THE JOINTS OF MAMMALS COMPARED WITH THOSE OF MAN: A COURSE OF LECTURES DELIVERED AT THE ROYAL COLLEGE OF SURGEONS OF ENGLAND. By F. G. PARSONS, F.R.C.S., *late Hunterian Professor.*

PART II.—JOINTS OF THE HIND LIMB.

THE HIP JOINT.

SOME of the chief points which attract attention in the hip joint of man are the three thickened parts of the capsule called the ilio-femoral, ischio-femoral, and pubo-femoral ligaments, as well as the intra-articular ligamentum teres running from the bottom of the acetabulum to the head of the femur, and otherwise free in the interior of the joint. In the anthropoid apes the same thickenings of the capsule are found, and it is even said[1] that they are somewhat more prominent than in man. There is no doubt that the ligamentum teres is constantly present in the gorilla, chimpanzee, and gibbon, and it is a most remarkable thing that it is usually absent in the orang. In this museum there are the hip joints of two orangs, in one of which there is a fossa on the head of the femur where the ligament, if it had been present, would have been attached, while in the other specimen there is no such mark. In both these preparations the cotyloid notch and transverse ligament are present as in man.

In the lower or cynomorphine monkeys the ligamentum teres is always present, and resembles the same structure in man, though it seems almost certain to me that it can never be put on the stretch. The three thickened parts of the capsule are present, but are not so well defined as in man; the ilio-femoral band can easily be made out, but its Y-shaped appearance is not evident; I believe that its prominence in the higher apes and monkeys must be a physiological result connected in some way with the conversion of the hind limb from a supporting to a

[1] Keith.

brachiating organ, since, as we shall see, it is not present in lower mammals. It can hardly be an adaptation to the erect position, since in the anthropoids the line of the centre of gravity of the body does not fall behind the centre of the hip joint, as in man, and the semi-erect position is assisted by the contact of the knuckles with the ground. In man, however, it undoubtedly assists in maintaining the erect posture. I have been unable to find any evidence to support Bland Sutton's ingenious suggestion that it is in any way connected with the presence or absence of the gluteus quartus (ventralis). The only proof that the ilio-femoral band is a degenerated gluteus quartus which would be at all convincing to me would be to see one or more human subjects in which the gluteus quartus is present and the ilio-femoral ligament absent, though how the erect position would be maintained in such a case I do not know.

In the lemur the hip joint corresponds with that of the lower monkeys, and the ligamentum teres is present and well marked. In the Cheiroptera the fruit bat (Pteropus) has the hip twisted in such a way that the original front of the knee looks backwards and outwards and the plantar surface of the foot forwards. The lesser trochanter is therefore on the outer side; it is situated inside the capsule of the joint, and has an articular summit. When the foot is moved toward the mouth, *i.e.* when the hip is flexed and abducted, this trochanter comes in contact with an articular surface just above the acetabulum, reminding one somewhat of the antitrochanter of birds. There is a well-marked ligamentum teres, which is short, though it never appears to be put upon the stretch. Anyone who has watched a fruit bat taking a grape or other fruit will readily see that this twisting of the hip is an adaptation to allow the knee to flex forward and the foot to be brought into contact with the mouth; the foot in this way is able to take the place of the hand, which in this case has been converted into an organ of flight. In the insectivorous bat (Plecotus), the need of using the foot as a hand is not so great, and we do not find the hip so completely twisted round as in the fruit bat; indeed, the knee looks more outward than backward, and the lesser trochanter does not articulate with the ilium. As in Pteropus, the ligamentum teres is well marked.

In the Insectivora, both the mole and the hedgehog have no ligamentum teres: the latter is one of several instances which cause me to doubt the universal validity of Bland Sutton's statement that "those mammals in whom a ligamentum teres is absent also lack a gleno-humeral band," because the hedgehog certainly does possess a gleno-humeral band.

In the Carnivora, as in most of the lower mammals, the capsule of the hip is not specially thickened at any one point; the ligamentum teres, however, is thick and well marked in the land Carnivora, at least it is so to my knowledge in the Felidæ (cat, leopard, lion), Viverridæ (civet, genet, ichneumon, and suricate), Hyænidæ (*Hyæna striata*), Procyonidæ (*P. lotor*), Canidæ (dog and fox), Ursidæ (black bear), and Mustelidæ (polecat, stoat, weasel, and otter). It is stated to be absent in the sea otter (*Enhydra marina*), though it is certainly present in the common otter (*Lutra vulgaris*). It is absent in the walrus (*Trichecus rosmarus*) and the seal (*Phoca vitulina*), which are the only two specimens of the aquatic carnivores (Pinnipedia) I have observed.

