

ON THE HOMOLOGY AND MORPHOLOGY OF THE POPLITEUS MUSCLE: A CONTRIBUTION TO COMPARATIVE MYOLOGY. By GORDON TAYLOR, M.A., M.B., B.S., B.Sc. Lond., *late Pathological Assistant, Cancer Investigation Department, Middlesex Hospital*; and VICTOR BONNEY, M.S., M.D., B.Sc. Lond., F.R.C.S., M.R.C.P., *Lecturer on Practical Midwifery, Middlesex Hospital, Physician to Out-Patients, Chelsea Hospital for Women, Emden Research Scholar, Cancer Investigation Department, Middlesex Hospital.*

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WHILE engaged in the dissection of a specimen of *Felis domestica*, our attention was attracted by the fact that the *lowest and most external fibres* of the popliteus muscle appeared to pass uninterruptedly into the tibialis portion of the deep flexor of the pedal digits; indeed, almost a third of the muscle joined the flexor tibialis (*vide* fig. 5).

On closer inspection, a minute tendinous intersection was found to be present in the muscular substance; but certain of the fibres undoubtedly passed into the more distal muscle without any interruption in their continuity.

The obvious suggestion was that these represented the *condylo-radialis* of Windle, which occurs frequently in the anterior extremity. Indeed, the attachment of the two muscles had a fair amount of similarity—namely, a muscular slip arose from the external condyle of the femur (the representative of the internal humeral condyle) and passed to join the flexor tibialis digitorum pedis—the representative of the flexor radialis of the forearm.

We decided to investigate this point by means of dissections of various types, but we found that the matter was more involved than at first sight appeared, and that a proper determination of the homology of this muscle necessitated a comprehensive morphological survey of the flexor group of muscles of the posterior tibial region, and, beyond this, a consideration of the homologies existing between them and the corresponding group in the fore limb.

In this endeavour, dissections have been made of the hind limb of the following members of the various mammalian orders, with the exception of

the Cetacea and Sirenia, in which a hind limb is either rudimentary or absent altogether.

Two specimens of lizard have also been investigated.

Reptilia.

Lacertilia.

Varanus flavescens.

Varanus exanthematicus.

Mammalia.

Monotremata.

Echidna hystrix (Spiny Ant-eater).

Marsupialia.

Trichosurus fuliginosus (Sooty Phalanger).

Trichosurus vulpecula (Vulpine Phalanger).

Macropus melanops (Black-faced Kangaroo).

Hypsiprymnus rufescens (Rufus Rat Kangaroo).

Edentata.

Bradypus tridactylus (Three-toed Sloth).

Dasypus villosus (Hairy Armadillo—two specimens).

Ungulata.

Cervidæ. *Cervus axis* (Axis Deer).

Bovidæ. *Ovis aries* (Common Sheep).

Ovis burrhel (Burrhel Wild Sheep).

Gazella Arabica (Arabian Gazelle).

Subungulata. *Hyrax Capensis* (Cape Hyrax).

Rodentia.

Myomorpha. *Mus musculus* (Mouse).

Hystricomorpha. *Atherura Africana* (African Brush-tailed Porcupine).

Cavia cobaya (Guinea-pig).

Lagomorpha. *Lepus cuniculus* (Rabbit).

Carnivora.

Felidæ. *Felis domestica* (Domestic Cat—several specimens).

Viverridæ. *Suricata tetradactyla* (Suricate).

Herpestes griseus (Grey Ichneumon).

Canidæ. *Canis familiaris* (Dog).

Canis vulpes (Fox).

Ursidæ. *Ursus Malayanus* (Malay Bear).

Mustelidæ. *Lutra vulgaris* (Otter).

Insectivora.

Erinaceus Europæus (Hedgehog).

Cheiroptera.

Cynonycteris collaris (Collared Fruit-bat).

Primates.

Lemuroidea. *Lemur catta* (Ring-tailed Lemur).

Anthropoidea. *Platyrrhini*—*Cebus fatuellus* (Brown Capuchin).

Catarrhini—*Macacus rhesus* (Rhesus Monkey).

Papio porcarius (Chacma Baboon).

The following is a detailed account of the popliteus and upper attachments of the flexores tibialis et fibularis, as found in the dissections of the foregoing animals.

The lower attachments of the latter two muscles were only investigated in so far as was necessary to identify them.

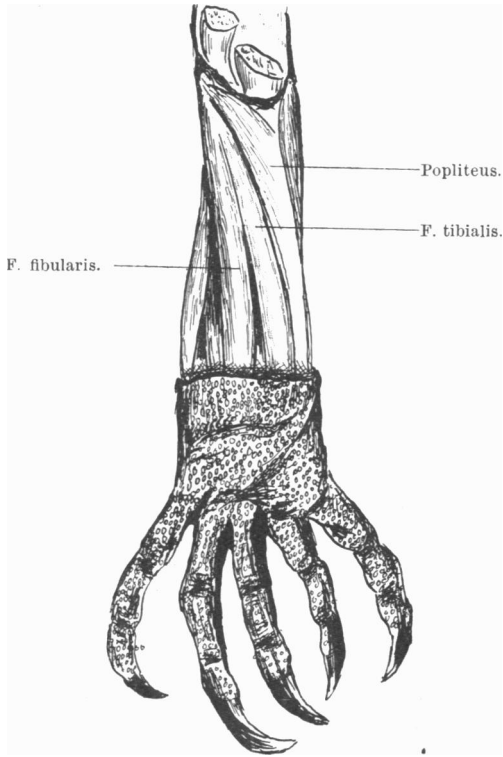


FIG. 1.—Posterior tibial region of *Varanus exanthematicus*.

