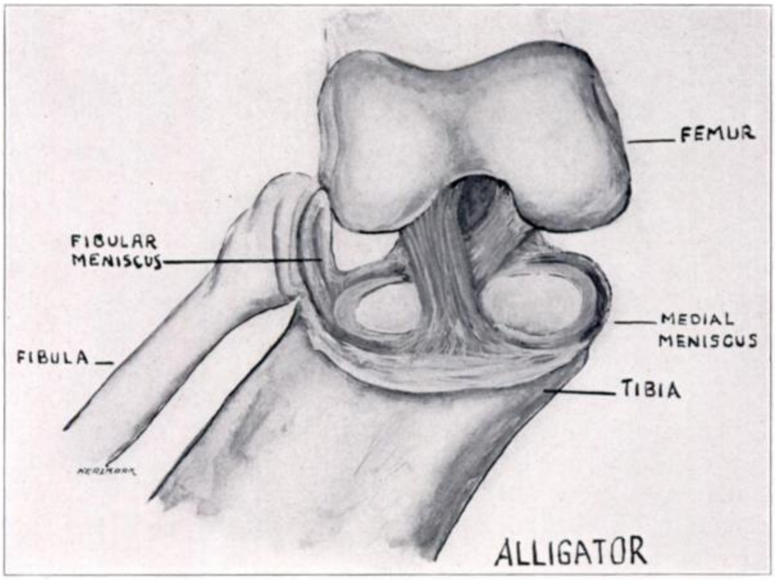

FIG. 3

its lateral border and is at right angles to it, so as to be interposed between the fibula and the lateral surface of the femur with which it articulates. A thin synovial membrane could be made out, but no patella.

The mammals have come a long way since their remote ancestors crawled about the slimy banks of their primeval swamps. One of the best examples of the simpler mammals is the *opossum*. This animal is a marsupial, has well-developed limbs, and can move quite rapidly. The knee joint shows the femoral condyles with a marked groove between them. The tibia has a sloping surface which extends anteriorly from the joint. The ligamentous termination of the extensor muscles of the thigh has a ligament which branches off at right angles to it to insert into the upper border of the sloping surface of the tibia, while the overlying tendon inserts into the lower border of the oblique surface of the tibia. There is no patella, but the extensor tendon is thickened over the joint line to form a rudimentary patella. There are two very well-developed

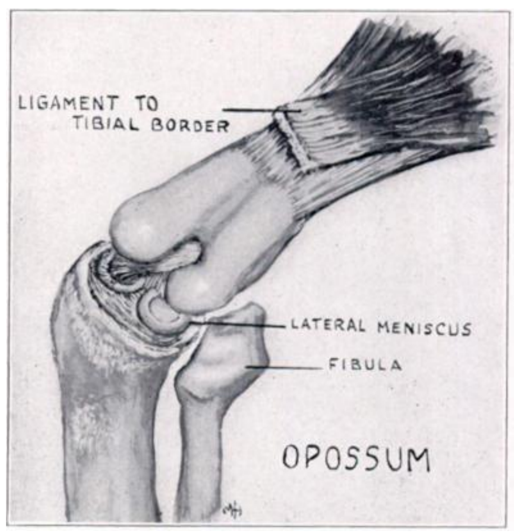

FIG. 4

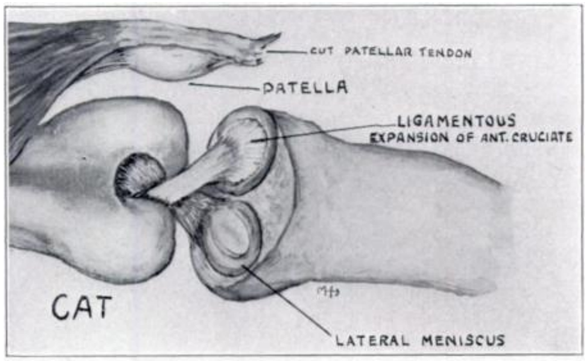

FIG. 5

semilunar cartilages. The lateral meniscus has a prolongation posteriorly which corresponds to the posterior cruciate ligament. The ligamentum mucosum is well developed and inserts into the tibia between the two menisci. The head of the fibula is enlarged and extends above the joint line to the lateral condyle of the femur, but no intra-articular cartilage is seen as in the alligator.