In the Ungulata, the horse, as Bland Sutton has pointed out, has the ligamentum teres divided into two parts, the upper of which, the cotyloid portion, corresponds to the usual ligamentum teres of mammals; while the lower part, which Chauveau and he term the pubio-femoral portion, passes out through the cotyloid notch and runs forwards and inwards to join the linea alba at its junction with the pubes. It is perhaps doubtful whether it is advisable to speak of this portion of the ligamentum teres as pubio-femoral, because it suggests an identity with the pubo-femoral part of the capsule, a suggestion which, as far as I know, is not intended; probably abdomino-femoral would be a better name. In the ox, sheep, deer, antelope, and chevrotain this abdomino-femoral ligament is not seen, though the rest of the ligamentum teres is well marked. In the goat a large part of the ligament passes out of the cotyloid notch, and is attached to the dorsal part of the capsule after the manner described later in Pedetes. In the rhinoceros, according to Sutton, the ligamentum teres is absent, but I have never had the opportunity of dissecting this animal. In the elephant, specimens in this Museum show that it is wanting in both the

Indian and African species. In Hyrax, Bland Sutton failed to find the ligament, but in my specimen the arrangement was interesting; it was attached by a vertical linear fold to the lower half of the head of the femur; this fold was not entirely free in the joint cavity, but its lower edge was continuous with the lower part of the capsule. When the ligament reached the acetabulum, the greater part of it was continued out through the cotyloid notch, and was attached to the pubes outside the joint; it thus corresponded with the abdomino-femoral band in the horse, and is a point in favour of Bland Sutton's contention that the ligamentum teres is the continuation of some extra-capsular structure. There is a similar specimen in the Museum of this College which shows very much the same arrangement.

In the Rodentia the ligamentum teres is, as far as I know, always present, at least I have found it in a fairly large and representative series of animals.

In the Cape jumping hare (*Pedetes caffer*) it was a somewhat delicate structure, and, as in the goat, horse, and Hyrax, passed out of the joint through the cotyloid notch, but instead of turning ventralwards to the abdomen, or being attached to the pubes, as in the two latter animals, it turned backwards and became continuous with the dorsal part of the capsule, which it tended to tighten in extreme flexion of the joint. The capsule of the hip in this animal suddenly became very thin just before its attachment to the neck of the femur, so that the outer edge of the thick part forms a sphincter round the neck, and it is this sphincter which is drawn tight by the ligamentum teres during extreme flexion. This may possibly be an adaptation to the jumping habits of the animal, but it is certainly another instance of the continuity of the ligamentum teres with extra capsular structures.

It is interesting to notice in this connection that some of the human anatomy text-books remark that fibres of the ligamentum teres are continued out of the hip through the cotyloid notch.

In the Edentata, Bland Sutton found the ligamentum teres absent in the sloth and pangolin. In the latter animal I can confirm his observations from a specimen in this Museum, as well as from a dissection of my own. In both the two-toed (Cholœpus) and three-toed sloths (Bradypus) his experience agrees with my own, but in the lesser ant-eater (*Tamandua tetradacyla*) the ligament is present and free in the joint, although it consists chiefly of synovial membrane without fibrous tissue. In the armadillo the arrangement of the ligamentum teres was identical with that already recorded in Hyrax, but the lower part of the head of the femur shows a vertical notch as if the sphere was not completed here. This points to the truth of the theory that the ligamentum teres is originally continuous with the capsule, but is cut off by the "confluence of the lateral wings of the caput femoris," as Keith says. It is, at all events,

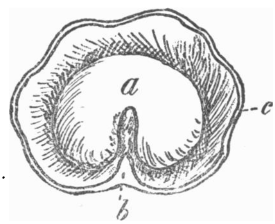

FIG. 1.—Hip joint of Armadillo (Dasypus). *a*, head of femur; *b*, ligamentum teres; *c*, capsule cut.

quite evident that one must not jump to the conclusion that absence of the ligamentum teres is a characteristic of the Edentata, though when it is present in them, it is usually in a rudimentary condition.

In the Marsupialia the ligamentum teres seems to be constant and well marked. I have found it in the Kangaroos (*Macropus rufus* and *Petrogale xanthopus*), and as far as I could determine, it was put on the stretch during extension of the hip in these animals. It was also seen in the native bear (Phascolarctus), the Tasmanian devil (Dasyurus), the flying and ground phalangers, and the bandicoot (Perameles).

In the Monotremata (Ornithorhynchus and Echidna) there is no ligamentum teres, nor could I find any trace of such a structure.

Summary of the Hip Joint.—The ventral part of the capsule is thickened in man and the anthropoids to form the ilio-femoral ligament; this thickening gradually disappears in the lower monkeys. In the quadrupeds the dorsal part of the capsule is generally the thickest. The ligamentum teres may be entirely absent, as in the orang, the hedgehog and mole (? other Insectivora), the Pinnipedia, the elephant, sloth, pangolin, and the Monotremata, though I cannot think of anything common to all these animals which could account for its absence, beyond the fact that they are all slow movers. When the ligament is present it may be free in the joint as in most mammals, partially fused with the pubic portion of the capsule, as in the Hyrax and the armadillo, or some of it may be traced to the outer side of the capsule through the cotyloid notch, as in the goat, horse, Hyrax, and Cape jumping hare.

Taking these two latter groups into consideration, the presumption is that the ligamentum teres was originally an extra capsular tendon or other fibrous band which was attached below the head of the femur, and gradually pushed its way into the interior of the joint cavity through the pubic part of the capsule.[1]

Knee Joint.

In contrasting the anatomy of man's knee with that of other mammals the following points should be kept in mind. In man the external lateral ligament is attached to the head of the fibula, and is a rounded cord; the internal lateral ligament is a flat strap, which is prolonged down the inner side of the tibia for some distance; the posterior ligament is reinforced by oblique fibres from the semi-membranosus muscle; the semilunar cartilages are, as their name implies, both semilunar, and are attached at each end to the head of the tibia, but the external one sends an oblique bundle of fibres up to the femur in close connection with the back of the posterior crucial ligament; the superior tibio-fibular articulation does not, as a rule, communicate with the knee; and the ligamentum mucosum is attached by a delicate fold of synovial membrane to the posterior part of the trochlear surface of the femur, but is not continuous with the synovial membrane lining the crucial ligaments.