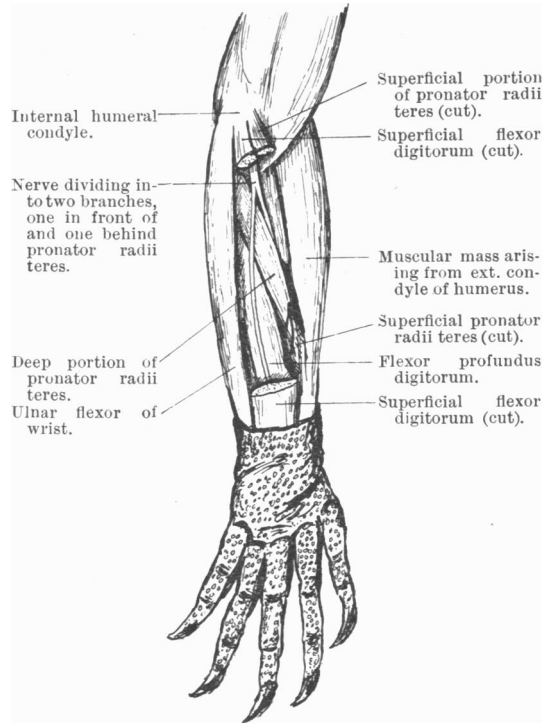


FIG. 2.—*Varanus flavescens*.
Ventral surface of antibrachium.

RESULTS OF DISSECTIONS.

Varanus exanthematicus, *Varanus flavescens* (vide figs. 1 and 2).—In both of these forms the popliteus arises (1) from the head of the fibula, (2) from the meniscus femoro-fibularis; the latter attachment is only a slight one.

The meniscus femoro-fibularis is connected with the external femoral condyle by the ligamentum femoro-fibulare.

The muscle consists of fibres which may be somewhat artificially

separated into 2 layers. There is not, however, in our specimens the distinct separation between these 2 layers which Fürst figures in *Varanus Gouldii*. The nerve passes superficial to the muscle. No fibres of the popliteus

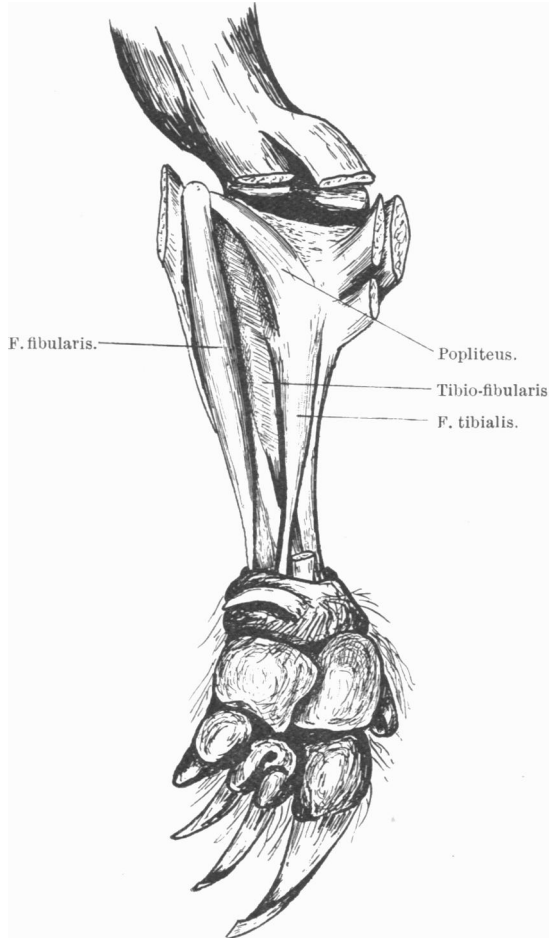


FIG. 3.—*Echidna hystrix*.

pass into the flexor muscle of the digits. Both flexor tibialis and flexor fibularis arose from the head of the fibula.

Echidna Hystrix.—The popliteus is attached above to the mesial aspect of the processus capituli fibularis, and below to the upper half of the tibia. There is a deeper stratum of transverse fibres, which Fürst calls the "pars

interossea" as opposed to the "pars propria." This is certainly a separate interosseus muscle, the "tibio-fibularis." It constitutes the third or deepest muscular stratum of the leg.