The line of ascent now brings us to the placentalia, of which an excellent example is the *cat*. The limbs are muscular, and the joints are designed for efficient function under strenuous conditions. A well-developed patella is observed with its patellar tendon inserted into the tibia well below the joint line. A ligamentous band runs off beneath this tendon to attach to the transverse ligament. The condyles are well developed and a deep groove lies between them, which always indicates speedy locomotion. The medial meniscus is a narrow band of fibrocartilage, formed by a thickening of the coronary ligament, and is attached at the medial border to the expansion of the anterior cruciate ligament. This expansion of the anterior cruciate ligament spreads out as a thin membrane to cover the entire medial tuberosity, disappearing under the free edge of the medial meniscus. The posterior cruciate ligament inserts by two branches into the posterior edge of the tibia, but does not spread over the cartilaginous surface of the lateral tuberosity. The head of the fibula is small and articulates with the tibia only.

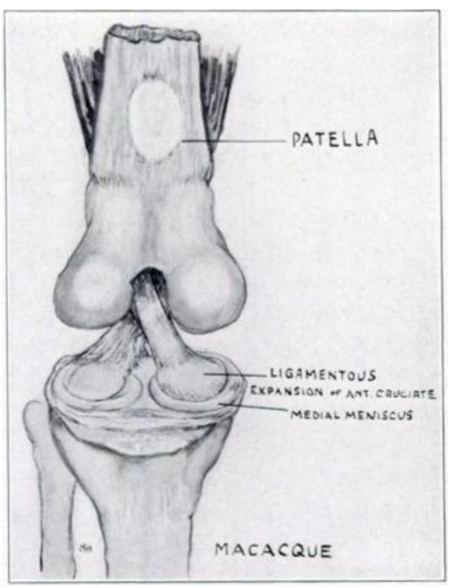

FIG. 6

The highest development in the animal kingdom is attained by the primates. These are the monkeys whose limbs are well adapted to strenuous running, climbing, jumping, and swinging.

As an example of the more primitive of this group, the knee of a *macaque* was studied. This