In the lower monkeys (rhesus, vervet, baboon, capuchin, and spider monkeys) much more rotation is allowed at the knee than in man, and this is the case during both flexion and extension, consequently smooth cartilage-covered facets are found between

[1] In reference to this, see Sutton on 'Ligaments,' p. 40.

the lateral ligaments and both tuberosities of the tibia, while the internal lateral ligament is not attached to the internal tuberosity and then prolonged down the shaft as in man, but passes straight from the internal condyle downward and forward to the inner surface of the shaft of the tibia.

The lower attachment of the external lateral ligament in the rhesus monkey is to the front of the upper surface of the head of the fibula, but in the spider monkey to the outer side of the neck; it was also noticed that the fibres of this ligament were twisted in such a way that those rising posteriorly from the femur became external and anterior when they reached the fibula. The ligamentum mucosum is continuous with the synovial membrane lining the anterior crucial ligament, so that there is an antero-posterior septum dividing the lower part of the joint into two halves, and making it impossible to pass a probe between the ligamentum mucosum and the anterior crucial ligament, as can so easily be done in man. The posterior ligament of the capsule is not a well-marked structure, and lacks the oblique expansion of the semi-membranosus, which is so characteristic of it in man. The crucial ligaments are not connected, and in Macacus rhesus I found that the synovial cavity of the joint was continued between them. The internal semilunar cartilage closely resembles that of man, but the external one, instead of being attached posteriorly just behind the spine of the tibia, is continued obliquely across the back of the posterior crucial ligament to the outer side of the internal condyle of the femur. In man this external cartilage acquires a new attachment behind the spine, but the older one still remains as an oblique band of fibres, closely connected with the back of the posterior crucial ligament, and sometimes spoken of in human anatomy as the ligament of Wrisberg. We shall see later that the simian attachment of this cartilage is the generalised mammalian type, and that man's arrangement is specialised for some purpose, probably as an adaptation to the erect position which results in strong and continual extension of the knee, with great strain on the intra-articular cartilages, especially the outer one, a strain which would possibly result in displacement were it not for the extra security gained by an attachment immediately behind the spine of the tibia. I have not had the opportunity of dissecting the knee of any of the anthropoids, but I am told by Keith and Duckworth that the arrangement in it more closely resembles that of the lower monkeys than that of man. In the baboon, vervet, and spider monkey the anterior and posterior attachments of the external semilunar cartilage, which otherwise are as in Macacus, are connected by a broad band resembling the rest of the cartilage, so that the structure is really circular instead of crescentic. In Ateles, too, a fibrous band runs from the anterior part of each semilunar cartilage in such a direction that they both meet in

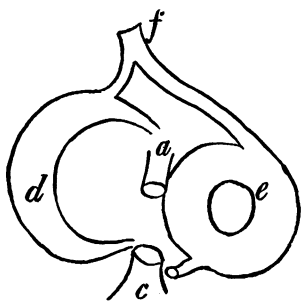

FIG. 2.—Knee joint of Spider Monkey (Ateles). *a*, anterior crucial ligament; *c*, posterior crucial ligament; *d*, internal semilunar cartilage; *e*, external semilunar cartilage; *f*, transverse ligament.

front of the internal cartilage, and become merged in the antero-internal part of the capsule. They are less well developed in other monkeys, and I think that the transverse ligament of the human knee must be a remnant of them.

In all the monkeys which I have examined the superior tibio-fibular joint communicated with the knee. In the knee of the lemur the arrangement and attachments of the semilunar cartilages and lateral ligaments closely resembled those of the rhesus monkey already described, but the ligamentum mucosum, instead of being firmly attached to the femur, was not connected with it at all. The chief difference, however, between the knees of monkeys and lemurs lies in the superior tibio-fibular joint. This joint in the lemur allows of free forward and backward gliding movements when the knee is flexed, but not when it is extended. The ligaments attached to the head of the fibula are four, two superior or external lateral of the knee; also an anterior and a posterior ligament. Of the two superior, which connect the fibula with the femur, the anterior is the usual external lateral ligament; while the posterior, I have little doubt, is the divorced tendon of the popliteus, the fleshy part of which is attached to the tibia and fibula to form part of the tibio-fibularis or rotator fibulæ. The anterior tibio-fibular ligament is a rounded horizontal bundle, considerably longer and

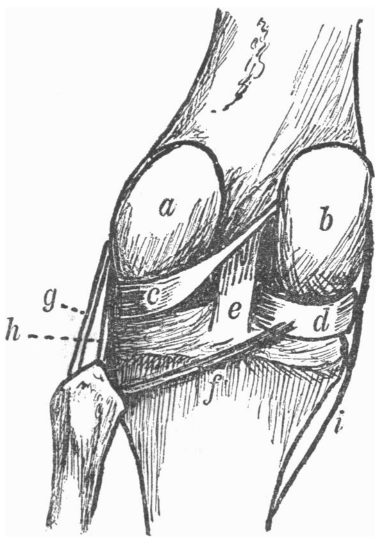

FIG. 3.—Knee joint of Lemur from behind. *a*, external condyle; *b*, internal condyle; *c*, external semilunar cartilage; *d*, internal semilunar cartilage; *e*, posterior crucial ligament; *f*, posterior tibio-fibular ligament; *g*, long external lateral ligament; *h*, tendon of popliteus converted into a ligament; *i*, internal lateral ligament.