The tibialis portion of the deep flexor of the digits arises from the tibia below the popliteus insertion, but no fibres of the latter muscle pass into the flexor tibialis.

The flexor fibularis has the usual origin from the upper part of the fibula (*vide* fig. 3).

Trichosurus fuliginosus.—From the upper extremity of the fibula there arises a stratum, which consists of the following muscles—in order from above downwards, and from within outwards: (1) Popliteus; (2) a fasciculus, intimately associated with the popliteus at its origin, but passing below directly into the flexor tibialis; (3) flexor tibialis; (4) tibialis posticus; (5) flexor fibularis.

(2) and (3) are separated by the nerve-twigs proceeding to supply the popliteus.

The flexor tibialis ends in a sesamoid in the sole of the foot.

The flexor fibularis supplies all the digits, and also gives off from its superficial aspect in the middle of the leg the superficial flexor of the toes (*vide* fig. 4).

Trichosurus vulpecula.—The arrangement of muscles of the hind limb is the same as in *T. fuliginosus*; but the flexor fibularis does not give origin to the superficial flexor, as in the other species.

Macropus melanops.—Popliteus arises (1) from the external femoral condyle by means of a strong tendon; (2) from a sesamoid developed in the aforesaid tendon; (3) from the head of the fibula, slightly. The insertion is into the upper fifth of the tibia.

From the superficial aspect of the muscle near its inferior border a muscular slip takes origin, of which the fleshy belly, measuring about $1\frac{1}{4}$ inches in length, passes into a long filiform tendon which is attached to the tarsus. The direction of the muscular fibres in this slip corresponds with that of the popliteal fibres.

The flexor fibularis is a powerful muscle arising from fibula and tibia, and supplies all the 4 digits.

The long tendinous slip, with the fleshy belly at its proximal end, would appear to be a flexor tibialis, because of its superficial position, for a tibialis posticus would not be superficial to the popliteus. Its insertion into the tarsus is not an insurmountable objection, for the flexor tibialis may end in the tarsus in certain rodents, and it ends in a sesamoid in the phalangers.

If the slip referred to be the flexor tibialis, then *no* tibialis posticus is present.

Hypsiprymnus rufescens.—The popliteus arises from external femoral condyle. There is the usual insertion.

The flexor fibularis is a powerful muscle, and, as in *Macropus*, arises from tibia and fibula.

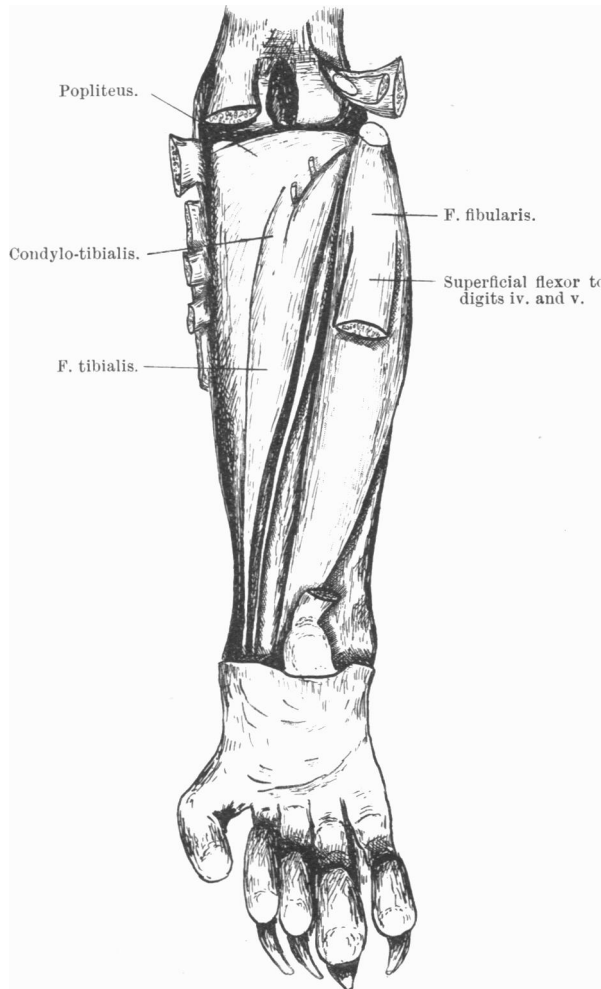


FIG. 4.—*Trichosurus fuliginosus*.

The tibialis is a similar minute fleshy slip, with a filiform tendon, but does not arise from the superficial aspect of the popliteus, but, running along the lower border of the latter muscle, it can be traced up to the fibular head. It ends as in *Macropus*, on the tarsus.

Bradypus tridactylus.—The popliteus arises from the external femoral condyle, and is inserted into the upper two-thirds of the tibia. No fibres pass into the flexor tibialis, but a muscular bundle of considerable dimensions arises from the external supracondylar ridge of the femur, proximal to the origin of the external head of the gastrocnemius. This passes down the limb, deep to the last mentioned muscle, and joins the flexor fibularis on its superficial and inner aspect.

