THE PHYLOGENY OF THE PLANTAR MUSCULATURE.

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WITH 9 TEXT FIGURES.

In three papers which have appeared in this JOURNAL I have given the results of a comparative study of the flexor muscles of the antibrachium, hand and crus, and have shown that in each of these parts there is an arrangement of the musculature in definite layers, which can be identified in the amphibia, reptilia and mammalia. And, further, it was shown that there is a close correspondence in the arrangement of the musculature of the antibrachium and crus in the lower forms. There remain to be determined the existence of an arrangement in primary layers in the plantar musculature and the correspondence of these layers with those occurring in the palm. In the present paper I shall consider especially the question of the primary layers of the plantar musculature and their differentiation.

The material which has served for this study consisted of series of transverse sections of the same forms that were employed in my study of the crural flexors, **04**, except that, through the courtesy of Dr. M. J. Greenman, Director of the Wistar Institute of Anatomy, I have been able to add to the mammalian series a representative of the Insectivora, *Scaphanus* sp.?, which, unfortunately, however, proved to be of only subordinate value for my purpose, owing to the extensive transformation of the plantar musculature into tendinous structures. I have also had opportunity for studying the plantar muscles of *Iguana tuberculata,* through the courtesy of my colleague, Dr. J. E. Reighard.

I. THE PLANTAR MUSCLES OF THE URODELE AMPHIBIA.

The plantar muscles of *Amblystoma* are arranged in four primary layers, which correspond, layer for layer, with those occurring in the palm. In a transverse section through the foot a little distal to the bases of the metatarsal bones, the arrangement represented in Fig. 1 is seen. Superficially, immediately beneath the integument, is the strong plantar aponeurosis (*pa*), beneath which lies a continuous layer of muscle tissue,

the *flexor brevis superficialis* (*fbs*). Dorsal to this is a layer, consisting at this level of four distinct portions, which is the *flexor brevis medius* (*fbm*); resting directly upon the metatarsals is the third layer, showing indications of division into a number of subordinate portions, and forming the *flexor brevis profundus* (*fbp*); and, finally, extending between the adjacent surfaces of contiguous metatarsals, are the representatives of the fourth layer, the *intermetatarsales* (*im*).

The plantar aponeurosis and flexor brevis superficialis. The plantar aponeurosis is the direct continuation of the strong aponeurosis which covers the muscles of the crus, and over the metatarsals it divides into five slips, which pass to the various digits; the slips to the hallux and

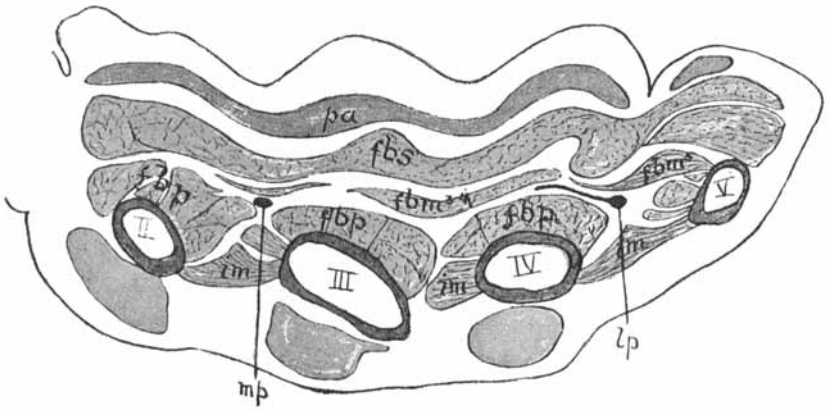


FIG. 1. Transverse section through the foot of Amblystoma. *fbm* = flexor brevis medius; *fbp* = flexor brevis profundus; *fbs* = flexor brevis superficialis; *im* = intermetatarsales; *lp* = lateral plantar nerve; *mp* = medial plantar nerve; *pa* = plantar aponeurosis; *II-V* = metatarsal bones.

minimus had already separated at the level of the section shown in Fig. 1. More proximally, over the tarsals, the aponeurosis receives upon its dorsal surface the insertion of the majority of fibers of the plantares profundi of the crus, these muscles acting on the phalanges through the aponeurosis. In tracing a series of sections from the crus downwards into the foot one finds the plantares gradually diminishing in size as their fibers insert into the aponeurosis, until they are represented only by a few slips which are prolonged further distally than the main masses of the muscles. But just as one begins to expect these slips to completely disappear, they begin to enlarge and more distally form the continuous sheet of muscle which is represented in Fig. 1 as the flexor brevis superficialis, this muscle, accordingly, appearing to be the direct continuation of the plantares pro-

