THE PHYLOGENY OF THE CRURAL FLEXORS.

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WITH 14 TEXT FIGURES.

In an earlier paper (1903) I presented the results of a comparative study of the flexor muscles of the antibrachial region and showed that it was possible to trace step by step the changes by which the arrangement occurring in the Urodelous amphibia was converted into that characteristic of the mammalia. In the amphibia the muscles in question possess a definite arrangement in layers and it was shown that these layers have a fundamental significance, since, notwithstanding the almost innumerable modifications and differentiations which they present in higher forms and the apparently enormous differences which exist between the amphibian and mammalian forearm musculatures, yet the layers could be recognized throughout and consequently afforded a basis for the reconstruction of the phylogeny of the mammalian muscles.

It became of interest, consequently, to ascertain whether a comparative study of the crural flexors would reveal a similar fundamental arrangement in layers and so afford a basis for their phylogenetic reconstruction, and, if so, an opportunity for a satisfactory consideration of the much-discussed question of the serial homology of the arm and leg musculature. In the following pages the results of such a study are recorded in so far as they bear upon the first of the two problems mentioned, namely, the phylogeny of the crural flexors. The question of the serial homology of the arm and leg musculature I hope to discuss later in connection with some other general questions relating to the morphology of the vertebrate limb.

The methods and forms employed in the present study were essentially the same as those made use of in the investigation of the arm muscles. The arrangement and relations of the muscles were studied in serial transverse sections and the forms employed were *Amblystoma tigrinum* as a representative of the Urodele amphibia, *Scincus sp?* as

a representative of the reptilia and the opossum (*Didelphys virginiana*),[1] the mouse, the cat and man as representatives of the mammalia.

I. THE CRURAL FLEXORS OF THE URODELOUS AMPHIBIA.

A transverse section through the upper part of the crus of Amblystoma shows the arrangement of parts represented in (Fig. 1). Superficially upon the posterior surface of the section is seen a strong, somewhat crescentic, muscular mass, which, employing a terminology consistent with that used in the descr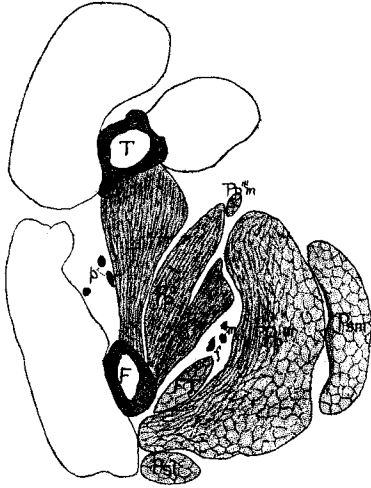iption of the antibrachial muscles, may be termed the *plantaris superficialis medialis* (*Psm*). It may be remarked in passing that while the terms used by Eisler, 95, in his careful and suggestive paper on the homology of the extremities are also employed here, their application is very different, since Eisler has failed to recognize the muscle now referred to as a distinct constituent of the crural flexor mass, that muscle which he terms the plantaris superficialis lying beneath the muscle now under consideration and forming what I shall describe as the plantaris profundus III.

FIG. 1.—Transverse section through the upper part of the crus of *Amblystoma tigrinum. F,* fibula; *f,* ramus superficialis fibularis; *FT,* fibulo-tarsalis; *I,* interosseus; *m,* ramus superficialis medialis; *p,* ramus profundus; *Pp I-III,* plantares profundi I-III; *PpIII m,* plantaris profundus III minor; *Psl,* plantaris superficialis lateralis; *Psm,* plantaris superficialis medialis; *T,* tibia.

In addition to this most superficial muscle, there is upon the outer side of the leg another muscle (*Psl*) which must also be referred to the superficial layer and which may be termed the *plantaris superficialis lateralis.*

Beneath the superficial layer formed by these two muscles lies a larger

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[1] As on a former occasion, I am indebted to my friend, Dr. C. F. W. McClure, for the opossum material which was used, and I desire to express my appreciation of his courtesy in placing at my disposal material without which my studies would necessarily have been very incomplete.

To my assistant, Mr. F. S. Bachelder, I am greatly indebted for assistance in the work, since he kindly undertook the preparation of all the serial sections that were required. He also studied with me the arrangement of the muscles and nerves of the amphibian crus and so much of this paper as treats of these structures is to be regarded as our joint work.

muscle mass whose fibres have a markedly oblique direction and which will be spoken of as the *plantaris profundus III* (Pp^{III}). Beneath the fibular border of this there is a small oval muscle whose fibers are cut transversely and which is the *fibulo-tarsalis* (*FT*), while opposite its tibial border there is a very slender muscle which may be termed the *plantaris profundus III minor* ($Pp^{III}m$). Still more deeply seated are two layers of muscle whose fibers are directed obliquely downward and tibia-wards, the *plantares profundi II* and *I* (Pp^{II} and Pp^{I}), and finally, extending almost directly across between the fibula and tibia is a muscular sheet which may be termed the *m. interosseus* (*I*).

A comparison of such a section with one taken through the forearm of Amblystoma will show that a remarkable similarity exists between the two. There is exactly the same number of layers and the same direction of the fibers in the different layers. Indeed, the resemblance is so close that the two sections might easily be confused in a casual examination. A discussion of their resemblances and the significance of these will, however, be postponed until a later occasion, and I shall pass on now to a consideration of the various muscles mentioned above.

And first as to the *plantaris superficialis medialis* (*Psm*). As already noted, this muscle is not regarded by Eisler as a part of the crural musculature and in this view he is in agreement with his predecessors. The muscle is continuous above with the lower end of the muscle named ischio-flexorius by Hoffmann, 73, the caudo-pedal by Humphry, 72, and the external flexor of the crus by Perrin, 93, and, indeed, is the terminal part of that muscle. From dissections there is little reason to regard it otherwise than as these authors have done, but its relations as seen in sections, especially when these are compared with sections through the forearm, speak so strongly for the view here set forth that I have no hesitation in advancing it. And especially so since there are two other facts bearing favorably upon it, namely (1) the insertion of the muscle into the plantar aponeurosis, which occurs a short distance below the knee joint, and (2) the fact that in Amblystoma the ischio-flexorius is crossed at the knee joint by a well-marked tendinous inscription, which marks, I believe, the line of junction of the ischio-flexorius proper with the plantaris superficialis medialis. The ischio-flexorius of Hoffmann is, according to this view, a compound muscle formed by the end to end union of a true ischio-flexorius with a plantaris superficialis medialis.[2]

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[2] If I understand aright Humphry's, 72, description of the caudo-pedal muscle of Cryptobranchus, there is in this form also a tendinous inscription in the muscle in the neighborhood of the knee joint. If this be so, it is

The *plantaris superficialis lateralis* (*Psl*) is a muscle which has invariably been described as the femoral head of the large superficial muscle which I term the plantaris profundus III. From the remarkable similarity of the muscles of the forearm and crus in the urodele amphibia it might be expected that the same constancy in the relations of the superficial and deep flexors of the leg to the femur and crural bones as obtained in the corresponding muscles of the crus in their relations to the humerus and antibrachial bones would be found, and it was on this ground that I was first led to refer this muscle to the superficial layer and to regard it as distinct from the plantaris profundus III. Further study only served to confirm the correctness of this view by revealing a consistent phylogeny for the crural flexors based upon it.

The muscle takes its origin from the flexor surface of the external condyle of the femur and is separated by a distinct interval from the upper part of the origin of the plantaris profundus III. It passes down the fibular side of the leg, quite distinct from the plantaris profundus and passes over into a rather feeble tendon, which is inserted into the outer border of the fibula near its lower extremity. Throughout its whole extent, therefore, it is distinct from the plantaris profundus III in Amblystoma.

The *plantaris profundus III* (*Pp^{III}*) is the largest of all the muscles of the crus and is described by Humphry, **72**, as the flexor sublimis digitorum, by Hoffmann, **73**, as the femoro-fibulæ-digiti I-V, by Perrin, **93**, as the external flexor of the digits and by Eisler, **95**, as the plantaris superficialis major, all these authors, as has already been noted, including in the muscle the plantaris superficialis lateralis. It arises in Amblystoma from the posterior surface of the upper part of the fibula and its fibers are directed downwards and somewhat tibially to be inserted into the under (dorsal) surface of the plantar aponeurosis, through which it acts upon the digits.

From the upper part of the tibial border of this muscle a slender slip (*$Pp^{III}m$*) separates and passes almost vertically downwards to fade out in connective tissue in the neighborhood of the ankle joint, in close proximity to the tibial border of the plantaris profundus I. This is evidently the muscle described by Eisler as the plantaris superficialis minor and has apparently been overlooked by Perrin. It seems to be,

interesting to note that in the caudo-pedal of Cryptobranchus there is not only an end to end union of the ischio-flexorius proper and the plantaris superficialis medialis, but also of the former and what may be termed an ischio-caudalis.

in Amblystoma, a derivative of the plantaris profundus III and may be termed the *plantaris profundus III minor.*

The fibulo-tarsalis (*FT*) arises from the posterior surface of the upper part of the fibula and extends vertically down the crus, lying immediately behind the fibula, to be inserted into a strong tendinous band which extends transversely across the sole of the foot at about the level of the distal row of tarsal bones. This muscle is the fibulo-plantaris of Eisler, the deep common flexor of the phalanges of Perrin, the fibulæ-metatarsi et digiti I-V of Hoffmann and the flexor profundus digitorum of Humphry.

The *plantaris profundus II* (*Pp^{II}*) also arises from the posterior surface of the fibula and takes an oblique direction downwards and tibially to be inserted into the deeper (dorsal) surface of the plantar aponeurosis. It is the *plantaris profundus I* of Eisler, the internal flexor of the digits of Perrin and the femoro-fibulæ metatarsi I-III of Hoffmann.

The *plantaris profundus I* (*Pp^{I}*) arises from almost the whole length of the fibula and from the tarsus and is directed downward and tibially to be inserted into the lower end of the tibia, into the tibiale and the tarsale I; I did not find any insertion into the plantar aponeurosis in Amblystoma. This is the muscle described by Perrin as the direct rotator of the foot, and is apparently represented in Menopoma, according to Eisler, by four more or less distinct muscles which have been named the plantares profundi II and III, the fibulo-tibialis and the fibulo-tarsalis. Humphry and Hoffmann have not recognized it as distinct from the plantaris profundus II.

Finally, the *interosseus* (*I*) is a strong band of muscle fibers which extend almost directly across between the tibia and fibula, occupying the position of the interosseous membrane of the higher mammalia. It is the pronator tibiæ of Humphry and the fibulæ-tibialis of Hoffmann.

In the study of the arm flexors much light was thrown upon their phylogenetic modifications by their nerve supply and the same holds good for the crural flexors. It must be remembered, however, that with the modifications which the muscles undergo in the various groups, a modification of the nerve trunks also occurs, and in making use of the nerve supply for the identification of muscle equivalents in the different groups, these changes in the paths followed by the nerve fibers must be taken into consideration. The final test in the identification of a motor nerve is its end organ, the muscle; that is a definite quantity in the problem. But the path by which a given nerve reaches its end organ is not necessarily the same in all cases; the nerve, as a rule, will seek the most direct route

to its destination, but that route need not be exactly the same in all forms. The tendency, however, is largely towards conservatism, and even when the bulk of the fibers composing a given nerve trunk, adopt, in the higher vertebrates, a new path, some will be apt to retain the original course and so serve as guides for the determination of topographic relationships. I have elsewhere (1903, pp. 466-7) expressed in general terms the con-
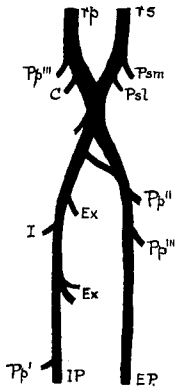

FIG. 2. — Diagram of the crural nerves in *Amblystoma tigrinum*. *C*, cutaneous branch; *EP*, external plantar; *Ex*, branches to extensor surface; *I*, branch to interosseus; *IP*, internal plantar; *Ppl-III*, branches to plantares profundi I-III; *Psm*, branch to plantaris superficialis medialis; *rp*, ramus profundus; *rs*, ramus superficialis.

clusions in regard to the value of nerve supply in determining muscle homologies to which my studies of the muscle and nerves of the forearm have led me.