Dasypus villosus.—The popliteus arises from the external condyle of the femur; it is inserted into the upper half of the tibia. The flexor fibularis is a very powerful muscle. The flexor tibialis is smaller than the fibularis, and arises (1) from the tibia; and (2) some of the lowermost and outermost fibres of the popliteus pass into the muscle.

Cervus axis.—The popliteus arises from the external condyle of the femur, and is inserted into the upper third of the tibia. Some of the lower and outermost fibres gain an attachment to a tendino-aponeurotic band on the external and deep aspect of the uppermost part of the flexor tibialis.

From this tendinous band, some of the fibres of the flexor tibialis also arise.

This arrangement obtains in our other ungulata, viz.—*Gazella Arabica*, *Ovis aries*, and *Ovis burrheli*.

Hyrax Capensis.—The popliteus arises from the external femoral condyle, and has the usual insertion. No fibres pass into the flexor tibialis, which is distinctly smaller than the flexor fibularis. There is no tibialis posticus.

Mus musculus.—No popliteal fibres pass into the flexor tibialis.

Atherura Africana.—The popliteus arises from the external femoral condyle, and is inserted into the upper third of the tibia. A small fasciculus passes into the flexor tibialis. Flexor fibularis is a large muscle arising from both tibia and fibula. Flexor tibialis is comparatively small. A tibialis posticus is present.

Cavia cobaya and *Lepus cuniculus* show no trace of popliteal fibres passing into flexor tibialis.

Felis domestica.—The popliteus arises from external femoral condyle. The tibialis has three heads of origin: (1) a tibial head; (2) a fibular head; (3) a popliteal head.

The size of this latter head appears to vary. In the first specimen that we dissected, a very large proportion of the muscle passed with the popliteus to the external femoral condyle; but in subsequent dissections of other specimens the size of this head was much smaller, or did not exist at all.

The fibularis and tibialis posticus each arises by two heads, from the fibula and tibia respectively (fig. 5).

Suricata tetradactyla.—The popliteus arises from the external femoral

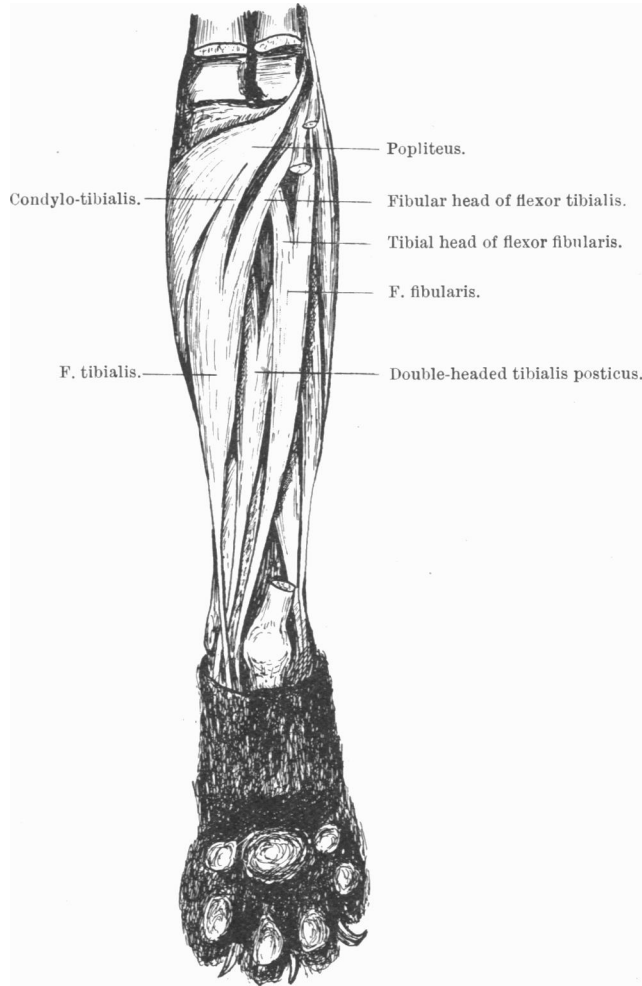


FIG. 5.—*Felis domestica*.

condyle, and is inserted into the upper two-thirds of the tibia. Its outermost and lowest fibres are directly continuous with those of the flexor tibialis.

The flexor fibularis is the largest muscle of the flexor stratum.

Herpestes griseus and *Canis familiaris* show no trace of popliteal fibres passing into the flexor tibialis.

Canis vulpes.—A similar condition obtains here.