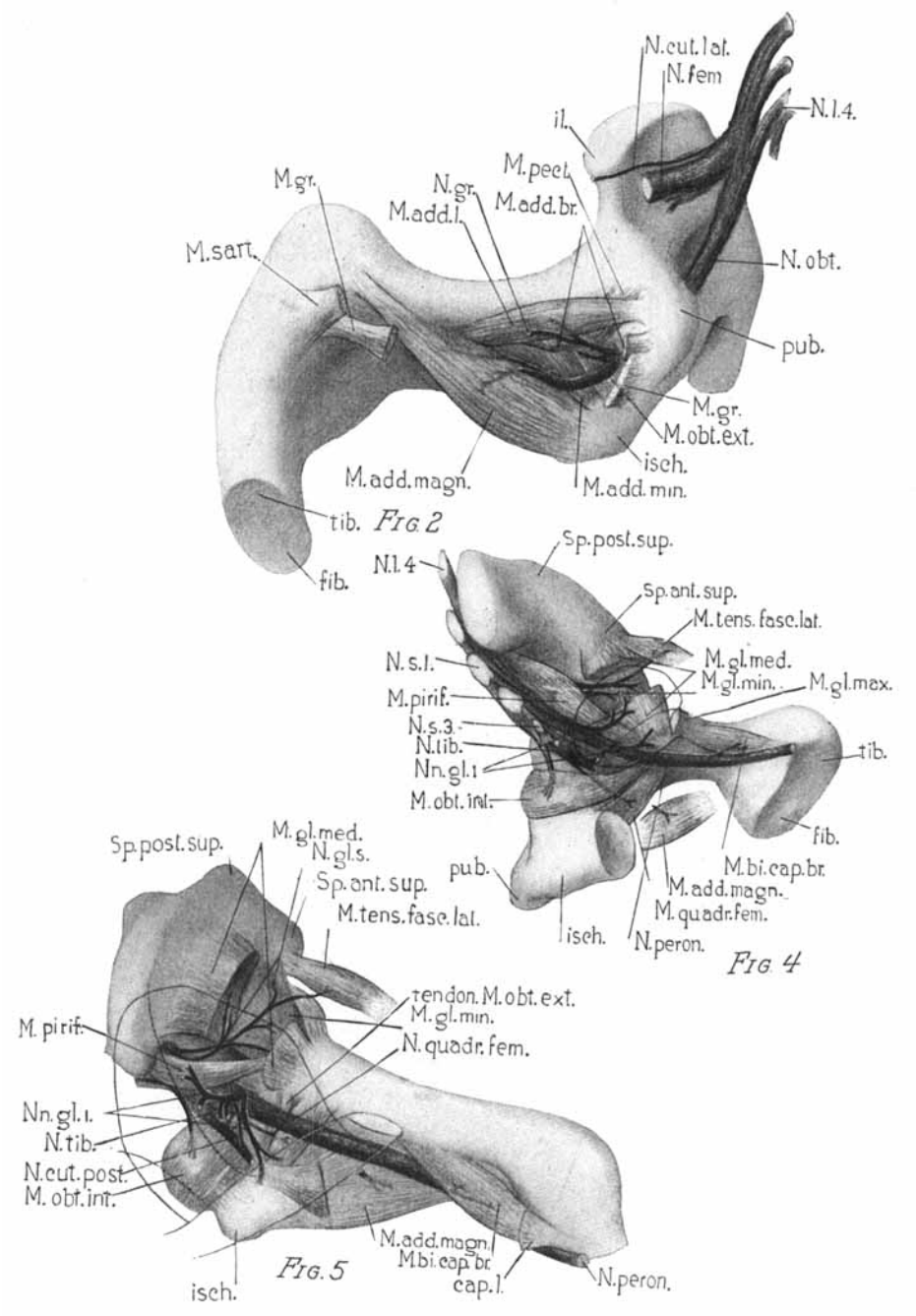


FIG. 2

FIG. 4

FIG. 5

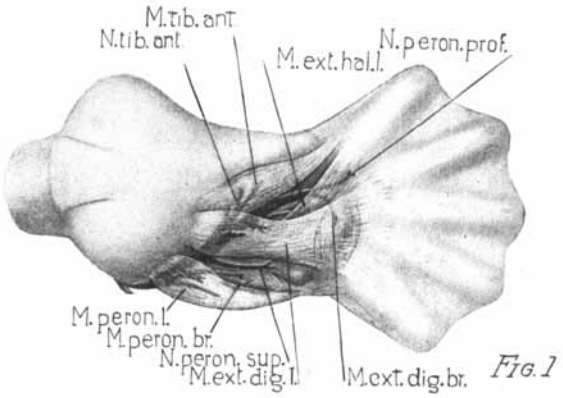


FIG. 1