In Amblystoma, immediately above the knee joint, two distinct nerve trunks occur upon the posterior surface of the leg (Fig. 2). They are formed by the division of the sciatic nerve after it has given off the peroneal nerve and are what Humphry, **72**, has termed the internal and external popliteal nerves. They do not, however, correspond in composition to the nerves so named in the mammalia, and for this reason they will be spoken of here as the *ramus plantaris profundus* (*rp*) and the *ramus plantaris superficialis* (*rs*). They lie, at first, one on either side of the sciatic artery, but as they are traced downwards the ramus profundus passes slightly laterally so as to come to lie in front of the ramus superficialis, and a little later the two stems fuse, only to separate again, some interchange of fibers apparently taking place, however, during the fusion, and a further interchange is carried out by means of a cross connection between the two stems a little lower down.

From the ramus superficialis above the fusion branches are given off to the plantaris superficialis medialis (*Psm*) and to the plantaris superficialis lateralis (*Psl*), and below the fusion to the plantaris profundus III (*Pp^{III}*) and the plantaris profundus II (*Pp^{II}*). Just as these nerves are given off the stem is passing over the upper border of the plantaris profundus III and its course is then downwards and outwards between the fibulo-tarsalis and the plantaris profundus II (Fig. 1, *f*), or to a certain extent through the substance of the fibulo-tarsalis. It thus reaches the fibular side of the crus and descends towards the foot, lying between the lateral border of the fibulo-tarsalis and the origin of the plantaris profundus II. Beyond this it will be unnecessary to follow it at present.

The ramus profundus (*rp*) gives off above the fusion a branch to

the plantaris profundus III (Pp^{III}) and below the fusion a branch
(*Ex.*) which passes downward and forward through a notch on the crest
of the tibia and is supplied to the muscle which has been termed the
tibialis anticus. The main stem then gives off a branch (*I*) to the
interosseus, and having in its downward course passed successively over
the upper border of the plantares profundi III-I, it passes over the upper
border of the interosseus and is continued downward on the extensor sur-
face of that muscle (Fig. 1, *p*). Before reaching the foot it gives off
a branch and then divides into two stems, one of which, together with
the branch, passes to the muscles upon the dorsum of the foot, while the
other passes backwards beneath the lower border of the interosseous
muscle, gives off a branch to the plantaris profundus I and continues
onward to be distributed to the plantar surface of the foot.

In order to understand the significance of this arrangement of the
nerves it will be necessary to compare it with what occurs in the arm.
In this but a single nerve trunk, the brachialis longus inferior, enters the
flexor surface of the antibrachium and it divides into a ramus profundus
and a ramus superficialis. The former has a course almost identical
with that of the ramus profundus of the crus and supplies the pronator
quadratus and the palmaris profundus I, which have the same topo-
graphical relations as the interosseus and plantaris profundus I supplied
by the ramus plantaris profundus. The latter nerve, however, also con-
tains some extensor fibers which are lacking in the deep nerve of the
antibrachium, the separation of the præaxial and postaxial fibers having
taken place higher in the arm than in the leg.

The ramus superficialis of the antibrachium divides into two portions,
a ramus superficialis medialis and a ramus superficialis ulnaris, the
latter of which possesses relations similar to those of the ramus plantaris
superficialis after it has given off its branches to the plantares profundi
III and II. It would seem, therefore, that these branches may well be
regarded as equivalent, in part at all events, with the ramus superficialis
medialis of the arm, while the main stem below their origin may be
considered the equivalent of the ramus superficialis ulnaris and be termed
the *ramus superficialis fibularis.*

But the ramus superficialis medialis of the arm supplies not only the
palmares profundi III and II, but also the palmaris superficialis. In
the leg the branches which are distributed to the muscles which I have
identified as forming the plantaris superficialis, are given off from the
ramus superficialis above the point of its fusion with the ramus pro-
fundus, so that a difference from the arrangement in the arm exists in
that there is no concrete ramus superficialis medialis, its branches aris-

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ing independently at different levels.   And, furthermore, a more import-
ant difference exists in the origin of a branch to the plantaris profundus
III from the ramus profundus above its point of fusion with the ramus
superficialis.   This might seem to vitiate any direct homology between
the ramus plantaris profundus and the ramus palmaris profundus, but,
on the other hand, it may be a part of the same lack of differentiation of
the plantar nerves which is evidenced in the retention of extensor fibers
in the ramus plantaris profundus.   In Cryptobranchus, according to
Humphry, 72, both the ramus profundus and the ramus superficialis
send branches to the plantaris profundus III, and in Menopoma, to judge
from Eisler's figures, 95, the two stems separate only at the upper border
of the plantaris profundus II, from which it may be presumed that the
branches to the plantaris profundus III are given off from the common
stem above the bifurcation.   Whether the high or the low bifurcation be
the more primitive condition, it is difficult to say, but it is at least plausi-
ble to suppose that the fusion of the two trunks in Amblystoma presents
opportunities for the transference of fibers destined for the plantaris
profundus III (and possibly II) from the ramus profundus to the ramus
superficialis, since, apparently, the fibers which form the lower cross
connection between the two stems are destined for the supply of the
plantaris profundus II.

   However that may be, it seems clear that in the plantar nerves there
is less definiteness in the differentiation of the nerve fibers into special
trunks than occurs in the palmar nerves, a fact which is shown by the
inclusion of præaxial fibers in the same trunk with postaxial ones
throughout the entire length of the crus and by the inclusion of fibers
destined for superficial muscles in the same trunk with others for the
deep muscles.

   Tabulating the nerve supply of the plantar muscles according to the
origin of the fibers from the two main stems the following arrangement
is obtained :—

>   Plantaris superficialis medialis,
>   Plantaris superficialis lateralis,
>   Plantaris profundus III (in part),   } Ramus superficialis.
>   Fibulo-tarsalis,
>   Plantaris profundus II,

>   Plantaris profundus III (in part),
>   Plantaris profundus I,   } Ramus profundus.
>   Interosseus,

but, if the interpretation of the plantar nerves given above on the basis
of a comparison with the arm nerve be accepted, the tabulation will be as
follows :—

Plantaris superficialis medialis, Plantaris superficialis lateralis, Plantaris profundus III, Plantaris profundus II,	Ramus superficialis medialis.
Fibulo-tarsalis,	Ramus superficialis fibularis.
Plantaris profundus I, Interosseus,	Ramus profundus.

II. The Crural Flexors in the Lacertilia.

A goodly number of papers dealing with the myology of the hind limb of members of the group Lacertilia have appeared, that of Gadow, **82**, being one of the most comprehensive. It has been the custom, however, to employ for the various muscles a terminology based upon that used for the mammalia, a procedure which carries with it implications of homologies which in some cases do not exist and in the majority of cases are at best merely partial ones. Since in the present study the lacertilian myology is being approached from below, rather than from above, and since in the amphibia the characteristic feature of the crural muscles is their arrangement in layers, I propose to employ for the reptilian muscles a terminology which will indicate their relations to the amphibian condition, using the terms employed by Gadow, for instance, only for purposes of identification.

A transverse section through about the middle of the crus of Scincus presents the appearance shown in Fig. 3. At first sight the differences from the arrangement in Amblystoma are very apparent, but a closer inspection will reveal marked similarities, which a study of the nerve supply will but serve to emphasize. The topographical relations of the muscles may, however, first be considered, with a view to determining how far a layered condition can be recognized.

It is a characteristic of the amphibian superficial plantar layer that it arises from the femur and is inserted below into the plantar aponeurosis. In Scincus one finds superficially upon the posterior surface of the crus three muscles, a plantaris superficialis medialis (*Psm*), a plantaris superficialis lateralis (*Psl*), and between the two a long slender muscle which may be termed the plantaris superficialis tenuis (*Pst*). Of these the *plantaris superficialis medialis* differs from the other three in that it arises from the head of the tibia, instead of from the femur as might be expected if it be really a portion of the superficial plantar layer. Examining its origin more closely it will be seen to arise not only from the head of the tibia but also from the posterior surface of a strong tendon which passes from the head of the tibia to the internal condyle of the femur. The existence of this tendon and the relation of the muscle

to it is of great importance in determining the true significance of the muscle, for they indicate, apparently, a primary attachment of the muscle to the femur. The tendon, indeed, represents the proximal portion of the muscle which has undergone degeneration in association with a new attachment made by the muscle below the knee joint, the resulting condition being strictly comparable with what has occurred in connection with the peroneus longus of man, this muscle having similarly shifted its upper attachment from the femur to the fibula, its upper part being represented by the external lateral ligament of the knee joint.
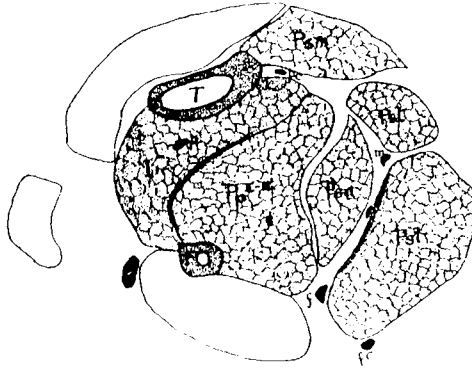

FIG. 3.—Transverse section through the upper part of the crus of *Scincus sp.* F, fibula; *f*, ramus superficialis fibularis; *fc*, fibular cutaneous nerve; *I* interosseus; *m*, ramus superficialis medialis; *p*, ramus profundus; *pc*, cutaneous branch from ramus profundus; *PII-III*, plantaris profundus II-III; *Psa*, plantaris superficialis accessorius; *Psl*, plantaris superficialis lateralis; *Psm*, plantaris superficialis medialis; *Pst*, plantaris superficialis tenuis; *T*, tibia.

An examination of the origin of the plantaris superficialis medialis as described for other lacertilia seems to give support to this view. It is true that throughout the reptilia in general the muscle takes its origin from the tibia. In Euprepes, however, Fürbringer, 70, describes it, under the name of the gemellus internus (epitrochleo-tibio-metatarsalis ventralis) as arising both from the head of the tibia and from the internal condyle of the femur, and, according to Gadow, 82, it (gastrocnemius, caput internum) arises in Ophryoessa principally from the posterior surface of the internal condyle, only a few fibres taking origin from the tibia. It is clear then that one is dealing here with a muscle which was either primarily attached to the femur and in the majority of the reptilia has made a secondary connection with the tibia, or else was primarily attached to the tibia and has secondarily migrated, so far as its origin is concerned, upward to the femur.

There seems to be little question but that the former of these two

possibilities is the easier of accomplishment; it is not a migration, but the formation of a new attachment in the course of the muscle and the degeneration of the part above. And, as already noted, there is evidence of the occurrence of such a process in at least one of the muscles found in man. On this view the tibial superficial muscle of the lacertilian crus is to be regarded as having in reality a femoral origin and agrees in its primary relations with the other superficial muscles.

Traced downwards the plantaris superficialis medialis becomes a broad band which inserts into the tibial border of an aponeurotic sheet (Fig. 4, a) which represents a portion of the superficial layer of the plantar aponeurosis and receives also the insertion of the plantaris superficialis lateralis.
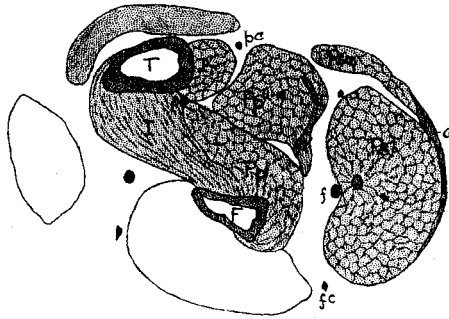

FIG. 4.—Transverse section through the lower part of the crus of *Scincus sp.* a, superficial portion of plantar aponeurosis; a', deep portion of plantar aponeurosis; f, ramus superficialis fibularis; F, fibula; fc, fibular cutaneous nerve; I, interosseus; I', vertical fibers of interosseus; p, ramus profundus; pc, cutaneous branch of ramus profundus; Ppl,plantaris profundus I; PpII-III, plantaris profundus II-III; Psl,plantaris superficialis lateralis; Psm, plantaris superficialis medialis; T, tibia.