Ursus Malayanus.—The popliteus arises from the external femoral condyle. The muscle is inserted (1) into the upper half of the posterior surface of the tibia. (2) Some of the outer and deeper fibres are inserted into the tibial half of a tendinous band, running from fibula to tibia, along the

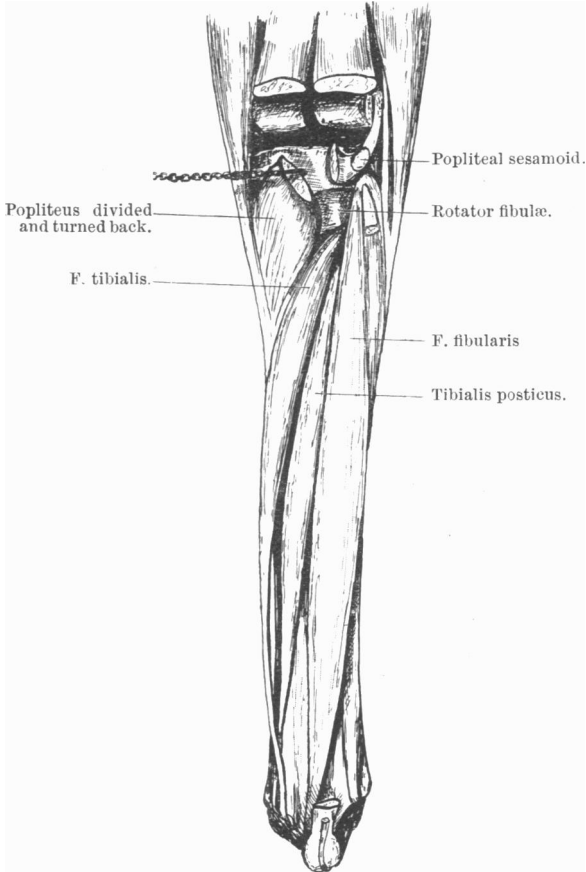


FIG. 6.—*Lemur catta*.

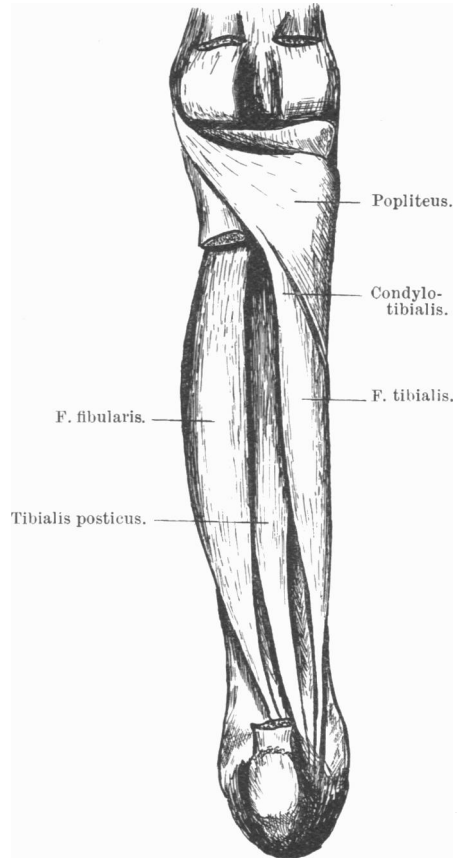


FIG. 7.—Posterior tibial region of *macacus rhesus*.

upper border of the tibialis; the flexor tibialis arises from tibia, head of fibula, and the tibio-fibular tendinous band referred to.

Lutra vulgaris.—The popliteus arises from the external femoral condyle, and inserted into the upper half of the tibia.

The tibialis arises as in *Ursus*, but in addition some fibres are attached to some tendinous bundles on the lower border of the popliteus.

The tenuissimus emerged from the postero-inferior border of the flexor cruris lateralis, and extended right down to the os calcis, remaining fleshy to within a third of an inch of its insertion.

Erinaceus Europæus.—No fibres of popliteus passed into flexor tibialis.

Cynonycteris collaris.—A popliteus was not present. Fürst also failed to find it in a Pteropus and a Vespertilio.

Lemur catta.—The popliteus comes from the external femoral condyle, though at first sight it appears to arise from the fibular sesamoid; but the tendon can be distinctly traced onwards underneath the external lateral ligament, to the external condyle. The tendon appears to be degenerate.

The sesamoid is closely bound to the head of the fibula.

Beneath the popliteus is a rotator fibulæ, which stretches across the uppermost part of the interosseous space. This muscle is evidently a persistent portion of the primitive interosseous muscle, known as the tibio-fibularis. No popliteal fibres pass into the flexor tibialis (*vide* fig. 6).

Papio porcarius.—The popliteus arises from the external femoral condyle; a few of its lowermost fibres are continuous with the flexor tibialis, a minute tendinous intersection intervening.

Macacus rhesus and *Cebus fatuellus* show a similar arrangement, but no tendinous intersection appears to be present (*vide* fig. 7).

The results of our dissections may be briefly expressed as follows:—There is intimately associated with the popliteus a distinct band of muscular fibres whose upper attachment varies *pari passu* with that of the popliteus, and which passes below into the flexor tibialis.

Such a muscular slip is *present* in the following animals:—

<i>Marsupialia.</i>	Trichosurus fuliginosus. Trichosurus vulpecula. Macropus melanops. Hypsiprymnus rufescens.
<i>Edentata.</i>	Dasypus villosus (2 specimens).
<i>Rodentia.</i>	Atherura Africana.
<i>Carnivora.</i>	Felis domestica (some specimens). Suricata tetradactyla.
<i>Primates.</i>	Cebus fatuellus. Macacus rhesus. Papio porcarius.