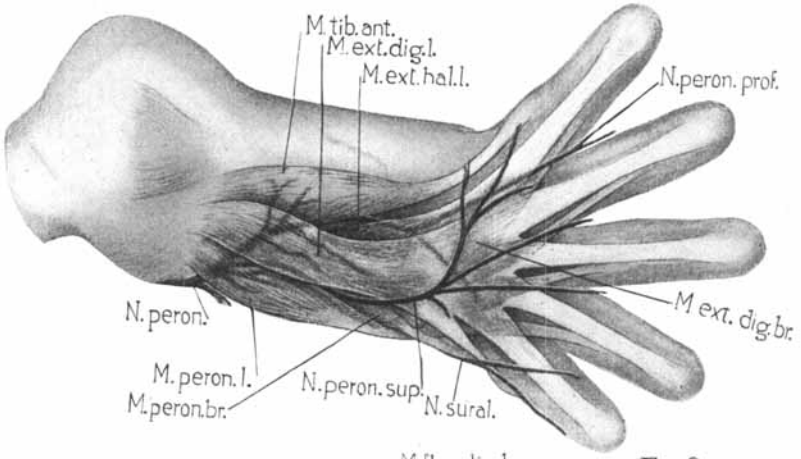


FIG. 2

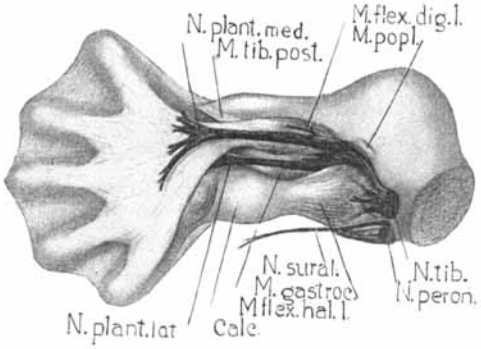
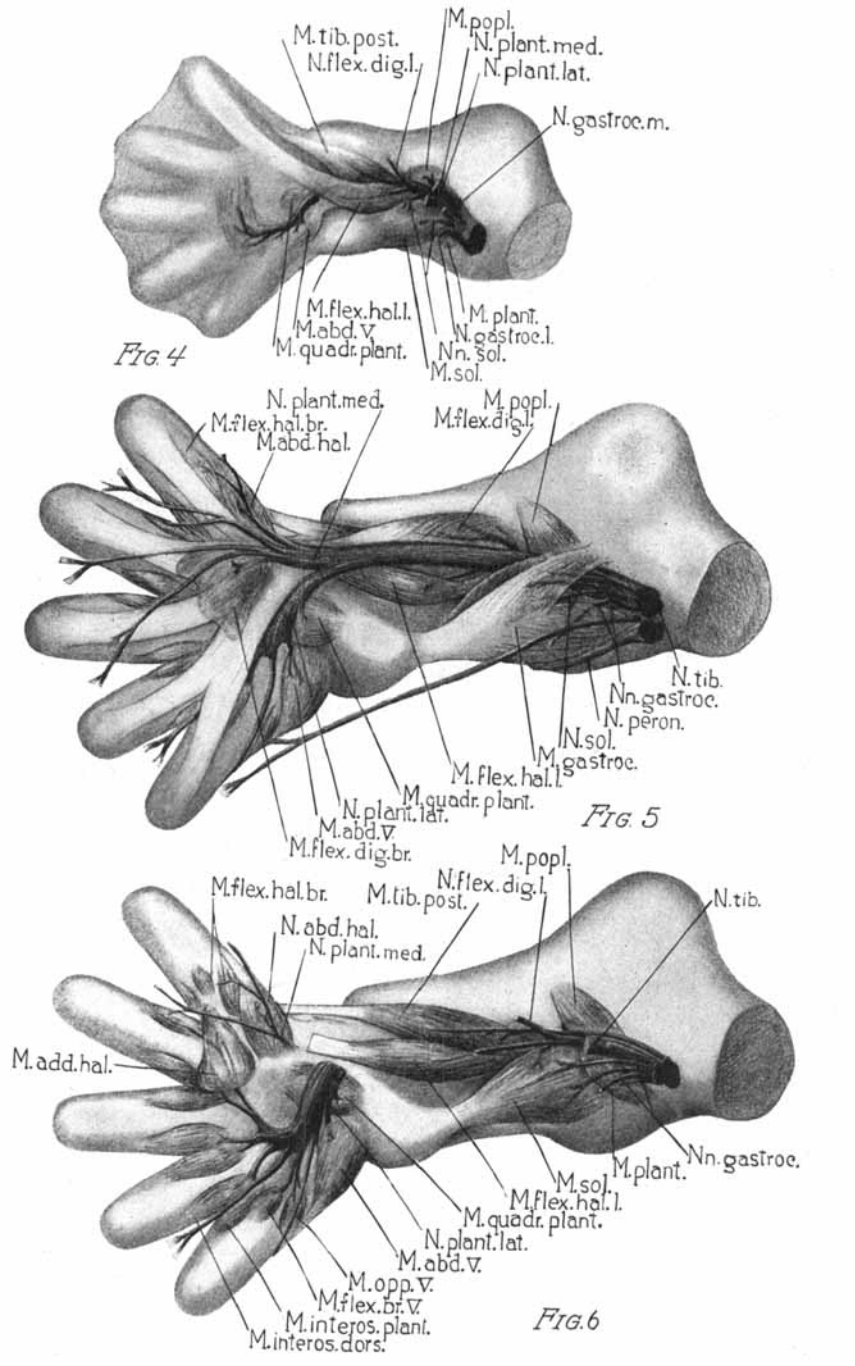