The *plantaris superficialis tenuis* (Fig. 3, *Pst*) takes its origin above the knee joint from a sesamoid cartilage developed in a tendon arising from the fibular border of the flexor tibialis externus (Gadow) and passes downwards to unite with the tibial border of a portion of the plantar aponeurosis which covers the posterior surface of the plantaris profundus II-III (Fig. 4, a'). The muscle is slender throughout its entire course. At first it lies superficially between the medial and lateral superficial plantars, but lower down it is covered by the fibular edge of the medialis and at about the middle of the crus fuses with the posterior surface of the deep plantar mass, or, as it is better expressed above, inserts into the tibial border of a portion of the plantar aponeurosis which covers the deep plantar mass.

This muscle does not seem to be present in all lacertilia. Thus Perrin, 93, fails to find it in Uromastix and I have not succeeded in observing

it in dissections of Phrynosoma. On the other hand Perrin finds it in Varanus and apparently in Lacerta and Gongylus, and Gadow, **82**, regards it as a typical portion of his flexor longus digitorum of which it forms the caput accessorium. It seems to be a muscle separated from the fibular border of the plantaris superficialis lateralis, a view which receives confirmation from the statement of Gadow that it is sometimes fused above with that muscle. Its apparent absence in certain forms may upon this view be regarded as due to its failure to separate from the parent muscle.

The *plantaris superficialis lateralis* (Fig. 3, *Psl*) is a rather large muscle which takes its origin by a tendon from the posterior surface of the lateral condyle of the femur. A sesamoid cartilage is imbedded in the tendon just above the line where the muscle fibres begin to make their appearance and, as the tendon is traced downwards, it is found to broaden out into a thin sheet covering the anterior (deep) surface of the muscle and gradually fading out below, with the exception of a narrow band which continues on to the region of the ankle joint, becoming enclosed by the muscle substance (Fig. 4). Just when the tendon begins to fade out an aponeurotic layer (Fig. 4, *a*) appears on the posterior (superficial) surface and increases in strength as it passes downwards, becoming a part of the plantar aponeurosis. It is with the inner border of this that the plantaris superficialis medialis and the tendon which descends from the border of the flexor tibialis externus and gives rise to the plantaris superficialis tenuis, unites.

As the muscle substance is traced downwards it is seen to be continued past the ankle joint into the plantar region of the foot. In the upper part of the muscle the fibers are all parallel, arising from the tendon of origin, but lower down fibers arise from the slender tendon which continues the tendon of origin downwards and have a somewhat radiating arrangement (Fig. 4). Tracing out the two sets of fibers, it is found that the upper ones insert into the upper part of the plantar aponeurosis, while it is those which arise from the prolongation of the tendon of origin that form exclusively the lower part of the muscle and are continued over the tarsus to be inserted into the plantar aponeurosis, and the sesamoid cartilage developed in it over the fifth metatarsal.

In addition to these three muscles there is yet a fourth (*Psa*) which is apparently to be reckoned as a portion of the plantaris superficialis. It arises from the posterior surface of the external condyle of the femur below the plantaris superficialis lateralis and passes downward under cover of that muscle to about the middle of the crus, where it unites with the plantaris profundus III-II, or rather, inserts into the portion of the plantar aponeurosis covering that muscle (Fig. 4, *a'*).

Gadow, **82,** and Perrin, **93,** both describe this muscle as a portion of the flexor longus digitorum (fléchisseur des quatre premiers doigts), that is to say of the plantaris profundus III-II, making it a femoral head of that muscle. It may be that it is really a portion of the plantaris profundus group of muscles which has secondarily extended its origin to the femur and that its absence in Ophryoessa and Cnemidophorus, as noted by Gadow, is due to this upward migration not having taken place. On the other hand it seems more probable that the origin from the femur is a primary condition, the muscle being a separation of the deeper portions of the plantaris superficialis lateralis. Its union with the plantaris profundus presents no more obstacle to this view than the similar union of the superficialis tenuis; both the plantaris profundus and the plantaris superficialis insert primarily into the plantar aponeurosis, so that a union of the two sets of muscles is not at all impossible. On account of its associations with the deep plantar muscles it will be spoken of as the *plantaris superficialis accessorius.*

The plantaris profundus group of muscles is represented in the lacertilia by three distinct muscles, one of which is to be regarded as representing the plantares profundi III and II of the amphibian crus, while the other two represent the plantaris profundus I. The *plantaris profundus III-II* (Fig. 4, $Pp^{II\text{-}III}$) is the muscle termed by Gadow the flexor longus digitorum, caput internum, and by Perrin the tête interne du fléchisseur des quatre premiers doigts. It takes its origin from the upper half of the fibula and to a slight extent from the outer surface of the head of the tibia, and increases rapidly in size as it descends the crus, forming the most voluminous muscle of the calf of the leg. At about one-third of the length of the crus an aponeurotic layer appears upon its posterior surface (Fig. 4, a') and into this the plantaris superficialis accessorius and the plantaris superficialis tenuis insert. As it approaches the ankle joint the aponeurosis increases in strength and becomes tendon-like, the fibres of the muscle terminating upon it, and at the ankle joint a sesamoid bone (Fig. 5, s) is developed upon its tibial border, the last remaining muscle fibers and also the plantaris profundus I accessorius inserting into this. With the development of the sesamoid bone the whole aponeurosis or tendon becomes thick and almost cartilaginous, but as it is traced onward into the foot it again becomes tendinous and gives off a slip from its fibular border. This passes to the fifth digit, sending off a slip to the fourth, and the main portion of the tendon passes on beneath the superficial muscles of the planta to divide eventually into tendons which pass to the three inner digits. All the five tendons pass to the terminal phalanges of their respective digits and give origin in their course to the lumbrical muscles.

The amphibian plantaris profundus I is represented in Scincus by two distinct muscles. The first of these, which may be termed simply the *plantaris profundus I* (Figs. 4 and 5, Pp^I), arises from the posterior surface of the lower part of the fibula and is directed obliquely downward and inward. It passes over into a flat tendon which lies beneath (anterior to) the tibial border of the tendon of the plantaris profundus III-II, and, indeed, is to a certain extent connected to the deep surface of the sesamoid bone developed in that tendon. It separates from it again, however, and is continued on over the large tarsal bone of the first row (astragalo-calcaneus) and is inserted into the two inner bones of the second row of the tarsus. This is the muscle which has very generally been recognized as the tibialis posticus.
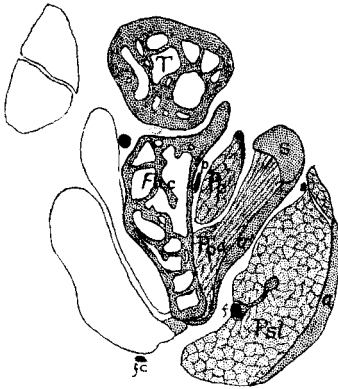
The second muscle, which may be termed the *plantaris profundus I accessorius* (Fig. 5, Pp^Ia), arises from the plantar surface of the fibular portion of the large astragalo-calcaneous (*Fac*) and is directed obliquely inward and downward, passing posteriorly to the lower part of the plantaris profundus I (Pp^I), to be inserted into the sesamoid bone (*s*) developed in the tendon of the plantaris profundus III-II.

Finally, there is a well developed *interosseus* muscle (Figs. 3 and 4, *I*) which passes across from the fibula to the tibia, filling up the interval between the two bones through almost its entire length. In the upper part of the muscle (Fig. 3) the fibers have an almost vertical direction, but, as it is traced downwards, the lower fibers, which pass over to the tibia anterior to the higher ones, become more and more oblique, until finally in the lower part of the crus (Fig. 4) all the fibers are exceedingly oblique, some almost transverse, and the vertical upper fibers are seen as a small bundle (I^I) lying upon the posterior surface of the tibia, completely isolated from the oblique ones. The higher vertical fibers are inserted into the outer (fibular) and posterior surfaces of the lower half of the tibia, while the lower oblique fibers pass to its anterior and inner surfaces, wrapping around the lower end of the bone.

FIG. 5.—Transverse section through the ankle of *Scincus sp. a*, superficial portion of plantar aponeurosis; *a*, deep portion of plantar aponeurosis; *f*, ramus superficialis fibularis; *FAC*, fibulare-astragalo-calcaneus; *fc*, fibular cutaneous nerve; *p*, ramus profundus; *PpI*, plantaris profundus I; *PpIa*, plantaris profundus I accessorius; *s*, sesamoid bone in deep portion of plantar aponeurosis; *T*, tibia.

Before passing to a consideration of the nerve-supply of these muscles a few remarks may be made in the way of a comparison of the plantar aponeurosis of the lacertilia with that of the amphibia. In the latter, just as was the case with the palmar aponeurosis, it forms a continuous sheet which receives the insertion of the crural flexors and gives origin to the plantar muscles of the pes, the only indications of a layered condition to be seen in it being at its upper and lower borders, where it becomes partly divided into subjacent layers corresponding to the layers of muscles inserting into or arising from it. In the lacertilia the conditions are slightly different. Covering the posterior surfaces of the plantaris superficialis lateralis there occurs a distinct aponeurotic layer (Figs. 4 and 5, a) which receives the insertion of the fibers of that muscle and is also joined by the tendon of the plantaris superficialis medialis. As it is traced downwards this aponeurosis separates in the neighborhood of the ankle joint into a thinner and narrower superficial layer and a thicker and deeper layer. The former gradually verges towards the fibular side as it passes into the foot and is finally lost over the outer side of the fifth metatarsal bone. The deeper layer gives rise from the deep surface of its medial half to the superficial layer of the plantar muscles, while its lateral portion, developing a sesamoid cartilage which receives the insertion of the fibers of the plantaris superficialis lateralis, inserts into the fifth metatarsal.

In addition to this superficial layer a deeper layer of the aponeurosis also occurs (Figs. 4 and 5, a'), this being the aponeurosis with which the plantaris profundus III-II becomes connected and which is continued onward as the tendons of that muscle to be inserted into the terminal phalanges of the digits.

There are then in the lacertilia two principal portions of the plantar aponeurosis as compared with the continuous aponeurosis of the amphibia. A deeper portion has separated from a more superficial one to form the tendons of the plantaris III-II and having also inserted into it portions of the plantaris superficialis. Probably too the tendon of insertion of the plantaris profundus I, on account of its attachment to the sesamoid bone developed in the tendon of the plantaris profundus III-II, is to be regarded as a separated portion of the original aponeurosis and, if this be the case, all the crural flexors primarily insert into the plantar aponeurosis as in the amphibia.

Turning now to the nerves of the crus. In sections just above the knee the sciatic nerve is represented by three trunks. One of these (Fig. 6, A), when traced onwards, curves around the outer border of the fibula to the dorsal surface of the crus and need not concern us further. The other two are supplied to the flexor surface.

One of them (F) passes down into the crus upon the fibular side of the plantaris superficialis lateralis and gives off a couple of large cutaneous branches (C) which are distributed to the fibular side of the leg, one of them (Figs. 4 and 5, *fc*) passing far down the crus in the groove between the fibular border of the plantaris superficialis lateralis and the peroneus. The main stem in its downward course gradually verges medially, so that it comes to lie beneath the plantaris superficialis lateralis (Figs. 4 and 5, *f*) and, indeed, becomes partly enclosed in the substance of that muscle. It appears to give off no branches in the crus, nor could any twig to the plantaris superficialis lateralis be found arising from it. At the ankle it passes into the foot towards its fibular border, and is then recognizable as the external plantar nerve.

FIG. 6.—Diagram of the crural nerves of *Scincus sp.* *A*, nerve to extensor surface; *c*, cutaneous nerves; *EP*, external plantar; *F*, ramus superficialis fibularis; *I*, branch to interosseous; *IP*, internal plantar; *m*, ramus superficialis medialis; *Mp*, common trunk of ramus superficialis medialis and ramus profundus; *PpI*, branch to plantaris profundus I; *PpIa*, branch to plantaris profundus I accessorius; *PpII-III*, branch to plantaris profundus II-III; *Psa*, branch to plantaris superficialis accessorius; *Psl*, branch to plantaris superficialis lateralis; *Psm*, branch to plantaris superficialis medialis; *Pst*, branch to plantaris superficialis tenuis; *rp*, ramus profundus.