It is doubtfully present in the following:—

	All the Ungulata, except hyrax.
<i>Carnivora.</i>	Ursus Malayanus. Lutra vulgaris. Felis domestica (some specimens).

It is entirely absent in the following:—

Lacertilia.	Varanus flavescens. Varanus exanthematicus.
Monotremata.	Echidna hystrix.
Edentata.	Bradypus tridactylus.
Ungulata.	Hyrax Capensis.
Rodentia.	Mus musculus. Lepus cuniculus. Cavia cobaya.
Carnivora.	Canis familiaris. Canis vulpes. Herpestes griseus.
Insectivora.	Erinaceus Europæus.
Chiroptera.	Cynonycteris collaris.
Primates.	Lemur catta.

THE PRIMITIVE PROXIMAL ATTACHMENT OF THE MUSCLES OF THE POSTERIOR TIBIAL REGION.

In the *hind limb of the lizard* it will be remembered that *not only did the popliteus arise from the fibula*, but that the *flexor tibialis arose from the fibula as well*, there being, paradoxical as it may appear, no origin of the F. "tibialis" from the tibia (*vide* figs. 1 and 2).

A dissection of the same region in the fore limb revealed the same interesting condition, viz.—That the *flexor "radialis" arose entirely from the ulna*, there being *no radial origin to this muscle*. In the fore limb the superficial flexor (sublimis) arose as usual from the internal condyle, so that we have the very suggestive fact that *both superficial and deep flexors arose from the post-axial side of the limb*.

We believe this to be the primitive arrangement in both the forearm and leg regions, and we suggest that it is correlated with a caudal-ward movement at the elbow-joint and knee-joint necessary for the method of progression by sprawling or swimming, which obtains in the lower vertebrata.

HOMOLOGY OF THE POPLITEUS.

It is usually stated that the popliteus is the homologue of the pronator radii teres. Keith, however, in his *Myology of the Catarrhini* puts forward the suggestion that it represents the *deep part only* of this muscle, and that the superficial portion may be represented in man by an occasional slip from the external head of the gastrocnemius.

Hepburn has found a similar slip in the chimpanzee.

With Keith's suggestion we entirely concur. In dissecting the fore-limb of our two specimens of *Varanus*, we found that the *pronator radii teres* was composed of two distinct parts:—

(1) A superficial portion arising from the internal condyle.

(2) A deep portion arising from the upper part of the shaft of the ulna, close to its head.

The median nerve passed between these two portions, whilst the anterior interosseous nerve passed downwards behind a deep portion, embedded in the substance of a well-developed interosseous radio-ulnar muscle (*vide* fig. 1).¹

In the hind limb of *Varanus*, the popliteus arose as before stated from the head of the fibula, and was inserted into the tibia in its upper half. Beneath it was the interosseous layer of muscle, known as the tibio-fibularis, and it was covered by the superficial mass of flexor muscles with which it, as well as the flexores tibialis et fibularis, were intimately connected (*vide* fig. 2).

It will be seen then that the popliteus of *Varanus* exactly corresponds, both in origin, insertion, and relations, with the *deep portion* of the *pronator radii teres*. The superficial of the latter muscle is probably represented in the hind limb of *Varanus* by some of the fibres of connection which exist plentifully between the superficial and deep layers of muscle, and which, arising in common with a gastrocnemius mass, attain an extensive aponeurotic insertion into the inner border of the tibia.

From a consideration of all the foregoing facts it is obvious that the popliteus belongs to the same stratum as the F. tibialis et fibularis, and that it is a differentiated part of the muscle-sheet, which also gives rise to the F. tibialis and F. fibularis.

Moreover, we have seen in the lizard how this muscle-sheet is primitively post-axial at its proximal attachment.

In the fore limb also the corresponding muscle group—that is, the *deep* portion of the pronator radii teres, and the F. radialis et ulnaris—are likewise post-axial in origin.

THE PHYLOGENETIC VARIATIONS IN THE UPPER ATTACHMENT OF THE POPLITEUS.

In a primitive limb, as in *Varanus*, the tibia and fibula move freely upon one another; indeed, the need of some means of attaining the rotatory movements of the limb necessary for propulsion or progression is probably

¹ Since writing the above, we have examined the dissections of the antibrachium of *Ornithorhynchus anatinus* and *Echidna aculeata* in the Museum of the Royal College of Surgeons, and were much interested to find that an *ulnar* head to the pronator radii teres exists in both of them.

the factor which has determined the existence of two bones in the middle segment of either limb. *When the necessity for such a movement is no longer required, the bones tend to become fused.* Coincidentally with the loss of movement between the tibia and fibula, changes in the muscle will inevitably follow. Rotatory movement between the two bones of the leg is absent in the majority of the mammalia, and is confined (if one except the case of the Lemur) to the *Monotremes and less specialised members of the Marsupialia.*

It is an interesting and suggestive fact that the rotatory mechanism seen in the lizards should be retained in these early and primitive mammalian orders.