better defined than in other animals, and at its inner end is attached to the front of the external tuberosity of the tibia. The fourth ligament corresponds to the posterior ligament of the superior tibio-fibular joint in man, but instead of being attached to the tibia it runs upward and inward behind that bone till it reaches the back of the internal semilunar cartilage. During flexion of the knee the fibula is free to glide forward and backward on the outer tuberosity of the tibia, but as soon as the knee is extended the external lateral ligaments which run downward and backward become tense, and prevent the fibula moving backward; at the same time, during extension of the knee the internal semilunar cartilage becomes longer from before back, and puts the posterior ligament connecting it with the head of the fibula on the stretch, so that the fibula can now move neither forward nor back. I confess that I do not know what advantage the lemur gains from this mobility of the superior tibio-fibular joint, but we shall see a very similar arrangement in many of the arboreal marsupials, and possibly it may be of use in tree-climbing, though why the arboreal monkeys do not possess the same arrangement is difficult to say.

In the Cheiroptera, the fruit bat (Pteropus), as I have already pointed out, has the flexor surface of the knee turned forward. No movement except flexion and extension is allowed, and it is interesting to notice that there are no traces of semilunar cartilages, an indication, I think, that these structures are chiefly intended to provide two separate joints, one above for hinge movements, and another below for rotatory or gliding movements. This arrangement reminds us of what we have already met with in the temporo-mandibular joint.

The external lateral ligament, which of course is internal in the bat, is double, and consists of a superficial and a deep part. I have little doubt that, as in the lemur, the deep part is really the tendon of the popliteus which has lost its muscular portion, not, in this instance, because that portion has been separated from it to move the fibula on the tibia, but because, having no rotating work at the knee to do, and no power of moving the head of the fibula, it has disappeared from sheer want of work. The internal lateral ligament is not continued down the shaft of the tibia, and the crucial ligaments show nothing remarkable. The patella is absent, a fact which is probably correlated with the disuse of the limbs as organs of progression. In the long-eared bat (Plecotus), which will serve as an example of the insectivorous bats, the knee joint does allow a certain amount of rotation, and in it semilunar cartilages are found as very delicate rings. This bat resembles the fruit bat, however, in the absence of any trace of a patella. In the Insectivora the hedgehog and mole have typical mammalian knee joints, the external semilunar cartilage is attached to the internal condyle posteriorly, and the crucial ligaments are unconnected; otherwise the joint is as in man. Since the tibia and fibula are firmly synostosed above and below in these animals, there can be no question of the superior tibio-fibular joint communicating with the knee.

The Carnivora, like the Insectivora, in the structure of their knee joint, maintain their reputation for being very generalised mammals, though some little interest attaches to the arrangement of the ligamentum mucosum; sometimes, as in the otter, it may form a vertical antero-posterior septum, reaching from the anterior crucial ligament as high as the lower margin of the trochlea; at other times, as in the bear and hyæna, the ligamentum mucosum is hardly attached to the femur at all.

In the bear (*Ursus Americanus*), the same twisting of the fibres of the external lateral ligament that has already been referred to in the monkey was well seen, and the direction of the twist was the same.

In the Ungulata the semilunar cartilages have the generalised mammalian attachments already described, but the external lateral ligament is modified to suit the disappearing fibula. In the horse, in which the upper part of the fibula is present, the ligament is attached as usual to the head of that bone. In the goat it is attached to the outer tuberosity of the tibia, and afterwards is prolonged down among the muscles as a fibrous cord representing the fibula. In the deer I could find no trace of a fibula, and the ligament ended in the outer tuberosity of the tibia. The characteristic twist of the external lateral ligament was well seen in the deer (*Cariacus rufus*) and the antelope (*Tragelaphus scriptus*), and the internal lateral ligament also showed a twist, though not so clearly as the outer. In the internal ligament, the posterior fibres at the femur became internal (superficial) and then anterior at the tibia—that is to say, the ligament was twisted in the opposite direction to the external lateral.

In all the ungulates which I have examined, the ligamentum mucosum has a very extensive attachment to the femur; in the ox it very nearly divides the knee into three joint cavities, one between the trochlea and the patella, and two others between the condyles and the tibia. In my specimen of the brocket deer (*Cariacus rufus*), the knee was completely divided into two chambers, by a reflexion of synovial membrane, running from the crucial ligaments to the tendon of the extensor longus digitorum, which rises from the outer side of the trochlea; the external condylo-tibial articulation is thus shut off from the rest of the knee joint. In the goat and chevrotain the ligamentum mucosum is well marked, and divides the two condylar parts of the joint from one another, but the trochlear portion communicates with both of them. In the Rodentia the knee joint resembles that of the Carnivora and Insectivora, in being typically mammalian in its arrangements.