FIG. 3


M. tib. post.
N. flex. dig. l.
M. popl.
N. plant. med.
N. plant. lat.
N. gastroc. m.
M. flex. hal. l.
M. abd. V.
M. quadr. plant.
Nn. sol.
M. sol.
M. plant.
N. gastroc. l.
FIG. 4
N. plant. med.
M. flex. hal. br.
M. abd. hal.
M. popl.
M. flex. dig. l.
N. tib.
Nn. gastroc.
N. péron.
N. sol.
M. gastroc.
M. flex. hal. l.
M. quadr. plant.
N. plant. lat.
M. abd. V.
M. flex. dig. br.
FIG. 5
M. flex. hal. br.
M. tib. post.
N. flex. dig. l.
M. popl.
N. tib.
N. abd. hal.
N. plant. med.
M. add. hal.
M. plant.
Nn. gastroc.
M. sol.
M. flex. hal. l.
M. quadr. plant.
N. plant. lat.
M. abd. V.
M. opp. V.
M. flex. br. V.
M. interos. plant.
M. interos. dors.
FIG. 6

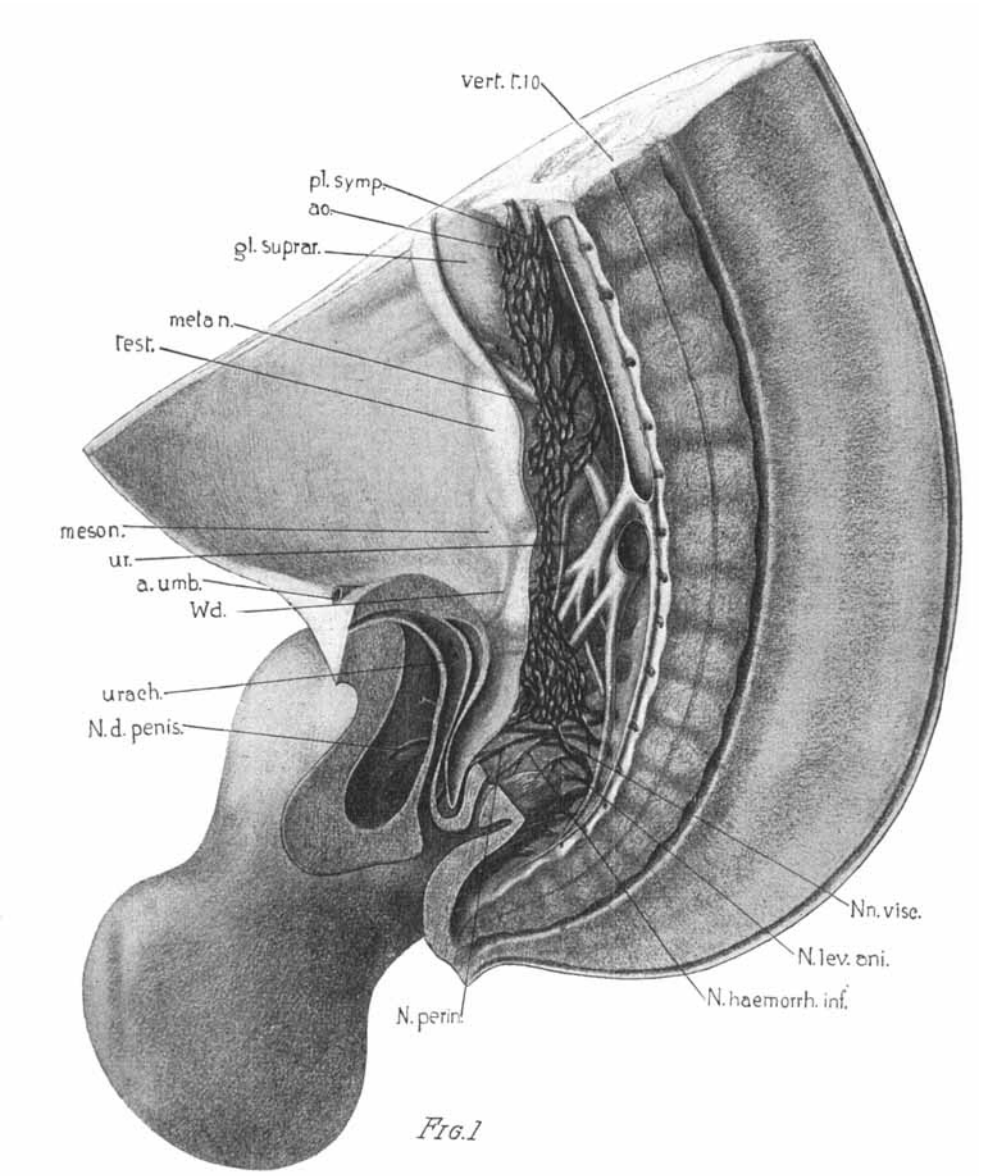

vert. r.10
pl. symp.
ao.
gl. suprar.
meta n.
rest.
meson.
ur.
a. umb.
Wd.
urach.
N.d. penis
Nn. visc.
N. lev. ani.
N. haemorrh. inf.
N. perin.