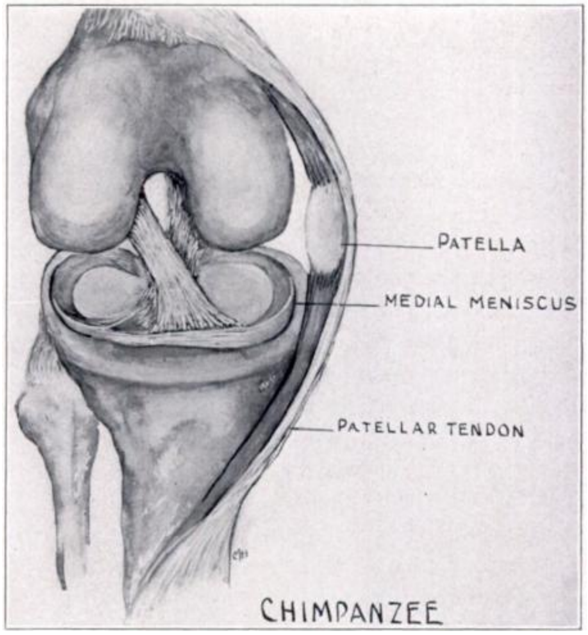

FIG. 7

animal has no prehensile tail, but its legs have an opposable hallux which makes the foot a grasping organ. The knee joint is well developed. The patella and patellar tendon are closely bound over the joint, allowing very slight excursion of the bone. The medial meniscus arises from the coronary ligament and extends only as a narrow circular rim around the tibial tuberosity. The anterior cruciate ligament is quite large and as it reaches the tibia it expands into a ligamentous membrane, covering over the entire medial articular surface of the tibia and disappearing under the free edge of the meniscus. The posterior cruciate ligament becomes attached to the lateral meniscus which is also very narrow and circular. The cruciate ligaments would seem to provide extra stability to the joint when greatly flexed, as well as when extended under traction as when the animal swings from a branch. The narrow menisci would appear to allow for rotation with little danger of tearing the interior thinned-out portion, as found in the human knee.

The simians are the most highly developed of the primates and the remarkable resemblance of the body structure to that of the human being is well known. The knee of a *chimpanzee* was dissected and studied with reference to the habits of the animal. This monkey assumes a partly erect posture, but helps to support its body with the forelimbs, using the backs of the phalanges for this purpose. The knee joint is held in a habitually flexed attitude, and the muscles are very well developed, the muscle tissue extending well down to the joint line. On dissecting the joint, it is seen that the rather small patella is tightly bound down over the joint by a strong patellar tendon. This allows for very slight excursion of the patella. The condyles are well developed, and the groove between them is much less pronounced than in the macaque. The cruciate ligaments are unusually large in proportion to the joint, but they do not expand over the articular surface as in the cat or the macaque. The menisci are crescentic and are more nearly like that of the human being but very narrow. The closely knit construction of the joint makes it remarkably well adapted for the strenuous work which it must do in primitive life.

EMBRYOLOGY

In tracing the evolution of the limbs, and especially of the knee, from the lowest vertebrates it is remarkably evident that, despite tremendous changes in other organs of the body, man has retained a great deal of the primitive features of the limbs. The bones of the legs of most mammals became greatly modified—for instance, the comparative elongation of the legs in horses and the disappearance of limbs altogether in whales—whereas in man, despite modification for plantigrade life, the original plan of structure is still clearly apparent.

Thus, in accordance with the biogenetic law or recapitulation theory, we should see the development of the limbs through the evolutionary stages in the embryo of man. At the end of the fourth week an elongated ridgelike elevation is seen on the dorsal border of the embryonic body. The limb buds arise from this ridge. It is held that this lateral ridge represents a row of fins and the limbs are specialized fin rays. These buds grow and extensions grow into them from the muscle plate and skin plate of each of the segments opposite the origin of the bud, and a nerve process from each of the corresponding segments of the spinal cord is sent into this mass. This segmental origin is seen only in the lower vertebrates and is inferred for the higher vertebrates.

By the seventh week the cartilage centers have appeared for the majority of the bones of the lower extremity. In the earliest stages the limb buds are so placed that the lower limb is rotated outward, while the upper limb is rotated inward. This is a position normally found in the primitive amphibians. This period, reached about the second month, may be called the reptilian stage.

Further development takes place, so that the cartilaginous skeleton gradually shows centers of ossification as the limbs elongate.

The knee joint up to the second month is a dense mass of tissue. The joint is flexed at nearly a right angle. The limb bones are formed from a center of chondrification within the unjointed skeletal blastema. At the periphery of these centers growth proceeds most rapidly, so that the centers approach each other, leaving the original blastema between them. This dense tissue or interchondral disc gives rise to the structures within the joint. A membrane called the perichondrium surrounds the growing cartilage and is derived from the peripheral part of the blastema. By the ninth week a joint space forms by the disappearance of the mesenchymal cells, first at the periphery and finally in the center. The perichondrium bridges across the limb segments to become transformed into a capsular ligament. In front of the joint this becomes denser to form the quadriceps tendon. The capsule now becomes lined with cells of the perichondrium to form the synovial membrane. The cartilaginous origin of this membrane is shown in certain pathological conditions in the adult whereby synovial villi give rise to cartilaginous nodules. Remnants of the interchondral plate project into the gap between the articular margins to form the menisci.