This nerve is evidently that referred to by Gadow, 82, as stem III, and, notwithstanding its somewhat different course in its upper part, is apparently equivalent in part to the *ramus superficialis fibularis* of Amblystoma, but, unlike it, is quite distinct from the branches which represent the ramus superficialis medialis, a difference which may well be correlated with the absence of an anastomosis between the flexor stems in the lacertilia.

The other main stem, before leaving the thigh, divides into two trunks (Fig. 6, *m.* and *rp.*), both of which pass downwards to the tibial side of the plantaris superficialis lateralis. The more posterior trunk (*m*), the stem I of Gadow, may from its distribution be termed the *ramus superficialis medialis.* Shortly after entering the crus it divides into several branches which are entirely confined to the crus and supply all the portions of the plantaris superficialis, as well as the plantaris profundus III-II.

The deeper branch (*rp*), the stem II of Gadow, may be termed the *ramus profundus.* It passes towards the tibia and divides into two branches, the posterior of which (Fig. 6, *c;* Figs. 3 and 4, *pc*) is cutaneous and is distributed to the skin over the tibial surface of the crus. The deeper branch enters the substance of the the the m. interosseus (Fig.

3, *p*) on its posterior surface and is continued downward through that muscle, to which it gives branches, and, emerging from it at the ankle, (Fig. 6, *p*) it sends twigs to the plantaris profundus I and to the plantaris profundus I accessorius and is then continued into the foot as the internal plantar nerve.

Accepting the interpretation of the nerves of the amphibian crus given above and comparing on the basis of their nerve supply the muscles of the amphibian and lacertilian crus the following result is obtained.

Nerve.	Amphibia.	Lacertilia.
R. superf. medialis,	Plantaris superf. medialis,	Plantaris superf. medialis.
	Plantaris superf. lateralis,	Plantaris superf. tenuis. Plantaris superf. lateralis. Plantaris superf. accessorius.
	Plantaris profundus III, minor, Plantaris profundus III, Plantaris profundus II,	Plantaris profundus III–II.
R. superf. fibularis,	Fibulo-tarsalis,	. . . .
R. profundus,	Plantaris profundus I, Interosseus,	Plantaris profundus I. Plantaris profundus I, accessorius. Interosseus.

It is clear from this that a close comparison based both upon the topographical relations and the nerve supply can be made between the crural flexors of the amphibia and those of the lacertilia, there being, however, in the latter a greater amount of differentiation of the original layers. It is interesting to note that just as in the lacertilian arm no representative of the ulno-carpalis could be distinguished, so too in the crus there appears to be no representative of the amphibian fibulo-tarsalis.

III. The Crural Flexors in the Mammalia.

In considering the crural flexors of the mammalia it will be convenient to depart from the method of description and nomenclature followed in the preceding pages, and to consider the various muscles as independent structures, employing the terms usually assigned to them in mammalian myology. In other words, the primary layers will be temporarily neglected, the reference of the individual muscles to them being considered later on.

A considerable amount of confusion seems to have existed with reference to the soleus and gastrocnemius. Thus, the latter muscle has been described as possessing but a single head in certain forms, the lateral head being described as the soleus; in others the soleus is supposed to be included in the lateral head of the gastrocnemius; and in one case even, the medial head of the latter muscle has been termed

the soleus. It becomes a question then what shall be termed a soleus and what a gastrocnemius, and since the human arrangement is the type with which all other mammalia are directly or indirectly compared, it will be advisable to base the definitions of the two muscles on that arrangement, and this is, essentially, that the gastrocnemius takes its origin from the femur and is a two-joint muscle, while the soleus has its origin from the bones of the crus and is a one-joint muscle. A more satisfactory distinction could be made by referring the two muscles to their respective primary layers, but for the present that given above may suffice.

FIG. 7.   FIG. 8.

FIG. 7.—Transverse section through the lower part of the crus of *Didelphys virginiana.* *ep,* external plantar nerve; *F,* fibula; *FF,* flexor fibularis; *ff,* nerve to flexor fibularis; *FT,* flexor tibialis; *Ge,* gastrocnemius lateralis; *Gi,* gastrocnemius medialis; *ip,* internal plantar nerve; *Pl,* plantaris; *PT,* pronator tibiæ; *rp,* ramus profundus; *T,* tibia; *TP,* tibialis posticus.

FIG. 8.—Transverse section through the upper part of the crus of *Didelphys virginiana.* *F,* fibula; *FF,* flexor fibularis; *Ge* and *Gel,* outer and inner portions of gastrocnemius lateralis; *Gi,* gastrocnemius medialis; *Pl,* plantaris; *PT,* pronator tibiæ; *s,* soleus; *T,* tibia; *TP,* tibialis posticus.

The *medial head of the gastrocnemius* is a practically constant element of the mammalian crus and presents little variation except in relative size. In the opossum (Figs. 7 and 8, *Gi*) it arises from the internal condyle and quickly passes over into a flattened tendon which descends the leg, gradually verging toward its outer border, until near the ankle joint it comes to lie to the outer side of the tendon of the gastrocnemius lateralis, in close proximity to which it is inserted into the os calcis. No union occurs between the two tendons except immediately at their insertion. In both the mouse (Fig. 10, *Gi*) and the cat (Fig. 9, *Gi*) the muscle unites with the gastrocnemius lateralis high up in the crus and the conjoined tendon inserts into the os calcis.

In contrast to the extreme simplicity of structure presented by the gastrocnemius medialis is the complexity of the *gastrocnemius lateralis* in all three forms here under consideration. In the opossum the muscle near its origin was found to consist of four bundles. Two of these (Fig. 8, *Ge*) arose close together from the outer surface of the lateral sesamoid cartilage of the knee joint and from the ligament extending from this to the external condyle, and were distinguishable not only by being separated by a band of connective tissue, but also by a difference in the direction of their fibers. A third portion (*Ge¹*) took its origin from the inner (tibial) surface of the lateral sesamoid cartilage, while the fourth portion (*s*) arose from the posterior surface of the head of the fibula, or, to be more precise, from the posterior surface of a tendon which arises from the posterior surface of the head of the fibula and is continued downwards to beyond the middle of the crus upon the deep surface of the compound muscle.
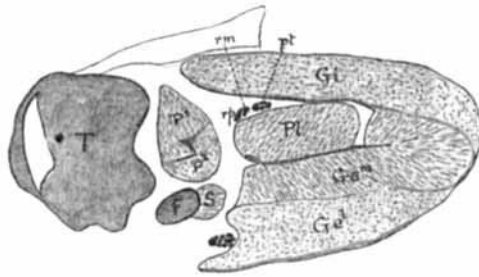
FIG. 9.—Transverse section through the upper part of the crus of the Cat. *F*, fibula; *Ge¹* and *Ge^m*, lateral and medial portions of the gastrocnemius lateralis; *Gi*, gastrocnemius medialis; *P¹* and *P²*, oblique and vertical portions of popliteus; *Pl*, plantaris; *pt*, posterior tibial nerve; *rm*, ramus superficialis medialis; *rp*, ramus profundus; *s*, soleus; *T*, tibia.

Below these four bundles became more or less confused, the connective tissue partition between the portions from the outer and inner surfaces of the sesamoid cartilage persisting for a greater distance than the others, and before its disappearance a tendon appears in the center of the outer sesamoid portions (Fig. 7) and gradually increases in size to become the tendon of the muscle. This is continued down the leg quite independent of the tendon of the gastrocnemius medialis, with which it is inserted into the tuberosity of the os calcis.

In the cat (Fig. 9) the lateral gastrocnemius arises together with the plantaris (*Pl*) from the patella by a strong aponeurotic sheet which is continued backward from the lateral border of that bone, and also from the downward continuation of this sheet which forms an invest-

ment for the outer surface of the plantaris for more than its proximal half. The muscle also takes origin from the lateral surface of the lateral sesamoid bone. The large muscle mass which results is intimately related to the plantaris, and in its upper part a thin sagittal aponeurotic plate appears dividing the muscle into almost equal portions (Ge^l and Ge^m). This sheet is continued all the way down the leg and below receives the insertion of the muscle fibers, becoming the tendon. In its upper part the muscle comes into contact with the gastrocnemius medialis (Gi), an aponeurotic plate intervening between them, however, and below, the tendons of the two muscles fuse completely to be inserted into the tuberosity of the os calcis, the tendon of the soleus also joining them shortly before their insertion, to form a typical tendo Achillis.[3]

In the mouse I cannot state the exact origin of the muscle (Figs. 10 and 12), but it has essentially the same structure as in the cat and has similar relations with the gastrocnemius medialis and plantaris.

Two other muscles are intimately associated with the gastrocnemius, the one more especially at its origin and the other at its insertion. These are the plantaris and the soleus.

The *plantaris,* notwithstanding its variability in man, is of very constant occurrence throughout the entire mammalian series, and has as a rule a much greater development and a more important rôle than in man. It is always closely associated at its origin with the gastrocnemius lateralis and is inserted below into the plantar fascia (occasionally into the os calcis) by which its action is transmitted to the digits. In the three forms here under consideration it forms what may be regarded as the medial anterior portion of the muscular mass formed by it and the gastrocnemius lateralis. It arises in the opossum (Fig. 8, Pl) from the medial half of the posterior surface of a tendon which extends downwards from the lateral fabella, and in the cat, from the fabella and from

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[3] In sections through the tendo Achillis one sees to the medial side a distinct tendon, connected to the true tendo by thin fascia beneath which lies the tendon of the plantaris as in a groove. This tendon might readily be mistaken for that of the gastrocnemius medialis, but it is in reality a thickening of the crural fascia and is quite independent of the muscle. It is attached below to the os calcis medially to the insertion of the tendo Achillis. Upon the lateral border of the tendo a similar thickening of the crural fascia occurs, but this fuses with the tendon of the gastrocnemius lateralis shortly before it is joined by the soleus. These fascial thickenings have been described for the dog by Ellenberger and Baum, 91, who trace them to the semi-membranous and biceps muscles, but they do not seem to have been noted for the cat, at least they are not mentioned in any of the works on that form to which I have access at present.

the strong aponeurosis which passes backwards from the outer border of the patella. Throughout the greater portion of its extent it is barely separable from the gastrocnemius lateralis (Figs. 9 and 10), but below it becomes tendinous and lies below (i. e., anterior to) and to the inner side of the tendon of the gastrocnemius lateralis, from which, however, it is quite distinct. At the ankle joint it lies to the medial side but posterior to the gastrocnemius and soleus tendon and spreads out into the thin but dense plantar aponeurosis. This covers the insertion of the tendo Achillis or its representatives and passes downward over the tuberosity of the os calcis, being attached to the outer surface of that bone by its outer border, but its inner border and the greater part of its central portion is free. Passing on into the foot it gives rise upon its deeper surface to the flexor brevis minimi digiti and may be continued onward as a series of fascial slips to the bases of the digits.
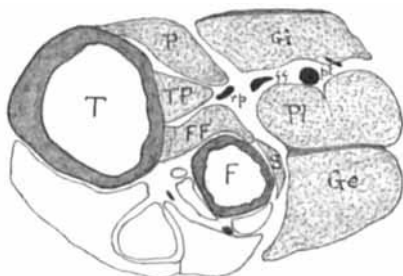
FIG. 10.—Transverse section through the upper part of the crus of the Mouse. *F*, fibula; *FF*, flexor fibularis; *ff*, nerve to flexor fibularis; *Ge*, gastrocnemius lateralis; *Gi*, gastrocnemius medialis; *P*, popliteus; *Pl*, plantaris; *pt*, posterior tibial nerve; *rp*, ramus profundus; *S*, soleus; *T*, tibia; *TP*, tibialis posticus.

The important point about the muscle, so far as its insertion is concerned, is its connection with the plantar fascia. That this is its true termination becomes evident in those forms such as Cuscus (Cunningham, 81) in which a plate of cartilage is developed in the fascia, the plantaris being inserted into the proximal border of this cartilage. To describe the plantaris as being continuous with the flexor brevis digitorum, as is sometimes done, merely leads to confusion; this muscle really arises from the plantar aponeurosis and the slips which extend to the bases of the digits are also portions of the plantar aponeurosis and have no primary relation to the plantaris.