In the Edentata, the three-toed sloth (Bradypus) has the synovial cavity between the patella and the trochlea completely shut off from that between the condyles and the tibia, and these latter, again, are separated from one another. In the armadillo the separation into three parts was not quite complete, while in the lesser ant-eater (Tamandua) and pangolin (Manis) the attachment of the ligamentum mucosum to the femur, although broad, does not nearly divide the joint into three. The lower attachments of the lateral ligaments in the armadillo are singularly low, and a great amount of rotation is allowed at the knee joint of this animal.

In the Marsupialia the knee and tibio-fibular joints have several points of interest. The crucial and lateral ligaments, and the semilunar cartilages, have the generalised mammalian attachments—*i.e.*, they are as in man, except that the posterior attachment of the external semilunar cartilage is to the internal condyle. The fibula, as Young has pointed out, is capable of a forward and backward movement at the superior tibio-fibular joint; the forward movement is checked by the external lateral ligament of the knee, while the backward is stopped by the long and strong anterior ligament of the tibio-fibular joint. I have had the opportunity of examining the knees of the following marsupials—Red kangaroo (*Macropus rufus*), Rock kangaroo (*Petrogale*), Wallaby (*Halmaturus*), Phalanger (*Phalangista vulpina*), Flying phalanger (*Acrobates pygmea*), Koala (*Phascolarctus*), Opossum (*Didelphys*), Tasmanian devil (*Dasyurus*), and Bandicoot (*Perameles*), and of these I think the phalanger showed the greatest specialisation of the joint, while the bandicoot had a much more generalised mammalian knee than the rest. In the koala, the phalanger, the opossum, and the Tasmanian devil, the great mobility of the fibula has produced the same effect on the popliteus that we noticed in the lemur; the fleshy part acquires an attachment to the fibula, while the tendon is converted into an extra external lateral ligament. In all the mar-

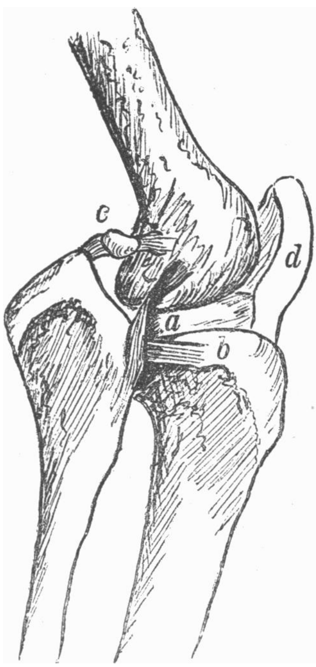

FIG. 4.—Knee joint of Opossum (Didelphys) from the outer side. *a*, external semilunar cartilage in front of twisted external lateral ligament; *b*, in front of anterior tibio-fibular ligament; *c*, tendon of popliteus, with sesamoid bone, forming an extra external lateral ligament; *d*, cartilaginous patella.

supials that I have examined, except the bandicoot, the patella is cartilaginous, and consequently these animals must want the leverage which this bone gives in extending the knee. Possibly the absence of a bony patella is made up for by the superior tibio-fibular joint. If the tibia and fibula are forcibly pressed together in the phalanger or the opossum, the head of the fibula will be seen to glide forward and inward, and, as the condyle of the femur is in contact with it during flexion of the joint, this forward and inward movement causes the knee joint to extend with considerable force; the extension of the knee thus started, is carried on by the external lateral ligament dragging the femur above its axis of rotation after the advancing head of the fibula. A circumstance which confirms me in the opinion that the leverage which the quadriceps extensor loses through the absence of the patella is made up for by the tibio-fibular muscle moving the fibula, is that in the bandicoot (Perameles) the tibio-fibular joint allows very little movement, the fibula never articulates with the femur, and the popliteus tendon, instead of being converted into an extra external lateral ligament, is continuous with its fleshy belly as usual. In this animal, therefore, the fibula can have little or no action in extending the knee, and we find that the patella, instead of being a pad of cartilage, as in other marsupials, is an elongated bone, as in most other mammals. It must not be imagined, however, that the loss of the patella is always compensated for by the mechanism I have described, for, in the kangaroos and wallabys, nothing of the kind exists; the fibula never touches the femur, and is not capable of great approximation to the tibia, nor does it in any way assist in the extension of the knee; in spite of this the patella is as distinctly cartilaginous as in the opossum or phalanger.

One ought not to leave the knee joint of the marsupials without noticing the great size which the external 'fabella' attains.

In the Monotremata, the Ornithorhynchus resembles the sloth in having the knee completely divided into three compartments by the ligamentum mucosum.

Both the external, and, as far as I could see, the internal semilunar cartilages, are attached to the femur posteriorly. The fibula articulates with the external condyle of the femur as well as with the tibia. The patella, unlike that of the marsupials, is large and is connected with the top of the fibula by a transverse ligament. The knee of the Echidna resembles that of Ornithorhynchus, except that the division of the joint into three is not quite complete. The anterior crucial ligament is divided into two bundles, which lie side by side, and the posterior horn of the internal semilunar cartilage turns up with the outer of these, and so is attached to the femur. The external semilunar is attached to the femur posteriorly, as in other mammals. The