In *Echidna hystrix*, and in both our specimens of *Trichosurus*, there was free movement between the bones of the leg; and in *Echidna* of the fibula on the femur, and in all the *popliteus*, had only a fibular (post-axial) attachment in the same manner as obtained in *Varanus*. The musculature of these mammals in the region under discussion only differed from that of the reptile in that the *F. tibialis* did not have a purely fibular origin (*cp.* figs. 1, 3, and 4).

The proximal attachment of these muscles in the leg of the more generalised Marsupials is therefore very fairly comparable with those of the homologous muscles in the antibrachium, as they exist in man.

In the highly specialised Marsupials, *e.g.* Kangaroo, and in all the remaining orders (except the sub-order of the Lemuroidea or Lemurs), the pseudo-rotatory movement between the leg bones has become lost, and coincidentally the *popliteus* having ceased to perform its original function as a fibular rotator, has become modified to act as a flexor of the leg, and has in consequence *acquired a new attachment* to the external condyle of the femur by *ascent*.

In the Kangaroo, the *F. fibularis* is the only functional deep flexor of the digits present, and the *F. tibialis* appears to be reduced to the small muscle arising from the superficial aspect of the *popliteus*, which has already been described.

In the ungulates, the *popliteus* has distally a very characteristic mode of attachment—*viz.*, to the upper edge of a fibrous arch, passing between the fibula and tibia.

This arch corresponds in position with the line of attachment of the human soleus, and we suggest that, in the case of Man, the soleus has extended along this arch from its primitive fibular origin until it has reached the tibia, thus cutting off the *popliteus* from the flexor tibialis, and at the same time pushing the latter muscle down on to the tibia, so that it no longer has a fibular head.

THE POPLITEAL FABELLA.

A fabella was developed in the tendon of the popliteus in most of the animals dissected by us, with the exception of the ungulates, and those animals in which it arose from the head of the fibula.

The fabella would therefore appear to be connected in some way with the ascent of the upper attachment of the muscle. It is developed from the fibro-cartilaginous ligamentum femoro-fibulare of Fürst, which in the lizard passes from the head of the fibula to the external condyle, and which the muscle in other forms utilises to attain its femoral attachment.

It scarcely appears likely to have been formed as a separated traction epiphysis of the head of the fibula, after the manner of fabella formation described by Parsons in the tendons of certain other muscles.

THE POPLITEUS OF THE LEMUR. (*Vide* fig. 6.)

The exceptional condition found in this animal requires special reference. The popliteus arises from the external condyle through a broad, flat tendon, which joins the muscle by the medium of a well-marked sesamoid, and which is very closely adherent to the head of the fibula.

Underneath the muscle is, as we have seen, a broad band of muscle fibres known as the rotator fibulæ. This muscle is not a part of the deep flexor sheet of which the popliteus represents a differentiated portion, but is to be regarded, as we have already stated, as a *persistent upper part of the interosseous tibio-fibularis of lower mammals*. To regard the popliteus as consisting of two strata independent of the tibio-fibularis, is to imply the existence of *four* primitive muscle strata in the leg, because we have already stated that we regard a portion of the gastrocnemius mass as equivalent in the lower limb to the superficial portion of the pronator radii teres in the upper limb.

It is very interesting to observe that in this animal, which alone of all the higher mammals manifests fibular rotation, the popliteus appears to be preparing through the sesamoid to redescend on to the fibula, doubtless to fulfil thereby the function of rotation, which is characteristic of the muscle in the primitive limb.

MORPHOLOGY OF THE "CONDYLO-TIBIALIS."

As stated on the opening page of this paper, our original intention was to ascertain the constancy of this slip in the various mammalian orders, and, if possible, to decide with what muscle of the fore limb it is homologous.

It would appear to us that its homologue in the anterior extremity is

the condylo-radialis of Windle. Professor Windle (*Journal of Anatomy and Physiology*, N.S., 4, 1899-90) has pointed out that the flexor mass of muscle in the forearm may be regarded as typically consisting of the following 6 parts—viz., flexor sublimis, flexor radialis, flexor ulnaris, condylo-radialis, condylo-ulnaris, and condylo-centralis.

Excluding the sublimis, the deep flexor will therefore consist of 5 parts, in a generalised mammal, such as a Carnivore or Insectivore. After the radialis and ulnaris, the commonest constituent is the condylo-radialis, which, according to Windle, arises typically from the internal humeral condyle, and joins the radial side of the common tendon, formed by the various components of the deep flexor stratum. A comparison between the condylo-tibialis and condylo-radialis shows that, not only do they bear a similar relation to the popliteus and deep portion of the pronator radii teres respectively, which, as we have seen, are to be regarded as homologous, but that they accompany the phylogenetic migrations of these muscles in a striking manner.

It is clearly apparent that there are certain stages in the phylogeny of the muscles derived from the deep flexor sheet of the forearm and of the leg.