The *soleus,* unlike the plantaris is not always distinguishable in the lower mammals. In both the cat and the mouse (Fig. 11, *s*) it is a well developed muscle which arises from the posterior surface of the upper part of the fibula (Figs. 9 and 10, *s*) and descends the leg beneath the

plantaris and lateral gastrocnemius, eventually becoming tendinous and uniting with the tendon of the latter muscle. In the opossum, however, it does not appear to exist as a distinct muscle and the conditions in this form probably serve to explain its apparent absence in others.

In the description of the gastrocnemius lateralis of the opossum it was noted that it possessed an origin from the head of the fibula. This head seems to be unrepresented in the gastrocnemius of the cat and mouse, and its relations to the rest of the muscle in the opossum present some interesting peculiarities. When it is first seen in tracing a series of sections downward it consists of a thin band of fibers (Fig. 8, s) which arise from a tendon extending downward from the head of the fibula, a portion of the flexor longus digitorum lying between the tendon and the bone. This muscle band is separated at this level from the deeper surfaces of the gastrocnemius lateralis and the plantaris by the tendon which extends downward from the lateral fabella and gives origin to the plantaris. As this tendon gradually fades out below a distinction between the muscle band under consideration and the gastrocnemius lateralis becomes less and less, until, finally, there is complete union of the two.

This fibular head of the opossum seems to represent the soleus of the higher mammalia, and the supposition of Cunningham, 81, and others that the so-called gastrocnemius lateralis of the marsupials includes also the soleus is correct, and the same is probably true of the dog and the other higher mammalia in which the soleus is stated to be lacking. As regards the monotremes it is to be noted that the lateral superficial crural flexor has been termed the soleus, and the gastrocnemius is regarded as lacking (Westling in Leche, 98), this nomenclature being adopted no doubt in view of the fact that the muscle arises from the peculiar process developed upon the upper end of the fibula in these forms and has no connection with the femur. If the fibular process represents a true outgrowth of that bone such a nomenclature would be justified, but it seems really to be an epiphysial structure and in all probability represents the lateral fabella of other forms. On this view the distinction which is made between the marsupial and monotreme muscle practically vanishes and it seems necessary to regard it as representing in both groups the gastrocnemius and soleus of higher forms.

The *long flexors of the digits* in the mammalia have been thoroughly discussed by F. E. Schulze, 66, and by Dobson, 83, and the former has pointed out that the arrangement occurring in man is quite different from that characteristic of the majority of mammals and as a consequence the nomenclature employed in human anatomy cannot be con-

sistently applied in the lower forms. He proposed, accordingly, and his proposition was accepted by Dobson, to speak of the two muscles usually recognized as the flexor longus hallucis and the flexor longus digitorum as the flexor digitorum fibularis and the flexor digitorum tibialis respectively. The proposition is certainly worthy of general acceptance and is almost necessary from the comparative standpoint, since in the majority of mammals the flexor digitorum fibularis (fl. longus hallucis) is the principal muscle and the flexor tibialis the subordinate one.

Dobson has pointed out that the relations of the two flexors is according to one of two types and that all the members of any family, if not order, of mammalia will present the same type. In one type the tendons of the two muscles fuse, while in the other they remain distinct, and notwithstanding that he found the aplacental mammalia presenting the second type of relation, Dobson concludes that the first is the more primitive, since, as he states it, " it is difficult to conceive that in any animals in which a definite separation of the tibial from the fibular flexors had once taken place—symmetrical reunion of these tendons could subsequently occur." With such a view the phylogenetic plan here being traced agrees, for an important part of this plan is the recognition of the plantar aponeurosis of the lower forms in the tendons of the long flexors, all the post-axial muscles of the crus, except the interosseus, having their insertion primarily into that aponeurosis, through which their action is extended to the digits.

The descriptions of the long flexors which Dobson has given for so many species of mammals are sufficiently thorough to warrant the omission of a detailed description of the arrangement observed in the forms I have studied, but for the sake of completeness and to bring out especially their relations to the plantar aponeurosis, or rather its mammalian representatives, a description of the arrangement observed in the opossum may be given.

The *flexor fibularis digitorum* (Figs. 7 and 8, *FF*) arises from the inner and posterior surfaces of the greater portion of the fibula. In its upper part it is separated by a strong aponeurosis from the adjacent tibialis posticus, and at about the middle of the leg a strong aponeurosis appears upon its posterior surface, separating the muscle from the more superficial plantaris. Traced downwards this aponeurosis gives rise upon its posterior surface to a muscle which increases rapidly in breadth, while the aponeurosis diminishes in that dimension, although thickening to form a structure to which the term tendon is applicable. The muscle is the flexor brevis digitorum, or rather a considerable portion of it, and need not concern us any further except in so far as its origin from

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what is usually described as the tendon of the flexor fibularis serves to confirm the homology of that tendon with part of the plantar aponeurosis of lower forms. Eventually all the fibers of the flexor fibularis insert into the tendon, the last of them disappearing some distance above the ankle joint.

The tendon is continued onward into the foot, lying in the median line between the os calcis and the inner malleolus, and at about the level of the distal row of tarsal bones the tendon of the flexor accessorius passes across it to be attached to its tibial border. This portion of the tendon then separates to pass on to an insertion into the base of the terminal phalanx of the first digit, and later the remainder of the tendon divides into four nearly equal tendons, which pass to the remaining digits. The relations of the lumbricales to the tendons will be considered on another occasion.

The *flexor digitorum tibialis* is, in contrast to the flexor fibularis, a rather slender muscle. It has usually been described as arising from the upper part of the tibia, but in my preparations I have not been able to trace it to that bone. I find it (Fig. 7, *FT*) taking its origin from the strong aponeurosis which covers the posterior surface of the strong pronator tibiæ (*PT*), and although it thus comes very close to the upper part of the tibia, no definite connection with that bone could be made out. The difference may be due to the fact that the individuals I studied were advanced fetuses, and that with advancing age the insertion reaches the bone, a process which, if it really occurs, is interesting as denoting a migration of the muscle tibia-wards. Its belly forms an irregularly quadrilateral mass lying between the pronator tibiæ internally and the flexor fibularis externally, and resting upon the tibialis posticus. At about the middle of the crus its tendon begins to appear upon its outer surface and into it the muscle fibers gradually insert, until in the lower part of the crus only the tendon remains, resting directly upon that of the tibialis posticus, by which it is separated from the posterior surface of the tibia. At the ankle joint it rests upon the internal malleolus and as it passes onward into the foot it separates from the tibialis posticus tendon and approaches the tendon of the flexor fibularis. At the level of the junction of the proximal and distal rows of the tarsal bones it gives origin to muscle fibers which represent a portion of the flexor brevis digitorum and pass downward and inward to join the rest of that muscle which arises from the tendon of the flexor fibularis.

A little farther on the flexor tibialis tendon becomes connected by fibrous tissue of varying density with the inner border of the flexor

fibularis tendon, but the actual tendon can be traced uninterruptedly onward and, as Dobson states, does not really unite with the flexor fibularis tendon, although the connection between the two may be sufficiently strong as to make a practical union. The tendon then begins to flatten out into a broad band which fades out gradually at the sides into the layer of the plantar aponeurosis with which the plantaris is associated, and eventually associates itself with the flexor brevis hallucis, inserting, in part at least, into the under surface of the cartilaginous spur.

In the other two mammals which I studied the general arrangement of the two flexors was similar to the above, except that the flexor brevis digitorum did not arise from their tendons. The flexor fibularis (Fig. 11, *FF*) is much the larger of the two muscles and sends tendons to all five digits, while the flexor tibialis, in the cat, unites with the tendon of the flexor fibularis before it divides into the terminal tendons. In the mouse the flexor tibialis (Fig. 11, *FT*) arises in common with the tibialis posticus and its tendon remains completely separate from that of the flexor fibularis and fades out into the plantar fascia. In the cat the muscle has an independent origin from the back of the upper part of the tibia.
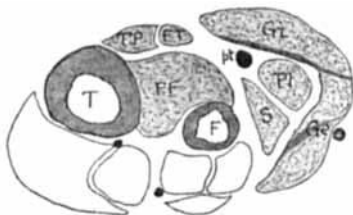

FIG. 11.—Transverse section through about the middle of the crus of the Mouse. *F*, fibula; *FF*, flexor fibularis; *FT*, flexor tibialis; *Ge*, gastrocnemius lateralis; *Gi*, gastrocnemius medialis; *Pl*, plantaris; *pt*, posterior tibial nerve; *S*, soleus; *T*, tibia, *TP*, tibialis posticus.

The *tibialis posticus* has also been described for a large number of forms by Dobson, 83, and I shall indicate only briefly its arrangement in the forms I have studied. In the opossum (Fig. 8, *TP*) it arises from the upper part of the fibula and from a strong aponeurosis which separates it from the adjacent flexor fibularis, and quickly passes over into a tendon which is continued down the leg, under cover of the tendon of the flexor tibialis, and passing behind the inner malleolus is inserted into the scaphoid bone. In the cat it arises from the upper part of the posterior surface of the tibia, becomes tendinous at about the middle of the crus and, passing into the foot in a groove on the inner surface of the tibia, is inserted into the scaphoid. In the mouse (Fig. 11, *TP*) it also arises from the upper posterior part of the tibia as a muscular mass from which later the flexor tibialis separates. It is a slender muscle, soon becoming a tendon and inserting into the internal cuneiform bone.

The *flexor accessorius pedis*, although apparently a muscle of the pes, is considered here with the crural flexors, since its affinities are altogether

with these muscles; the evidence for this statement will be presented
later. In the opossum it is a well-developed muscle forming what has
been termed by Coues, 72, the flexor brevis pollicis obliquus. Leche, 98,
however, records it as wanting in the marsupials and Cunningham, 81,
remarks that the muscle is wanting in Thylacinus and Dasyurus.
Dobson, 83, on the other hand, finds in Dasyurus a band passing from the
os calcis to the under surface of the flexor fibularis tendon and identi-
fies it, probably correctly, with the flexor accessorius and Young, 82,
in his account of the musculature of Phascolarctos, while stating that
" there is no flexor accessorius in the foot," goes on to say that a muscu-
lar bundle which arises from the os calcis and passes to a fibro-cartilagi-
nous backward prolongation of the plantar fascia is regarded by
Macalister as similar to it in its nature. McCormick, 87, suggests the
identity of one of the heads of his flexor brevis digitorum with the flexor
accessorius in *Dasyurus viverrinus,* but the brevity of his description of
this head and the absence of explanations of his figures prevent an
opinion as to the correctness of the suggestion. There cannot be the
slightest question as to the existence of the muscle in *Didelphys virgin-
iana,* and on account of its importance in the fundamental plan of the
crural muscles, to be discussed later, it seems quite probable that it may
be found in a rudimentary condition in the majority of the marsupials.

In the opossum it arises from the outer surface of the os calcis as a
distinct bundle of fibers which are directed inwards and distally. They
early pass over into a tendon which crosses the plantar surface of the
tendon of the flexor fibularis and unites with its outer border, that
portion with which it unites immediately separating to form the tendon
for the hallux. This description differs somewhat from that of Coues,
72, who regards the tendon of the hallux as representing the direct
continuation of the accessorius. Sections show very clearly, however,
that this is not the true state of affairs and that the arrangement is as
described above. In the cat the accessorius is a strong muscle of con-
siderable size, arising from the outer surface of the os calcis. Its thin
tendon passes obliquely across the tendon of the flexor fibularis and unites
with the greater part of its plantar surface, including the united flexor
tibialis tendon. In the mouse it is also well-developed, arising from the
outer surface of the os calcis and passing obliquely to the tendon of the
flexor fibularis, especially to that portion of it which becomes the long
flexor tendon of the hallux.

There still remains for consideration the muscle which has been
termed the *pronator tibiæ* in the monotremes and marsupials and in
the higher mammals the *popliteus,* assuming for the present that the
two muscles are identical.