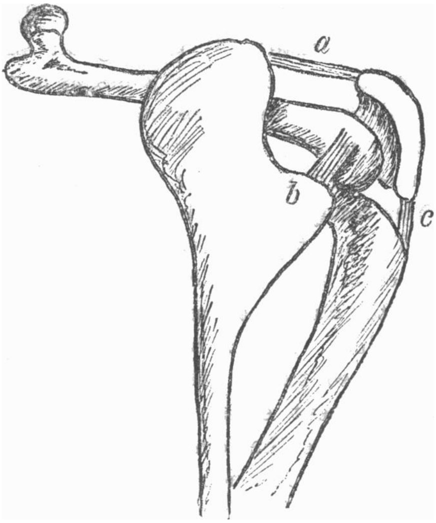

FIG. 5.—Knee joint of Ornithorhynchus from outer side. *a*, fibulo-patellar ligament; *b*, on fibula below external lateral ligament; *c*, ligamentum patellæ.

patella is very broad. The superior tibio-fibular joint communicates with the knee, and when the tibia and fibula are approxi-

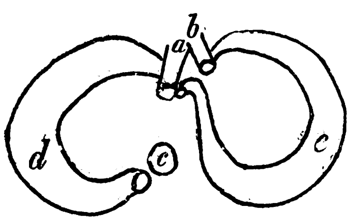

FIG. 6.—Knee joint of Echidna. *a* and *b*, double anterior crucial ligament; *c*, posterior crucial ligament; *d*, external semilunar cartilage; *e*, internal semilunar cartilage.

mated, the head of the latter glides forwards, as it does in marsupials.

Summary of the Knee.—The external lateral ligament of the knee in all mammals (including man) is twisted in such a way that the fibres attached posteriorly to the femur become external;

and then anterior when they reach the tibia. In some mammals a twist in the opposite direction is found in the internal lateral ligament. The ligamentum mucosum may be (1) quite unconnected with the femur as in the lemur; (2) slightly connected with it as in man; (3) forming an antero-posterior partition between the two condylar joints, as in most monkeys and the otter; (4) completely separating the knee into three cavities, two condylar and one trochlear, as in the three-toed sloth and duck mole; (5) separating the joint into two unequal parts, one trochleo-condylar and the other condylar, as in the brocket deer. The most primitive arrangement of the semilunar cartilages seems to be that both are attached posteriorly to the tibia, as in the duck mole and spiny ant-eater (Ornithorhynchus and Echidna). In man both horns of both semilunar cartilages are attached to the tibia. In other mammals an intermediate arrangement exists, and the external cartilage is attached posteriorly to the femur, the internal to the tibia. In the fruit bat, where no rotation of the knee occurs, there are no semilunar cartilages. In most monkeys the external semilunar cartilage forms a complete circle.

In certain marsupials the patella is cartilaginous, and this is coincident with a peculiar mobility of the superior tibio-fibular joint by which extension of the knee is assisted. In most mammals the superior tibio-fibular joint, when it is present, is continuous with the knee joint. Man is an exception to this.

THE ANKLE JOINT.

In contrasting the ankle joint of monkeys with that of man one is struck by the feeble development of the anterior fasciculus of the external lateral ligament. Keith has already pointed this out, and I am able to state that in my specimens of vervet and baboon the bundle was entirely absent, while in the macaque it was so feeble as to require careful looking for. This ligament in man checks lateral movement of the joint, and is most tense when the foot is at a right angle with the leg. I have had no opportunity of studying it in the anthropoid apes, but as far as my researches go, it is limited to certain monkeys and man, and therefore its presence is presumably connected with the maintenance of the erect position. In the spider monkey and lemur the middle fasciculus of the ligament is found attached to the anterior border of the external malleolus instead of to the tip of that process. The internal lateral ligament in all the monkeys I have examined (baboon, three macaques, vervet, capuchin, and spider monkey) is distinctly divided into an anterior and posterior band; of these the anterior consists of a superficial and deep portion. The superficial runs to the navicular bone, and then on to the metatarsus; it is described by Keith as the internal tibio-tarso-metatarsal liga-

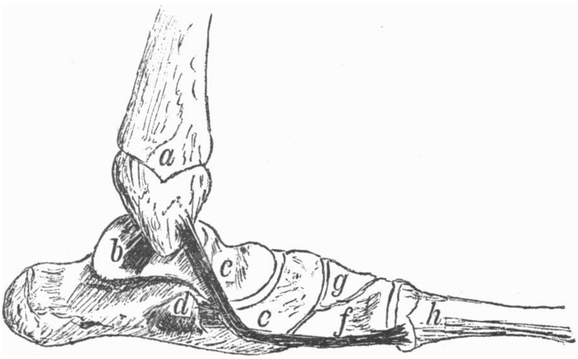

FIG. 7.—Ankle joint of Vervet Monkey (Cercopithecus) from inner side. *a*, tibia above epiphysial line; *b*, astragalus behind posterior fasciculus of internal lateral ligament; *c*, astragalus in front of anterior fasciculus of interior lateral ligament; *d*, sustentaculum tali; *e*, navicular; *f*, internal cuneiform; *g*, middle cuneiform; *h*, first metatarsal.

ment, while the deep part runs to the navicular bone and calcaneo-navicular ligament. The posterior part of the internal lateral ligament is not so strong, and runs downward and backward to the posterior part of the internal surface of the astragalus; it is broad and quadrilateral. The articular surface of the lower end of the monkey's tibia differs from that of man, in that it extends somewhat on to the front of the bone and comes into contact with the neck of the astragalus during dorsal flexion of the ankle; this arrangement has been noticed in some of the lower races of man. The inferior tibio-fibular joint of monkeys differs little from that of man, except that there is rather more synovial membrane.