The *first stage* is one in which the popliteus, flexor tibialis, and flexor fibularis all arise from the fibula, whilst in the forearm the *deep head* of the pronator radii teres, the radialis, and ulnaris all take origin from the ulna; such a stage is seen in the anterior and posterior extremities of the Lacertilia.

In the *second stage*, the other crural and antibrachial muscles retain their primitive attachments, but the flexor tibialis and flexor radialis extend their origins to the tibia and radius respectively. This condition is present in the Monotremata in both limbs, but in generalised Marsupials in the *leg* only, the muscles of the upper limb having passed into the third stage.

In the *third stage*, movement between the tibia and fibula having ceased to exist, the popliteus ascends to the external condyle of the femur, and carries with it some of the fibres of the flexor tibialis which represent the condylo-tibial slip under discussion; in the preceding stages, where the tendon of origin has not ascended to the outer condyle of the femur, the slip must be regarded as representing the connecting fibres with the flexor tibialis, which, in the primitive condition, extended continuously along the posterior aspect of the leg. In the antibrachium, though we cannot say definitely that the deep head of the pronator radii teres ascends to the internal condyle when movement between the bones ceases to exist, yet it is highly probable that some of the deeper fibres of the pronator radii teres in Carnivores, which undoubtedly arise from the internal condyle, represent the original *ulnar head* of the muscle; for it is noteworthy that the pronator

radii teres in the Cat is a deep, wedge-shaped muscle, extending right down to the upper extremities of the two bones of the forearm. None of the deep flexor layer of muscle extends beneath the pronator, and in thickness it certainly equals the conjoined superficial and deep flexor mass.

With this probable migration of the deep head of the pronator radii teres, the condylo-radialis is carried up also, to gain an attachment to the internal condyle.

But if such be the march of events, and if from the phylogenetic point of view the humeral origin of the condylo-radialis be more recent than the ulnar origin, then it may be objected that it appears rather strange that in Man, a mammal most specialised and the most highly evolved, the apparently older stage in the evolution of the muscle persists.

But we must remember that, in him, movement between the bones of the forearm has reappeared in an extreme degree.

Obviously, muscles producing this movement will act to greater advantage if the ulna be their fixed point of attachment; and hence the fact that a reptilian characteristic—viz., the deep layer of the pronator radii teres—has in him reappeared.

The human condition then constitutes a *fourth stage* in the phylogeny of the muscles derived from the deep flexor sheet of the antibrachium, and may be regarded as a reversion to a more primitive stage in adaptation to special requirements.

In the leg of the Lemur, in which movement between the bones has been similarly reacquired, *indications of this fourth stage* are apparent in the firm attachment that the popliteus attains to the head of the fibula, by the medium of the popliteal sesamoid.

In this fourth and reversionary stage, as seen in the arm of Man, the condylo-radialis descends to the coronoid process of the ulna, with the deep portion of the pronator radii teres, and exists as the accessory head of the *F. longus pollicis*, being thus strictly comparable to the condition of the condylo-tibial slip in those animals in which the upper origin of the popliteus is from the head of the fibula (see figs. 3 and 4).

The condylo-radialis in the antibrachium is always closely related to the flexor sublimis digitorum.

The condylo-tibial slip in the leg of the generalised Marsupials which we have dissected, and in which the popliteus arose from the fibula, always took origin in close relation with that of the soleus, which is generally looked upon as the representative of the flexor sublimis digitorum of the fore limb.

This we look upon as further evidence that the slip in question is the homologue of the condylo-radialis in the forearm.

CONCLUSIONS.

(1) That the superficial portion of the pronator radii teres is homologous in the lower limb with a portion of the gastrocnemius mass.

(2) That the deep portion of the pronator radii teres is homologous in the lower limb with the popliteus.

(3) That the deep portion of the pronator radii teres and popliteus arose primitively from the head of ulna and head of fibula respectively.

(4) That as movement between the tibia and fibula, and radius and ulna respectively, ceased to exist, the upper origin of the popliteus certainly, and the deep portion of the pronator radii teres probably, ascended to the external femoral and internal humeral condyles respectively.

(5) That in this upward migration they carried with them certain fibres of the flexor tibialis and flexor radialis respectively.

(6) That these fibres exist as the condylo-tibialis and condylo-radialis respectively.

(7) That in the Lemur, where movement between the tibia and fibula has reappeared, the popliteus appears to be descending to its primitive fibular attachment.

(8) That in Man, and to an extent in the Anthropoid Apes, in whom movement between the radius and ulna has reappeared, the deep portion of the pronator radii teres has descended to its primitive ulnar attachment, carrying with it the condylo-radialis

(9) That the fibrous arch from which the soleus arises in Man, is identical with the similar structure to which, in Ungulates, a large portion of the popliteus is attached, and is to be regarded as indicating the original line of the fibular origin of the popliteus.

We cannot conclude this paper without expressing our thanks to Mr Beddard, of the Zoological Society of London, for his kindness in placing so many specimens at our disposal.

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