In the opossum the pronator tibiæ is a muscular sheet which extends obliquely from the fibula to the tibia throughout the greater part of the length of those bones. It takes its origin partly from the inner border of the fibula, but mainly from the strong aponeurosis which separates it from the tibialis posticus and the flexor digitorum tibialis above and the flexor digitorum fibularis below. In its upper part the fibers are directed very obliquely, indeed, almost directly tibia-wards, to the upper part of the tibia, and in this upper portion the muscle is composed of two fairly distinct sheets of fibers, one lying anterior to the other and separated from it by a distinct layer of areolar tissue. Below (Fig. 7, *PT*), however, there is no such separation of two layers, and the fibers have a more vertical course. The partial separation above, already noted by Young, **81**, is apparently of " prophetic " interest in fore-
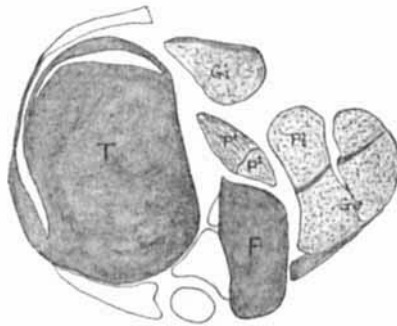

Fig. 12.—Transverse section through the crus of the Mouse just below the knee joint. *F*, fibula; *Ge*, gastrocnemius lateralis; *Gi*, gastrocnemius medialis; *P¹* and *P²*, oblique and vertical portions of popliteus; *Pl*, plantaris; *T*, tibia.

shadowing the differentiation of the muscle into an upper or popliteal portion and a lower or pronator tibial portion.

In the mouse the popliteus arises from a strong fibro-cartilaginous band attached above to the outer condyle of the femur. Those fibers which arise from the tibial side of the band (Fig. 12, *P¹*) have a much more oblique direction than the rest (*P²*) and are inserted into the tibia above them. No distinct indications could be discovered of a representative of the pronator tibiæ, *i. e.,* a lower portion of the muscle, although it is possible that some scattered fibers which lie anterior to the main mass of the flexor digitorum fibularis and have an oblique direction, may represent it. A separation between these fibers and the flexor was, however, at best indistinct.

In the cat the popliteus takes its origin from a sesamoid bone which is attached by a strong tendon to the outer condyle of the femur. The

muscle passes obliquely downward and inward over the knee joint (Fig. 9) and shows quite distinctly a composition from two masses of fibers, one of which (P^1), as in the mouse, has an oblique direction, while the other (P^2) is more vertical. No indications of a lower portion of the muscle could be found in the individual I studied, although it may be noted that both in the cat and in the mouse the interosseous membrane is more strongly developed than in the oppossum.

IV. The Nerves of the Mammalian Crus.

In the opossum, at the level where my sections began, there was a main nerve stem, the internal popliteal (Fig. 13), and on one side of it a stem for the internal gastrocnemius (GI) and on the other side
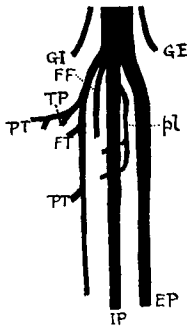

FIG. 13.   FIG. 14.

Fig. 13.—Diagram of the crural nerves of *Didelphys virginiana*. *EP*, external plantar; *FF*, branch to flexor fibularis; *FT*, branch to flexor tibialis; *GE*, branch to gastrocnemius lateralis; *GI*, branch to gastrocnemius medialis; *IP*, internal plantar; *pl*, branch to plantaris; *PT*, branch to pronator tibiæ; *TP*, branch to tibialis posticus.
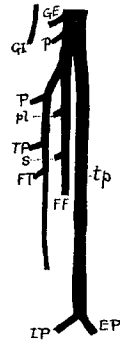
Fig. 14.—Digram of the crural nerves of the Mouse. *EP*, external plantar; *FF*, branch to flexor fibularis; *FT*, branch to flexor tibialis; *Ge*, branch to gastrocnemius lateralis; *Gi*, branch to gastrocnemius medialis; *IP*, internal plantar; *P*, branches to popliteus; *pl*, branch to plantaris; *s*, branch to soleus; *TP*, branch to tibialis posticus; *tp*, posterior tibial.

a branch for the external gastrocnemius (and soleus) (GE), and more externally the external popliteal which wound around the head of the fibula to the front of the leg. The internal popliteal descended into the crus between the two gastrocnemii, and soon after divided into five branches, of which two (EP and IP) were quite large, two others were much smaller, one of them (pl) passing exclusively to the plantaris, while the other one (FF) was distributed to the flexor digitorum fibularis.

The fifth branch (Fig. 7, rp) was of moderate size and passed

obliquely inwards, giving off branches to the tibialis posticus (*TP*), the pronator tibiæ (*PT*) and the flexor digitorum tibialis (*FT*), and then continued its course downward between the tibialis posticus and the flexor digitorum fibularis, without supplying either, and terminated near the ankle joint, apparently in the periosteum of the lower part of the tibia. The lowest of the branches which passed to the pronator tibiæ could be traced downwards in the muscle almost to the ankle joint and seemed to end there in periosteal branches to the lower end of the fibula.

The branch to the plantaris (*pl*) might be described as arising from the internal plantar nerve (*IP*) but with this exception neither the internal nor the external (*EP*) plantar nerves takes any part in the innervation of the muscles of the crus. After they have passed into the foot the external plantar gives off a branch, which passes mainly to the abductor minimi digiti, but also gives two twigs to the flexor digitorum accessorius.

In the mouse (Fig. 14) the internal gastrocnemius is supplied by a branch (*GI*) given off above the level of my highest section. The internal popliteal descends between the two gastrocnemii, gives off branches to the gastrocnemius externus (*GE*) and to the popliteus (*P*), and divides, opposite the knee joint, into three branches, two smaller ones and one large one. The latter (*tp*) is comparable to the posterior tibial nerve of human anatomy in many respects, although it takes no part in the innervation of the crural muscles but descends unbranching to behind the inner malleolus, where it divides into the external and internal plantar nerves (*EP* and *IP*), the former sending a branch to the flexor accessorius.

Of the two smaller branches, one (Fig. 14, *FF*; Fig. 10, *ff*) shortly after its formation gives branches to the plantaris (*pl*) and the soleus (*s*), but passes mainly to the flexor fibularis. The other smaller branch (Fig. 10, *rp*) gives off early in its course a branch to the popliteus (Fig. 14, *P*) and probably supplies the flexor tibialis also, although neither one nor the other of my series of sections permitted of perfect certainty of this point in this form. The branch then descends between the flexor fibularis and the tibialis posticus, giving off a branch to the latter, and, passing more deeply between the two muscles as it descends, finally rests upon the interosseous membrane and seems to terminate in the periosteum of the lower part of the fibula.

In the cat the arrangement of the nerves is in general the same as in the mouse. A branch is given off from the sciatic, before its division, to the internal gastrocnemius and another from the internal popliteal soon after its formation passes to the external gastrocnemius. A little

later the internal popliteal gives branches to the popliteus and to the plantaris, and shortly thereafter divides into two main trunks each of which is composed of subordinate bundles. These two main trunks lie one behind the other (Fig. 9), and the posterior larger one (*pt*) descends the leg without taking any part in the innervation of its muscles and below the ankle divides into the external and internal plantar nerves.

The other trunk is clearly composed of two portions. From one of these (*rm*) branches are distributed to the soleus and to the flexor fibularis, while the other (*rp*) early divides into four branches, one of which is distributed to the popliteus, another to the flexor tibialis, a third to the tibialis posticus, while the fourth, which is very small, passes downward in the aponeurosis between the tibialis posticus and the flexor fibularis gradually becoming smaller. I was not able to trace this last nerve to its termination, but in all its relations it corresponds to the branch to the periosteum in the mouse.

It may be recalled that in the lower vertebrates the nerves of the flexor surface of the crus were divisible into superficial and deep branches, and that of the former there were two main trunks, one of which, the ramus superficialis medialis, was entirely devoted, so far as its muscular branches were concerned, to the supply of the plantaris superficialis and the plantares profundi III and II. The other superficial trunk, the ramus superficialis fibularis, on the contrary, passed downward, supplying only the fibulo-tarsalis in the amphibia, and became the external plantar nerve. The deep branch, the ramus profundus, was distributed to the plantaris profundi I and the interosseus, and then was continued into the foot to form the internal plantar nerve.

Comparing with this the arrangement described above for the opossum, considerable similarity will be noticed. Thus descending the entire length of the crus there are two nerves, the external and internal plantar, the former of which has practically identical relations with the ramus superficialis fibularis of the lacertilia. In addition there is given off from the internal popliteal at or slightly above its division into the two plantar nerves a smaller stem which supplies the deep muscles of the crus and is continued down to the ankle joint as an exceedingly fine nerve, which is not, however, continued into the foot. In its topographical relations and in its crural muscular distribution this nerve seems to be the homologue of the reptilian ramus profundus, from which, however, it differs in being limited in its distribution to the crus.

In my study of the nerves of the antibrachium (McMurrich, 03) it was shown that the ramus profundus of the amphibia and reptilia extended into the manus, supplying in general the radial part of its palmar

surface, but that in the mammalia its palmar fibers became associated with the median nerve, its antibrachial portion persisting as the anterior interosseous nerve. Apparently a somewhat similar process has taken place in the crus. The tibial plantar fibers have separated themselves from the ramus profundus and have taken a more superficial course to form, in the opossum, the internal plantar nerve, though it can hardly be said that they have united with ramus superficialis medialis, which is represented by the branches to the plantaris soleus and flexor fibularis, together with the branches given off higher up to the two gastrocnemii.
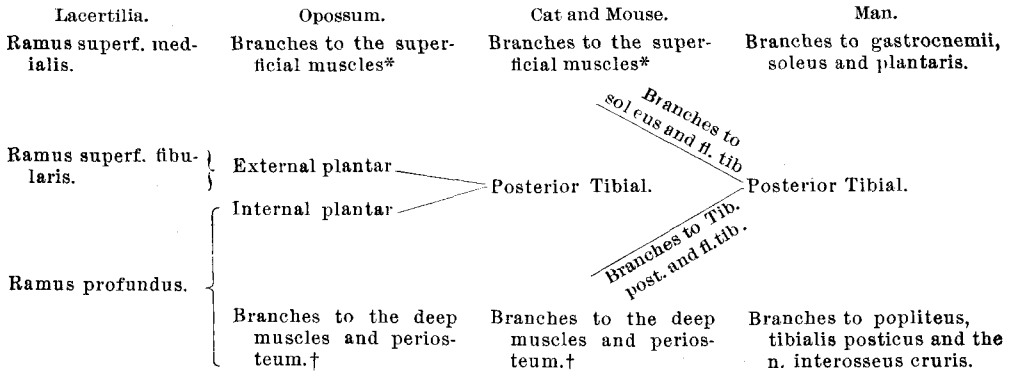
The condition in the opossum does not, however, complete the re-arrangement which is characteristic of the mammalia as a group, a further modification consisting in the union of the internal plantar fibers of the marsupial with the ramus superficialis fibularis (external plantar) to form the posterior tibial nerve. It is noteworthy, however, that even although this fused stem appears to be the prolongation of the internal popliteal, yet, in the mouse and cat, the ramus profundus arises from it at the knee joint and that in these forms it is proper to describe the internal popliteal as dividing into the ramus profundus and the posterior tibial, notwithstanding the discrepancy in the sizes of the two nerves. Furthermore the branches for the superficial muscles arise high up, some of them from the internal popliteal before it branches, while others may arise either at the point of bifurcation or even from the upper part of the ramus profundus.

Finally, it may be added, that in man a further modification occurs in the inclusion in the posterior tibial of certain of the fibers of both the ramus superficialis medialis and the ramus profundus, namely, of the former branches to the soleus and to the flexor fibularis, and of the latter a branch to the tibialis posticus and that to the flexor tibialis. Indications of the original conditions are, however, still to be seen in the origin in the popliteal space of a nerve which sends a branch to the popliteus and another to the tibialis posticus and is then continued down the crus, partly in the substance of the interosseus membrane, to end in the neighborhood of the ankle joint. This nerve, whose terminal prolongation down the crus was first thoroughly described by Halbertsma, **47**, as the n. interosseus cruris, is very evidently equivalent in its topographical relations to the ramus profundus of the lower forms, although some of its fibers destined for the tibialis posticus have separated from it and have joined the posterior tibial nerve. It therefore represents one of the primary branches of the internal popliteal and is deserving of more special mention than is accorded to it in the text-books of human anatomy.