FIG. 1

fundi. The continuity is, however, probably merely an apparent one, the fibers of the flexor brevis superficialis beginning to arise from the plantar aponeurosis before those of the plantares profundi have completed their insertion, so that there is a confusion of the two groups of muscles. The fact that one finds, first the continuous sheet of the plantares, then for a short distance three slender slips separated by portions of the plantar aponeurosis, and then again a continuous sheet of flexor brevis superficialis, seems to indicate that one has to do with two distinct muscles, especially when comparison is made with the arrangement in the hand, and when it is noted that the portions of the superficial flexor which pass to the marginal digits arise from the aponeurosis independently of the plantares, the portions continuous with these muscles passing only to the three central digits.

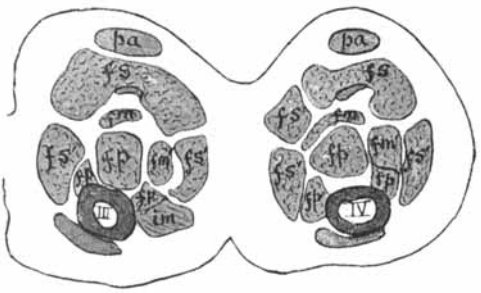


FIG. 2. Transverse section through the metatarsals of the third and fourth digits of Amblystoma near their heads. *fm* and *fm'* = central and lateral slips of flexor brevis medius; *fp* = slips of flexor brevis profundus; *fs* and *fs'* = central and lateral slips of flexor brevis superficialis; *im* = intermetatarsalis; *pa* = plantar aponeurosis; *III* and *IV* = metatarsal bones.

If the plantar aponeurosis and the flexor brevis superficialis be traced distally they will be found to split into as many slips as there are digits, the prolongations of the aponeurosis inserting into the terminal phalanges. In the muscle slips destined for the third and fourth digits the marginal portions (Fig. 2, *fs'*) separate and pass to an insertion into the sides of the heads of their metatarsals, these insertions being closely associated with those of the flexores breves profundi. A little more distally the central portion of each slip (*fs*) begins to undergo a transformation into connective tissue and gives rise to a tendon which applies itself to the dorsal surface of the slip derived from the plantar aponeurosis and fuses with it over the base of the first phalanx, the muscle fibers on either side of this central tendon inserting into the sides of the fibro-cartilages over the metatarso-phalangeal joint.

In the slip to the second digit there is a similar transformation of the median portion into tendon and an insertion of the muscle fibers adjacent to this tendon into the metatarso-phalangeal fibro-cartilages, but there is only one slip passing to the head of the metatarsal, namely, that to the fibular side. The slip to the fifth digit behaves essentially like that to the fourth or third, the only striking difference being the large size of the fibular metatarsal slip; but that to the first digit differs from the rest in that it fails to separate into subordinate slips, but inserts entirely into the metatarso-phalangeal fibro-cartilages.

In addition to the portions of the flexor brevis superficialis described above, another portion is probably represented by the *abductor quinti digiti*, or, as it may be more accurately termed, the *abductor ossis metatarsi V.*, which arises from the fibular border of the tarsus and inserts into the base of the fifth metatarsal, a sesamoid cartilage being developed at its insertion.

The *flexor brevis medius* takes its origin from the aponeurotic layer which lies immediately dorsal to the plantares profundi. It appears as four distinct slips, one of which (Fig. 1, *fbm*$^{3\,4}$) later divides, so that there is a slip for each digit. Toward the distal ends of the metatarsals the slips which pass to the third, fourth, and fifth digits divide into two portions, one of which (Fig. 2, *fm*), much smaller than the other, lies upon the plantar surface of the median slip of the corresponding flexor brevis profundus, while the other portion (*fm'*) rests upon the fibular slip of the same muscle. This latter portion inserts into the side of the head of its metatarsal, in more or less close association with the fibular slip of the flexor brevis profundus, and the smaller portion inserts into the metatarso-phalangeal fibro-cartilage. The slips to the second and first digits do not divide in this manner, but insert entirely into the articular fibro-cartilages.

The *flexor brevis profundus* is composed of three slips for each digit, a median and two lateral (Figs. 1 and 2). The lateral slips arise from the tarsal bones, and, in the cases of the marginal digits, partly from the plantar aponeurosis. The median slip, on the other hand, arises from the plantar surface of its metatarsal, and in the central digits separates the lateral slips, which, up to the level of its appearance, form a single mass. The lateral slips insert into the heads of the metatarsals, the fibular slips of the four tibial digits being intimately associated with the intermetatarsals, and the same slips of the third, fourth and fifth digits with the fibular slips of the flexor brevis medius for those digits. The median slips, which are the metatarso-phalangei of Humphry, **72**, extend further dis-

tally and insert in all five digits into the metatarso-phalangeal fibrocartilages.

In the third and fourth digits inter-phalangeal muscles, the phalangei of Humphry, also occur, passing from the plantar surface of the proximal phalanx to the base of the second one.