The thickening of certain parts of the capsule depends upon the strains to which the joint is subjected. The front portion was described as early showing strength to form the quadriceps tendon. Later the posterior portion becomes strengthened to prevent overextension. In man the condyles of the femur developed toward the popliteal space, thus isolating a part of the posterior capsule which remains within the joint and forms the cruciate ligaments.

We have seen how the reptilian knee joint revealed three menisci, due to the articulation of the fibula with the femur. Eventually, in the progress of evolution, the fibula became excluded from the joint and the fibulofemoral disc was included in the tendon of the popliteus.

In the embryo the upper end of the fibula is being excluded from the knee joint about the eighth week. At this stage there are five synovial cavities in this joint,—one between the patella and the femur, two between the femoral condyles and the primitive menisci, and two between the upper surface of the tibia and the menisci. About the fourth month these cavities become continuous, leaving the primary septa as the cruciate ligaments.

The circular form of the lateral meniscus and its continuity with the posterior cruciate ligament seen in the macaque are features in a knee joint where the power of rotation is highly developed. The menisci of the human embryo lose this circular form and the cruciate ligaments are only partly attached to them.

THE FUNCTION OF THE KNEE JOINT

From a consideration of the comparative anatomy, one may determine the function of the various structures which make up the joint.

Man is the only animal to assume the completely erect posture, and the knee joint is completely extended while bearing the weight of the body. The condyles of both the femur and the tibia find their largest development in the human knee joint. This affords extra surface for weight-bearing and adds to stability. The patella, which in the lower animals is rather poorly developed and has a very limited excursion, is in the human knee much larger and thicker and moves into a position directly above the joint line when the knee is fully extended. The increased thickness of the patella carries the patellar tendon more anteriorly and thus increases the tension on the quadriceps. This principle is used in the violin to increase the tension of the strings, the bridge corresponding to the patella.

The cruciate ligaments have been a subject of considerable controversy as to their importance in joint stability. Many methods for their repair have been devised in the belief that they are necessary in the proper function of the joint. In the animals dissected the cruciate ligaments were relatively much larger than those normally found in the human joint. In the cat and the macaque the cruciate ligaments expanded to cover the entire surface of the tibial condyle and were better developed than in any of the other animals. The tree-climbing, limb-swinging habits of these animals would induce us to believe that the cruciate ligaments act as check ligaments against rotation and subluxation when the knee is flexed.

The relatively small size of the cruciate ligaments in man would lead us to suppose that they are vestigial and relatively unimportant in knee stability. Embryological studies would tend to confirm this, as the cruciate ligaments were part of the posterior capsule and became isolated within the joint as the femoral condyles increased in size posteriorly.

The menisci are proportionately much larger in the human knee joint than in any of the animals dissected. The best development of these fibrocartilages in the animals was seen in the chimpanzee which assumes a semi-erect posture in walking.

These menisci are even better developed in the human knee which bears weight in the fully extended position. The value of these structures can be determined from a study of their function. In the extended position they fill in the space around the condyles and deepen the articular surfaces of the tibial condyles, thus adding stability. By this accurate approximation of the articular surface, a film of synovial fluid is spread to lubricate the cartilaginous surfaces. They act as shock absorbers where sudden strain is transmitted to the hyaline cartilaginous surfaces. Being of fibrocartilaginous structure rather than true hyaline cartilage, they have more power of growth and healing when injured.

In the small animals with knees habitually flexed, the menisci were small and very narrow. The alligator showed well-developed menisci, but this animal is relatively heavy and has a fibula which articulates with the lateral surface of the femoral condyle.

These findings would cause us to feel that the menisci are very important structures for weight-bearing knees.

Since the menisci are of fibrocartilaginous tissue and will regenerate if the synovial attachment is left intact, it would seem desirable when meniscectomy is indicated to remove only the torn portion, leaving a rim of meniscus attached to the synovia.