There occurs then in the vertebrate series a progressive modification

of the paths followed by the nerve fibers which supply the flexor muscles of the crus. Stated in general it consists of (1) a separation of the fibers destined for the internal plantar region from the ramus profundus and their assumption of a more superficial course, a process which occurs also in the antibrachium; (2) a breaking up of the ramus superficialis medialis into a number of branches which arise independently; (3) the union of the internal and external plantar nerves to form the posterior tibial; and, finally, the association of some fibers of both the ramus superficialis medialis and the ramus profundus with the posterior tibial.

Taking the reptilian arrangement for a starting point, the rearrangement as it is shown in the opossum, in the mammalia in general as represented by the cat and the mouse, and in man may be schematized thus:—

Lacertilia.	Opossum.	Cat and Mouse.	Man.
Ramus superf. medialis.	Branches to the superficial muscles*	Branches to the superficial muscles*	Branches to gastrocnemii, soleus and plantaris.
Ramus superf. fibularis.	External plantar		
	Internal plantar	Posterior Tibial.	Posterior Tibial.
Ramus profundus.	Branches to the deep muscles and periosteum.†	Branches to the deep muscles and periosteum.†	Branches to popliteus, tibialis posticus and the n. interosseus cruris.

Branches to soleus and fl. tib

Branches to Tib. post. and fl. tib.

* By the superficial muscles are here meant the gastrocnemii, plantaris, soleus and flexor fibularis.
† By the deep muscles are here meant the flexor tibialis, tibialis posticus and pronator tibiæ (popliteus).

V. THE HOMOLOGIES OF THE MAMMALIAN CRURAL FLEXORS.

Having now described the arrangement of the muscles in the three vertebrate groups selected for study and having also elucidated the modifications presented by the primary nerve stems, we are in a position to determine the homologies of the mammalian muscles with those of the lower forms. A comparison of the lacertilian and amphibian muscles has already been made and the comparison now to be drawn might be principally with the lacertilia, were it not that it will be necessary in the following pages to make frequent reference to the conclusions of Eisler, 95, who deduces the mammalian arrangement directly from the amphibian, neglecting altogether the reptilian. It will be convenient to consider the various muscles in succession and to take the arrangement seen in man as a type.

1. The *gastrocnemius* of man is formed by the union of two heads,

one from the external and the other from the internal condyle, and it unites with the soleus to form the tendo Achillis, inserting into the os calcis. Disregarding the soleus for the present, there are two possibilities to be considered with reference to the double origin of the gastrocnemius; either (1) it represents two originally distinct muscles which have united below, or (2) it represents the splitting in its upper part of an originally single muscle. The second of these possibilities may be dismissed on the ground that in the lower mammals the two heads, as a rule, remain distinct throughout their entire length. Eisler, in accepting the view that the two heads are primarily distinct muscles, takes the ground that one or the other of them has undergone an extensive migration, basing this conclusion upon the crossing of the two tendons which occurs shortly above their insertion, a peculiarity which has been considered in detail by Parsons, 94. The crossing, considered by itself, throws little light upon the question as to which muscle has undergone the supposed migration and Eisler, turning for evidence to the nerve supply, finds that Cunningham, 81, has observed in *Phalangista maculata* that the gastrocnemius medialis is supplied from the external saphenous (sural) nerve, which has a markedly fibular position and he concludes therefore that it is the gastrocnemius medialis which has migrated and that primarily it had its origin from the fibula and lay to the fibular side of the gastrocnemius lateralis, in which case there would be no crossing of the tendons.

The argument by which such a remarkable migration is deduced is open to criticism along several lines. In the first place the crossing of the tendons does not necessarily imply a migration of the muscles. It may be difficult to give a satisfactory explanation of it on another basis, and the migration theory, if correct, would certainly explain it, but it may be pointed out that the same crossing occurs also in the tendons of the flexor fibularis and the flexor tibialis digitorum in man, and yet a reversal of the relative position of the two muscles by migration seems altogether improbable. A theory which explains the one crossing will probably also explain the other, for, it may be noted, the tendons of the gastrocnemius and plantaris represent a superficial layer of the plantar aponeurosis into which both muscles primarily insert, while those of the two long digital flexors represent a deep layer of the same aponeurosis. The most probable factor in the production of the crossing is a physiological rather than a morphological one, a point which will be considered later on in connection with the discussion of the flexor tibialis digitorum.

In the second place it would seem that Eisler has placed too much

stress upon the supply of the gastrocnemius medialis by a branch of the external saphenous nerve. I have not been able to trace the origin of the nerve in the opossum, but one must conclude from Cunningham's statement, 81, that in the thylacine the nerve arises from the internal popliteal. In these two forms then, the thylacine and Phalangista, two different origins of the nerve occur, one of which favors Eisler's migration theory while the other is opposed to it. Which is the more primitive origin? I have not been able to find in the literature accessible to me any sufficiently detailed accounts of the arrangement of the nerves in other marsupials or in the monotremes, but, since there can be no question as to the identity of the lacertilian muscle termed above the plantaris superficialis medialis with the mammalian gastrocnemius internus, the origin of its nerve fibers may throw some light on the question. In Scincus it is supplied by a branch from the ramus superficialis medialis, i. e., from the more medial of the two superficial nerve trunks and according to Gadow, 82, this is the usual condition in the lacertilia which he studied, in Ophryoessa only does the branch come from the ramus superficialis fibularis. In the crocodiles the muscle is supplied by a branch from the ramus profundus and a weak branch from the superficialis medialis, while in the alligator it receives branches from both superficial nerves, that from the fibularis being the smaller. It seems, therefore, that there is a considerable amount of variation in the course of the nerve fibers in question, a fact which weakens an argument based solely on the path followed by a group of nerve fibers in a single species of mammal.

It seems to me that the muscle in question is primarily and finally a muscle of the tibial side of the crus, and that its homologue in that position can be found from the urodele amphibia to the highest mammalia. Eisler, as has already been pointed out, has failed to recognize the true plantaris superficialis of the amphibia and has thus been led widely astray in his attempts to homologize the amphibian and mammalian muscles. He finds the amphibian homologue of the gastrocnemius medialis in the fibulo-tarsalis (fibulo-plantaris, Eisler) and that of the gastrocnemius lateralis in the plantaris profundus III minor (plantaris superficialis minor, Eisler). It may be pointed out that both these muscles lie beneath the plantaris profundus III (plantaris superficialis major, Eisler) which Eisler identifies with the mammalian plantaris. This latter muscle, however, wherever it can be certainly identified, is in relation with the deeper portion of the gastrocnemius lateralis and would seem to be a derivative of the deeper portion of that muscle. Eisler's identifications would accordingly require an in-

version of the deeper and more superficial muscles, his fibulo-plantaris and plantaris superficialis minor coming to lie on a plane posterior to his plantaris superficialis major. Such a transposition can only be accepted on the strongest evidence, and of this, it seems to me, there is a failure.

Finally, as was pointed out in considering the antibrachial flexors, any theory which requires the migration of a muscle origin over a joint from below demands the closest scrutiny. Eisler's homologies make the gastrocnemius medialis have its origin primarily from the head of the fibula, and to reach the position it has acquired in the lacertilia and mammalia it must have migrated upwards over the knee joint as well as medially. If a plausible homology can be set forth which does not require this migration, the presumption is in its favor. In the forearm it was shown that the palmaris superficialis layer was distinguished from the other flexor layers by having its origin from the humerus, and that throughout the whole series of forms studied it retains that origin. The remarkable similarity which obtains between the amphibian antibrachium and crus leads to the expectation that in all probability the homologue of the superficial palmar layer will have the same relations, and the identification of the plantares superficiales medialis and lateralis with the gastrocnemii exactly fulfills the expectation.

The conclusions to which I have been led, then, are that the gastrocnemius medialis and lateralis of the mammalia are primarily separate muscles which insert into the superficial layer of the plantar aponeurosis, and that they represent the greater part of the superficial plantar layer of the amphibian crus, the gastrocnemius medialis corresponding to the plantaris superficialis medialis of both amphibia and lacertilia and the gastrocnemius lateralis to a portion of the amphibian plantaris superficialis lateralis and to the lacertilian muscle similarly named.

The *plantaris*.—There can be little doubt but that the plantaris is a derivative of the same muscle mass which gives rise to the gastrocnemius lateralis, or, to be more precise, that it represents the deeper medial portion of that mass. For it is typically associated with the gastrocnemius lateralis and is frequently united with that muscle in its upper part, occupying then the position indicated. It is already a distinct muscle in the reptilia, at least the muscle described above as the plantaris superficialis accessorius seems to be its homologue, although the relations which this muscle bears to the plantaris profundus III seems at first sight to preclude any such homology. But it must be remembered that after all the association is not directly with the profundus III, but with the plantar aponeurosis into which the profundus III also inserts.

As a result of the difference in the views of Eisler and myself regarding the amphibian homologues of the gastrocnemii, a difference also exists as to the homologue of the plantaris. Eisler finds it in his plantaris superficialis major, a muscle which, so far as its greater part is concerned, is fibular in origin and has been termed above the plantaris superficialis III. Acceptance of Eisler's homology would again require the migration of a muscle from below over the knee joint and, furthermore, as has already been pointed out, a transition of the planes occupied by the plantaris and the gastrocnemius, both of which phenomena the homology which I have deduced avoids.

It may be added (1) that the primary connection of the plantaris below is with the plantar aponeurosis, its insertion into the os calcis in man being a secondary condition, and (2) that its frequent absence is probably more correctly to be regarded as a failure to separate from the gastrocnemius lateralis, in connection with which idea its not unfrequent union with the tendo Achillis is of significance.

The *soleus,* the third element in the triceps suræ, is a muscle at first sight apparently peculiar to the mammalia, and among these is possibly unrepresented as a distinct muscle in the monotremes.[5] It has been described as lacking in a number of mammals, in such cases being probably included in the gastrocnemius lateralis. It has characteristically an origin from the fibula and this points strongly to its being a representative of the plantaris profundus group of muscles. The conditions in the lacertilia throw little light upon the question, but it is to be noted that the two superficial profundus layers are fused together in these forms. They are, however, clearly distinguishable in the amphibia and it is possible that they again become separated in the mammalia, a series of modifications similar to those which occur in the antibrachial flexors taking place. If this supposition be correct then it seems probable that the soleus represents the plantaris profundus III of the amphibia. The forms which I have studied do not furnish sufficient data for certainty as to this homology, but it seems to be the only one consonant with the facts at our disposal. Possibly a renewed study of the monotreme crus with this idea in mind may yield some light. Eisler, it may be added, regards the soleus as a derivative of the gastrocnemius lateralis.

The *flexor fibularis* and the *flexor tibialis* are so closely associated that at first one would have little hesitation in assigning them to a common

[5] The erroneous application of the term soleus to the muscle which arises from the epiphysial process of the fibula has already been noted.

origin, the two muscles standing to one another in much the same relation as the flexor profundus digitorum and the flexor longus hallucis of man. Their nerve supply is altogether different, however, since the flexor fibularis is supplied by the equivalent of the ramus superficialis medialis, while the flexor tibialis is supplied from the ramus profundus. There seems to be no good reason why this should be so if the two muscles belong to the same original layer, and one is forced to the conclusion that they have their origin from quite different layers. In the amphibia and lacertilia it has been shown that the plantares profundi III and II are supplied from the ramus superficialis medialis, while the plantaris profundus I and the interosseus are supplied from the ramus profundus. The flexor fibularis, accordingly, probably represents the plantaris profundus II, if the soleus be regarded as equivalent to the plantaris profundus III, while the flexor tibialis probably represents in part the plantaris profundus I. In other words the flexor tibialis is a muscle derived from the same primary layer as the tibialis posticus and is quite distinct from the flexor fibularis.