The *intermetatarsales* (Fig. 1, *im*), extend obliquely across the intermetatarsal spaces from the fibular to the tibial side. They are four in number, arising from the tibial sides of the bases of the second, third, fourth and fifth metatarsals, and inserting into the fibular sides of the heads of the first, second, third and fourth metatarsals in association with the fibular slips of the flexor brevis profundus of those digits.

The lateral plantar nerve is, as I have shown elsewhere, **04**, the continuation into the foot of the ramus superficialis fibularis of the crus, while the medial plantar is the continuation of the ramus profundus.

In the proximal tarsal region the lateral plantar nerve lies immediately upon the fibular border of the fibulare and the medial plantar upon the centrale. When the flexores brevi profundi appear they lie between the nerves and the bones, and still more distally, after the flexores breves medii have appeared, the nerves are situated between these muscles and the flexores breves profundi, the medial plantar over the interspace between the second and third metatarsals and the lateral plantar over that between the fourth and fifth (Fig. 1, *mp* and *lp*). The medial nerve gives off branches both medially and laterally, the lateral one meeting a medially directed branch from the lateral plantar opposite the inter-space between the third and fourth metatarsals, so that it becomes difficult to determine from which of the two nerves the branches to the muscles arise. It would seem, however, that the lateral plantar supplies all the muscles of the fifth digit and those inserting into the fibular side of the fourth, while the remaining plantar muscles are supplied by the medial nerve. Certain it is that the terminal cutaneous branches of the two nerves are distributed in such a way that the contiguous surfaces of the four tibial digits are supplied by the medial plantar and those of the fourth and fifth digits by the lateral plantar, the lateral surface of the minimus and the medial surface of the hallux being supplied by branches which descend from the crus.

This distribution differs materially from that described by Humphry, **72**, for Cryptobranchus. In that form the lateral plantar was found contributing to the supply of the third and second digits. In amblystoma it does not extend tibially beyond the fourth digit, the intermetatarsal between the fourth and third digits, for instance, being supplied by the medial plantar.

II. The Plantar Muscles of the Lacertilia.

The manus of the lacertilia compared with that of the urodeles showed a considerable increase in the number of muscle layers, the four urodelan layers being represented by seven. In the pes a similar increase occurs, but it is not carried to quite the same extent as in the manus, the flexor brevis medius layer being divided into only two layers instead of three.

In a previous paper, **04**, I showed that the aponeurosis of the crural flexors is, in the lacertilia, divided into a superficial and a deeper layer. The superficial layer is continued into the planta as a well marked aponeurosis (Fig. 3, pa_s) intervening between the integument and the flexor brevis superficialis, and contains several thickened bands which pass to

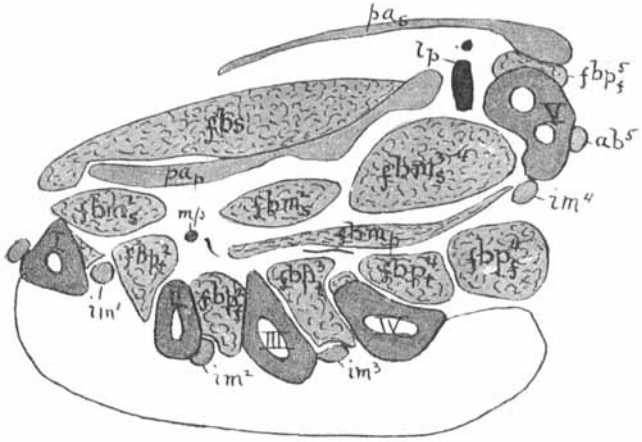


Fig. 3. Transverse section through the foot of Scincus, near the bases of the metatarsals. ab^5 = abductor quinti digiti; fbm_p = flexor brevis medius str. profundum; fbm_s = flexor brevis medius str. superficiale; fbp_t and fbp = fibular and tibial slips of flexor brevis profundus; fbs = flexor brevis superficialis str. superficiale; im = intermetatarsal ligaments; lp = lateral plantar nerve; mp = medial plantar nerve; pa_s and pa_p = superficial and deep layers of the plantar aponeurosis.

the digits and insert with the tendons of the flexor brevis superficialis. The layer is especially developed towards the fibular side of the foot, passing in Scincus to all the digits except the first, but in Iguana being limited to the third, fourth and fifth, only an exceedingly thin layer of fascia covering the muscles passing to the first and second digits. The slip to the minimus is a strong triangular sheet which easily separates from the rest of the aponeurosis.