In the lemur the ankle joint is practically identical with that of the monkeys, and there is no anterior fasciculus of the external lateral ligament; there is a good deal more movement, however, in the inferior tibio-fibular joint.

In the Cheiroptera the fruit bat (Pteropus) has the lower end of the fibula ending in a flat articular surface, which plays on a corresponding surface on the calcaneum. The joint between these two is completely shut off from the rest of the ankle joint, and there is a very definite extension of the synovial membrane of the ankle between the lower ends of the tibia and fibula.

In the Insectivora the hedgehog, mole, and shrew have the tibia and fibula fused together in the lower part of the leg. The external malleolus articulates by its tip with the calcaneum during dorsal flexion. As in all mammals below the higher Primates, the anterior fasciculus of the external lateral ligament is absent, and the middle fasciculus is attached to the front of the malleolus, and is nearly horizontal in direction. The posterior fasciculus is distinct, and connects the fibula with the astragalus as usual.

The internal lateral ligament is now seen in its generalised form; it consists of two definite bands—the anterior and more superficial passes to the navicular bone (tibio-navicular), while the posterior and deeper one is tibio-astragalar.

In the Carnivora the fibula is always distinct from the tibia at its lower end, and only the middle and posterior fasciculi of the external lateral ligament are present. Unlike the Cheiroptera and Insectivora, the fibula does not directly articulate with the calcaneum. In the Ungulata special arrangements are adopted to make the ankle a perfect hinge. In addition to the exact fitting of the lower end of the tibia into the deep trochlea of the astragalus the external lateral ligament is X-shaped, and so is tight in all positions of the joint. The deep portion of the X runs downward and backward, and is no doubt the middle fasciculus of the external lateral ligament of human anatomy, but the superficial limb which runs downward and forward has no representative in the more generalised ankles hitherto described. The anterior margin of the articular surface of the tibia is bevelled in most Artiodactyla; when the foot is dorsally flexed for rather over a right angle this margin comes in contact with the front of the facet on the astragalus, and movement of the ankle joint is brought to a standstill. It must not be imagined, however, that the foot cannot be dorsally flexed further than this, for the head of the astragalus continues the hinge movement, and rotates round a transverse axis until the astragalus is at right angles with the long axis of the foot. In this way dorsal flexion can be carried on until the metatarsals are nearly parallel with the tibia. The hinge-like steadiness of the ankle is increased by the external malleolus being concave from before back at its lower end, and articulating with a similar

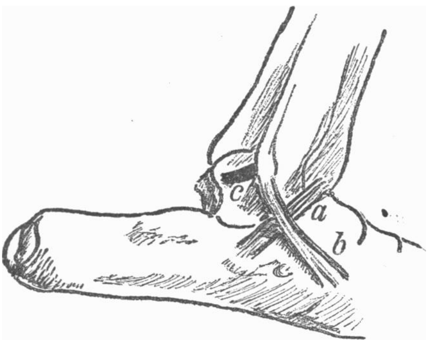

FIG. 8.—Ankle joint of Chevrotain (Tragulus) from outer side. *a*, middle fasciculus of external lateral ligament; *b*, extra ligament forming an X; *c*, posterior fasciculus.

convexity on the calcaneum. The internal lateral ligament consists of the two usual parts, the tibio-navicular, which is very strong, is superficial to and almost covers the tibio-astragalar portion; in addition to these there is another and more superficial band, which runs downward and backward across the tibio-navicular portion, and so forms an X on the inner side of the joint. The above description of the ligaments, which is taken from an examination of the ankle of the deer, antelope, and goat, seems to hold good for most ungulates; the bony surfaces are, however, liable to vary with the presence or absence of the lower end of the fibula. Hyrax is remarkable for the way in which the internal malleolus forms a spherical knob, which projects into a concavity on the inner side of the astragalus.

In the Rodentia the ankle is fairly generalised, the antero-posterior notch in the trochlear surface of the astragalus is very deep, and dorsal flexion of the ankle is stopped by the tibia and astragalus coming into contact anteriorly. The two bands of the internal lateral ligament are distinct, but the anterior one is sometimes, as in the case of Pedetes, attached to the sustentaculum tali instead of to the navicular. In the external lateral ligament of Pedetes and Dipus the same arrangement for forming an X ligament, already noticed in the Ungulata, is found. The external malleolus does not articulate with the calcaneum.

In the Edentata most of the species, such as Dasypus, Manis, and Tamandua, have a very generalised ankle, agreeing with that already described in the Carnivora and Insectivora. In Bradypus, however, the external malleolus forms a convex pivot, which fits into a concavity on the outer side of the astragalus, an arrangement resembling that of Hyrax, but on the opposite side of the joint.