This view may seem improbable on account of the close relation of the two muscles in their lower portions and on account of the distinctness of the tibialis posticus, but it must be remembered that the primary insertion of a considerable portion of the plantaris profundus I is probably into the plantar aponeurosis and that in the lacertilia it is in part united to the sesamoid cartilage developed in the tendon of the plantaris superficialis III-II. It is this aponeurotic portion of the profundus I which becomes the flexor tibialis, while the remainder of it constitutes the tibialis posticus, and, as will be shown later, the flexor accessorius digitorum pedis.

Eisler finds the homologue of the flexor tibialis in his plantaris profundus II and that of the flexor fibularis in his plantaris profundus I, thus coinciding with the opinion expressed above that the muscles belong to different primary layers and also with the identification of the two muscles, since the muscle he names the plantaris profundus I is identical with that which I have called the plantaris profundus II and that which he calls the plantaris profundus II is a part of my plantaris profundus I.

The remarkable transference of the action of the flexor fibularis from the fibular digits to the great toe which occurs in the mammalian series has received its most plausible explanation from Keith, 94, on functional grounds. It remains to especially emphasize in connection with his argument the primary insertion of both muscles into the deeper layers of the plantar aponeurosis, the different arrangements of the tendons

of the two muscles being but various differentiations, due to differences of strain, of an originally single aponeurosis and not a secondary fusion of distinct structures.

The significance of the *tibialis posticus* has already been indicated; from its relations and nerve supply it seems unquestionably a derivative of the plantaris profundus I, a view not at variance with that of Eisler, when allowance is made for the differences in our terminologies. Another derivative of the same layer is the *flexor accessorius digitorum pedis (quadratus plantæ)*, which represents a portion of the layer which takes its origin from the tarsal bones and is inserted into the plantar aponeurosis. The muscle certainly finds no place in the general plan of the plantar muscles and is clearly represented in the lacertilia, where it is supplied by a branch from the ramus profundus. Its supply from the external plantar nerve in the mammalia is readily explained on the basis of the separation of the plantar fibers from the ramus profundus to form a special more superficial nerve stem and to subsequently unite with the external plantar fibers to form the posterior tibial nerve, as has already been described. Its relations to the tendon of the long digital flexor is clearly a persistence of its original insertion into the deep layer of the plantar aponeurosis.

Finally as regards the *popliteus,* the most usually propounded homology is with the uppermost portion of the interosseus muscle, and, in truth, at first sight this seems to be a most plausible suggestion. There are, however, some difficulties in its way, one of the most important being its origin from the external condyle of the femur and another that in some forms it covers in, *i. e.,* lies posterior to the upper portions of the flexor tibialis and the tibialis posticus. On the other hand, its constant supply from the ramus profundus seems to imply in almost unmistakable terms its derivation from either the interosseus or the plantaris profundus I, and of the two the interosseus seems to be its most likely origin.

Eisler, though, recognizing a possibility of referring it to the interosseus, finally concludes that it is not properly a crural muscle at all in the sense in which the term crural is used here, but that it is a femoral muscle and the equivalent of the brachialis anticus of the arm. It is difficult to see how such an homology can be worked out in its details. It would imply that the muscle is a derivative of one of the femoral flexors, most presumably of the biceps or better of such a muscle as the cruro-coccygeus of the opossum, which sends a slip obliquely across the thigh to be inserted into the shaft of the tibia. It is to be noted, however, that this slip passes superficially to the upper part of the gastrocnemius, while the popliteus passes beneath, *i. e.,* anterior to that muscle.

The opossum has no muscle which corresponds exactly to the popliteus. It has the homologue of the interosseus well developed as the pronator tibiæ, but that muscle is entirely confined in its origin to the fibula, even its uppermost portion which has been homologized with the popliteus arising from that bone. It is only in the higher forms that a true popliteus is found and certain peculiarities in its structure in the mouse and cat seem to throw some light upon its significance. In both these forms, as has already been noted, two very distinct portions can be discerned in the muscle, a more tibial portion whose fibers have a very oblique direction and a more fibular portion whose fibers are more nearly vertical. A distinct line of demarcation between the two parts occurs in any transverse section of the upper part of the crus. Furthermore, the muscle receives two nerves, a fact which in so small a muscle is in itself noteworthy, and is all the more significant in that one of these nerves arises, in the mouse for instance, with that for the soleus from the internal popliteal stem, while the other arises from the branch which I have identified with the crural portion of the ramus profundus of the lower vertebrates. And, finally, the internal popliteal branch is supplied entirely to the more tibial oblique-fibred portion of the muscle, while that from the profundus passes entirely to the more fibular vertical portion.

The significance of these facts seems to be evident. The popliteus is a compound muscle, consisting of a portion derived from the plantaris superficialis and a portion which represents a part of the pronator tibiæ of the marsupials and the interosseus of the lower vertebrates. In other words the constitution of the mammalian popliteus is exactly equivalent to that of the pronator radii teres in the arm.

The idea that the muscle is a composite one furnishes a simple explanation of the condition occurring in some carnivores. Gruber, 78, has shown that in the dog, wolf and fox there exists, independently of the popliteus and lying to a certain extent beneath it, a short muscle extending between the upper portions of the fibula and tibia. This is the *m. peroneo-tibialis*. The same muscle occurs also in Viverra (Dobson, 83), and as an anomaly in man (Gruber, 77 and 78). The fact of the occurrence of such a muscle in certain carnivores while lacking in others is certainly reasonably accouted for on the supposition that its absence in the latter is only an apparent one. That is to say, it seems probable that the peroneo-tibialis of the dog represents the more vertical portion of the popliteus of the cat, the dog's popliteus being equivalent to the obliquely fibered portion of the cat's muscle. And similarly, the appearance of the peroneo-tibialis as an anomaly in man may readily be ex-

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plained on the ground of a separation of the profundus portion of the popliteus from the superficialis portion.

In the opossum the upper partially separated portion of the pronator tibiæ is very probably the equivalent of the peroneo-tibialis element, but what may be the representative of the superficialis portion of the popliteus it is difficult to say. A possible degenerated representative of it may be found in a strong tendon-like band which extends obliquely across the knee joint from the external fabellar cartilage to the head of the tibia, but such an identification can be at present merely a suggestion. More important, perhaps, are the relations which seem to exist between the plantaris and the popliteus as shown by anomalies in man, the popliteus having occasionally an accessory head which often coincides with the absence of the plantaris.

If the tendon mentioned above as occurring in the opossum really prove to be the representative in that animal of the superficialis portion of the popliteus, then there should be some muscular representative of it in lower forms. This may be found in that portion of the monotreme popliteus which arises from the epiphysial process of the fibula, and in the reptilia it may have a representative in the plantaris superficialis tenuis, although this seems at present very questionable. A study of a greater number of forms than I have had at my disposal will be necessary to trace out all the homologies of the popliteus, but I believe that the observations here recorded make the supposition as to the composite nature of the popliteus exceedingly probable.

In conclusion a few words may be said with regard to the modifications and homologies of the *plantar aponeurosis* throughout the series. In the urodele amphibia it is represented in the crus by the aponeurosis which covers the posterior surface of the plantaris profundus III and by the tendons of the plantares superficiales medialis and lateralis. It receives, therefore the insertions of these three muscles, together with that of the profundus II and a part of that of the profundus I, and gives origin to the superficial muscles of the plantar surface of the foot. With the increase in size of the lateral and medial portions of the plantaris superficialis, a portion of the superficial layer of the aponeurosis becomes separated to form the tendon of those muscles, while the rest of it is covered in by them and remains included in the tendon of the plantaris profundus III-II, part of it giving insertion to the plantares superficiales accessorius and tenuis.

This is the reptilian condition, and the transition from it to that of the mammalia is comparatively simple. The superficial layer of the aponeurosis in the mammalia is represented by (1) the tendon or tendons

of the triceps suræ, (2) the tendon of the plantaris and (3) the plantar aponeurosis of the foot, a portion of it (4), however, remaining included with the deep layer in the tendons of the flexores fibularis and tibialis. It is this fourth portion of the superficial layer which gives origin to the flexor brevis digitorum in those forms in which that muscle arises from the tendons of the long flexors.

The homologies of the crural muscles traced out in the preceding pages may be tabulated thus:

Amphibia.	Lacertilia.	Opossum.	Mammalia.
Plantaris sup. medialis.	Plantaris sup. medialis.	Gastrocnemius medialis.	Gastrocnemius medialis.
	Plantaris sup. lateralis.	Gastrocnemius lateralis (less included soleus).	Gastrocnemius lateralis.
Plantaris sup. lateralis.	Plantaris sup. accessorius.	Plantaris.	Plantaris.
	Plantaris sup. tenuis.	. . . .	Popliteus (superficial portion)?
Plantaris prof. III.		Soleus portion of gas-	Soleus.
Plantaris prof. II.	Plantaris prof. III–II.	troc. lat.	
		Flexor fibularis.	Flexor fibularis.
		Flexor tibialis.	Flexor tibialis.
Plantaris prof. I.	Plantaris prof. I.	Tibialis posticus.	Tibialis posticus.
	Plantaris prof. I access.	Flexor accessorius.	Flexor accessorius.
Interosseus.	Interosseus.	Pronator tibiæ.	Popliteus (peroneo-tibial portion).

SUMMARY.

1. In the crus of the urodelous amphibia the flexor muscles are arranged in five layers, the superficial one arising in the femoral region, the others, which have a more or less oblique direction, taking their origin from the fibula and slightly from the tarsus. They are inserted for the most part into the plantar aponeurosis, only the deepest layer inserting into the tibia. Between the second and third layers is a slender longitudinal muscle extending between the fibula and the tarsus.

2. The nerves of the flexor muscles of the amphibian crus are arranged in two main trunks, a ramus superficialis and a ramus profundus. The latter is continued into the pes as the internal plantar nerve. The former divides into rami mediales which are confined to the crus and a ramus fibularis which is continued into the pes as the external plantar nerve. The rami superficiales mediales supply the first, second and third layers of muscles, the ramus superficialis fibularis, the fibulo-tarsalis and the ramus profundus the fourth and fifth layers.

3. A complete separation of the præaxial and postaxial nerve fibers does not take place at the knee-joint in the amphibia, but the ramus profundus for a considerable portion of its course contains fibers which are distributed to the præaxial surface of the crus.

4. In the lacertilian crus the same muscle layers that occur in the

amphibia are readily distinguishable. The superficial layer has increased greatly in size and shows a differentiation into several muscles. The second and third layers have fused and the fourth layer has differentiated into two separate muscles. The fibulo-tarsalis has disappeared and the muscles have in general a more vertical direction than in the amphibia.

5. The arrangement of the nerve trunks in the lacertilian crus is essentially the same as in the amphibia. The separation of the præaxial and postaxial fibers takes place, however, above the knee joint.

6. In the mammalia the same layers of muscles can be distinguished although they have undergone greater differentiation into individual muscles than in the lower forms.

7. The plantar fibers of the ramus profundus are separated in the mammalia from the crural fibers and in the opossum form a more superficial stem, the internal plantar, which traverses the crus without taking part in its nerve supply. The other rami remain practically unaltered. In the higher mammalia a further change takes place in that the ramus fibularis (external plantar) and the internal plantar unite to form a single stem, the posterior tibial, and, in man, some of the fibers belonging to the ramus superficialis mediales and the ramus profundus become included in this.

8. The superficial layer of muscles retains throughout its origin from the femur and the deep layers theirs from the crural bones, with one apparent exception. Furthermore the insertion into the plantar aponeurosis is largely retained, although some shifting to the bones occurs.

9. The soleus represents the second layer of muscles and its absence in certain forms is probably due to its inclusion in the gastrocnemius lateralis.

10. The flexor fibularis and flexor tibialis belong to different layers, the former representing the third layer, while the latter is formed from a portion of the fourth layer, as is also the tibialis posticus.

11. The flexor accessorius digitorum (quadratus plantæ) is primarily one of the crural muscles and represents another portion of the fourth layer of muscles.

12. The popliteus is a compound muscle, being formed of a portion from the superficial layer, united with a portion of the fifth layer. The occasional occurrence of a distinct m. peroneo-tibialis in the higher mammalia is probably due to a failure of the two portions to unite.

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