The *flexor brevis superficialis* (Fig. 3, *fbs*) lies immediately beneath the superficial plantar aponeurosis and consists of a stratum superficiale

and a stratum profunduf. The *stratum superficiale* (Fig. 4, fb_s), takes its origin from the sesamoid bone developed in the tendon of the crural plantaris profundus II-III, and, therefore, from a portion of the superficial aponeurosis. In Scincus it forms a continuous sheet, lying at first to the medial side of the terminal portion of the plantaris superficialis lateralis and resting directly on the continuation of the tendon of the plantaris profundus II-III. As this tendon divides into slips for the five digits, the flexor superficialis divides into corresponding portions, each of these, as a rule, again dividing into two slips, which insert into either side of the base of the proximal phalanx, the tendon of the plantaris profundus II-III passing between them. The slip to the hallux could not be traced

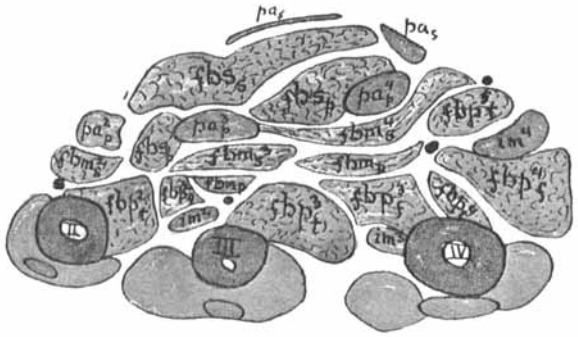


FIG. 4. Transverse section through the foot of Scincus near the heads of the second metatarsal. fbm_p = flexor brevis medius str. profundum; fbm_s = flexor brevis medius str. superficiale; fbp_f and fbp_t = fibular and tibial slips of flexor brevis profundus; fbs_p = flexor brevis superficialis str. profundum; fbs_s = flexor brevis superficialis str. superficiale; im = intermetatarsal ligaments; pa_p and pa_s = deep and superficial layers of the plantar aponeurosis; *II-IV* = metatarsals.

to the phalanx, but faded out over the tendon of the plantaris before reaching the metatarso-phalangeal joint.

In Iguana the muscle, though well developed, is limited in its insertion to the three tibial digits, the slip for the hallux early separating from the rest of the muscle and no slips passing to either the fourth or the fifth digit.

In addition to the flexor brevis superficialis the abductor quinti digiti (Fig. 3, ab^5) is probably to be assigned to the superficial plantar layer. In Scincus it is a small muscle which arises from the surface of a strong ligament extending from the fibular surface of the proximal tarsal bone to the base of the fifth metatarsal. As was the case with the corresponding muscle in the urodeles, its assignment to the superficial plantar layer is not beyond question, although it is indicated by the position of the muscle

and by the fact that it is supplied by a branch given off from the lateral plantar nerve before it bends dorsally to reach its final position between the middle and deep layers of flexors.

The *stratum profundum* (Fig. 4, fbs_p) of the flexor superficialis is represented by two muscles which take their origin from the plantar surface of the tendon of the plantaris profundus II-III before it separates into its terminal slips. The muscle lies in the intervals between the second and third and third and fourth of these terminal slips, and some of their fibers arise from the slips passing to the third and fourth digits. The more tibial muscle is directed fibularly in its distal course, and, passing over into a tendon, is inserted into the tibial side of the base of the proximal phalanx of the third digit, in close proximity to the slip of the flexor brevis medius str. superficiale to that digit. The more fibular muscle has almost the same relations, except that it fuses with the large slip of the flexor brevis medius str. superficiale to the fourth digit, forming a muscular mass which completely invests the plantaris profundus III-II tendon to the digit. The relations of the muscles are practically identical in both Scincus and Iguana; they seem to correspond to the muscles η and ζ of Gadow's, **82,** second layer and to those numbered 17 and 18 by Perrin, **93.**

The *flexor brevis medius* is represented by two distinct muscle layers. The *stratum superficiale* (Figs. 3 and 4, fbm_s), lies immediately dorsal to the tendons of the plantaris profundus III-II, and in Scincus consists at its origin of three portions. The tibial and middle portions arise from the plantar surface of the base of the second and fourth metatarsals and from the connective tissue covering those bones, while the fibular portion, much the strongest of the three, has an extensive origin from the fibular border of the fifth metatarsal. The tibial and fibular portions retain their individuality throughout, the former passing distally and tibially to be inserted into the first metatarso-phalangeal fibro-cartilage, while the latter passes to the corresponding structure of the fourth digit. The middle portion divides into two slips, which pass respectively to the metatarso-phalangeal fibro-cartilages of the second and third digits (Fig. 4, $fbm_s{}^{34}$).

In Iguana the arrangement of the layer is essentially the same as in Scincus, although there are some differences in detail. The muscles take origin in part from the tarsal bones, instead of from the metatarsals, and in part receive numerous fibers from the dorsal surfaces of the tendons of the plantaris profundus III-II. The tibial portion is strong and quite independent of the others; the median portion, which

has a considerable origin from the dorsal surface of the plantaris tendon as well as from the tarsus, passes to the second and third digits; while the fibular portion, which is strong, as it approaches the fourth metatarso-phalangeal joint, invests the fourth plantaris tendon and comes into such intimate connection with the fibular slip of the flexor brevis superficialis str. profundum as to be unseparable from it.