The Marsupialia are remarkable for the possession of a structure which is not found in the ankles of other mammals. My attention was first called to it by Mr Pearson, the Prosector of this College, in the Tasmanian devil. In this animal it closely resembles the semilunar cartilages of the knee, and lies between the lower end of the fibula and the astragalus. The two horns of the semilune are directed outwards, the posterior being attached to the fibula just behind the external lateral ligament, while the anterior one is attached to the calcaneum in front of the lower attachment of the same ligament. This structure is present in all the marsupials which I have examined, but is best seen in those in which the fibula is very movable, such as the Tasmanian devil, phalanger, and opossum. In the kangaroo it is present, but does not form a semilune; instead it runs obliquely downward and forward on the inner side of the external lateral ligament. I think that its attachments and its arrangement in the kangaroo point to its being derived from some of the inner fibres of the so-called middle fasciculus of the external lateral ligament, and its presence is possibly explained by the fact that in most marsupials there is a certain amount of rotation of the fibula on its long axis in addition to the ordinary hinge movement of the ankle. What I have seen of complete and partial menisci in joints makes me think that their presence generally indicates two or more different kinds of movement, and that their origin is more likely to be an ingrowth from the surrounding capsule than a modification of some ancestral structure. In the kangaroos the same X-like arrangement of the external lateral ligament seen in Ungulates and Pedetes is found.

In the Monotremata both Ornithorhynchus and Echidna have the internal malleolus knobbed, as in Hyrax, to fit into the inner side of the astragalus, and so form a pivot. The external lateral ligament consists of only one very strong fasciculus, but

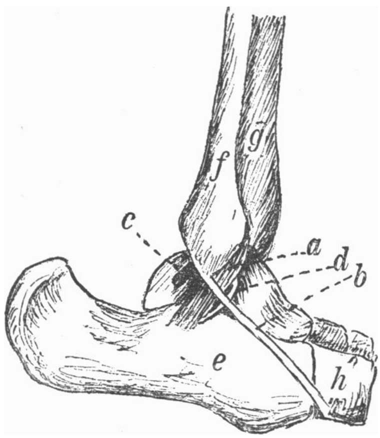

FIG. 9.—Ankle joint of Wallaby (Halmaturus) from outer side. *a*, mid fasciculus of external lateral ligament; *b*, extra fasciculus; *c*, posterior fasciculus; *d*, rudimentary interarticular meniscus; *e*, calcaneum; *f*, fibula; *g*, tibia; *h*, cuboid.

instead of being attached to the fibula it comes from the anterior margin of the lower end of the tibia close to the fibular articulation. It runs downward and backward to the calcaneum, and is evidently the middle fasciculus of the external lateral ligament of human anatomy. Its attachments and direction forcibly remind one of the arrangement of the fibres in the dorsal ligament of the carpus, which runs obliquely from the radius to the cuneiform in man and most other mammals.

Summary.—The anterior fasciculus of the external lateral ligament disappears in the lower Primates, and is probably an adaptation to the erect position. When the anterior fasciculus has disappeared the middle one occupies its point of attachment to the front of the external malleolus, but in the monotremes it is fixed to the front of the tibia; there is therefore some reason to think that the middle fasciculus of the

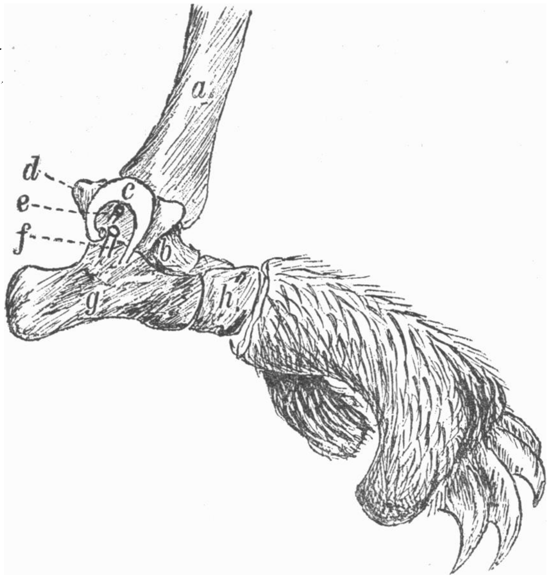

FIG. 10.—Ankle joint of Phalanger from outer side. (The fibula has been removed.) *a*, tibia ; *b*, head of astragalus ; *c*, interarticular meniscus ; *d*, ossification in meniscus ; *e*, posterior fasciculus of external lateral ligament ; *f*, middle fasciculus of external lateral ligament ; *g*, calcaneum ; *h*, cuboid.

external lateral ligament of the ankle is serially homologous with the dorsal ligament of the wrist joint, while the posterior fasciculus would probably be the serial homologue of the ulno-carpal band of the palmar ligament of the wrist, and the tibio-astragalar bundle of the internal lateral ligament of the ankle the serial homologue of the radio-carpal part of the palmar ligament of the wrist. This would leave the tibio-navicular bundle of the internal lateral ligament of the ankle as the serial homologue of the external lateral or radio-scaphoid ligament of the wrist.

Special protection against lateral movement of the ankle is attained in animals with a long foot, such as the ungulates, the kangaroo, and the Cape jumping hare, by additional lateral ligaments, which cross the permanent ones in such a way as to form an X.

In many marsupials a semilunar fibro-cartilage is interposed between the fibula and astragalus, and there are reasons for believing that this is derived from some of the fibres of the external lateral ligament. In these animals rotation as well as gliding and hinge movements take place at this joint, and this is one of the instances which make me believe that intra-articular menisci are formed in those joints where more than one kind of movement is present, and that, as in the bat's knee, they tend to disappear when only one kind of movement persists.