This layer seems to correspond to Gadow's, **82**, second plantar layer (less the slips η and ζ already referred to the flexor brevis superficialis str. profundum) together with slip α of his third layer. His second layer contains no slip to the hallux, while his third layer possesses two slips to that digit, one of which presents an appearance and arrangement similar to the hallucal slip of the flexor brevis medius str. superficiale of Scincus and Iguana. The same slip is described by Hoffmann, **90**, as the tarso-digitalis primus and by Perrin, **93**, as No. 30 flexor of the first phalanx. The latter author describes the middle slip as 9i, tarso-flexor of the digits, and the fibular slip as the external portion of 18, flexor of the fourth phalanx, the internal portion of that muscle being the slip of the flexor brevis superficialis str. profundum to the fourth digit.

The *flexor brevis medius stratum profundum* (Figs. 3 and 4, fbm_p) is a thin sheet which lies immediately dorsal to the str. superficiale and is separated from the flexores breves profundi by the deep branches of the plantar nerves. It arises from the bases of the fifth and fourth metatarsals and, to a certain extent, from that of the third, and its fibers are directed obliquely distally and tibially. It divides over the shafts of the metatarsals into four slips which pass to the fibular side of the metatarso-phalangeal fibro-cartilage of the first, second, third, and fourth digits. This muscle corresponds to the third plantar layer of Gadow, **82**, with the omission of slip α, and to the deductors of Perrin, **93**.

The flexores breves profundi (Figs. 3 and 4, *fbp*). These muscles form a layer resting directly upon the metatarsals and separated from the flexor brevis str. profundum by the deep branches of the plantar nerves. They form in Scincus ten slips, which do not, however, correspond by pairs to the five digits. So far as the three tibial digits are concerned a paired arrangement is clear, although the muscles for each digit arise from the next adjacent metatarsal. The fourth digit, however, has three slips attached to it, and the fifth only one, an arrangement which may indicate a transference of one of a pair corresponding to the fifth digit to the fourth.

Of the slips which pass to the metatarso-phalangeal fibro-cartilages of the first, second, and third digits, one (fbp_t) arises from the tibial surface and the other (fbp_f) from the plantar surface of the next adjacent metacarpal on the fibular side. In the case of the fourth digit one slip (Fig. 4, $fbp^4{}_t$) arises from a strong ligament which extends distally from the cuboid; a second slip ($fbp^4{}_f$) arises partly from this same ligament, which, much reduced in size, accompanies it throughout its course, and partly from the tibial surface of the fifth metatarsal; while the third ($fbp^5{}_t$) takes its origin from the head of the fifth metatarsal in close association with the intermetatarsal ligament. All three slips insert into the metatarso-phalangeal fibro-cartilages of the fourth digit.

The third slip from its position might readily be interpreted as a portion of the flexor brevis medius, stratum profundum. The fourth digit, however, has another slip which is plainly a part of that layer, and, furthermore, the deep branch of the lateral plantar nerve passes to its deep position between the slip under discussion and the flexor brevis medius, the slip, therefore, lying practically dorsal to the nerve layer and having the same relation to it as the other deep flexors. Its identification as one of these makes it seem probable that it really represents one of a fifth pair, its fellow being a slip (Fig. 3, $fbp^5{}_f$), which arises from a ligament extending between the talo-calcaneus and the base of the fifth metatarsal. It passes distally upon the fibular surface of the metatarsal, parallel to the lower part of the plantaris superficialis lateralis, from which it is separated by the lateral plantar nerve, and inserts into the fifth metatarsal near its distal extremity.

In Iguana I find essentially the same arrangement of the flexores breves profundi, although there are slight differences in detail. The first and second digits each receive two slips, but the slip to the third digit could not be divided into two portions. It arose, however, partly from the tibial surface and partly from the plantar surface of the fourth metatarsal and consequently agreed with the two slips found in Scincus. To the fourth digit three slips can be distinguished, of which that corresponding to $fbp^4{}_f$ is much the most prominent and completely conceals $fbp^4{}_t$, which is represented by a narrow and thin band of fibers, inseparable at its origin from $fbp^3{}_f$, although diverging from it distally. The third slip, which arises from the base of the fifth metatarsal, is quite small and after a short course unites with the fourth intermetatarsal. The single slip to the fifth digit is much stronger than in Scincus, covering the whole plantar surface of the metatarsal and having upon it in the median line the tendon of the flexor plantaris profundus.

The *intermetatarsales.* In Scincus and Iguana these muscles have the same structure and relations as the corresponding muscles of the hand. They are represented by four slender tendons (Figs. 3 and 4 *im*) which pass to the bases of the proximal phalanges of certain digits from certain metatarsals. The first tendon passes from the first metatarsal to the phalanx of the second digit; the second from the second metatarsal to the phalanx of the third digit; the third from the third metatarsal to the phalanx of the fourth digit; and the fourth from the fifth metatarsal to the phalanx of the fourth digit. Consequently the fourth digit receives the insertion of two of the tendons and the second and third digits each receive one.

The nerve supply of the plantar region presents some interesting differences from what obtains in the urodeles. At the level of the ankle joint the medial plantar nerve or ramus profundus is situated deeply, resting upon the talo-calcaneus dorsal to the plantaris profundus I, while the lateral plantar or ramus superficialis fibularis lies upon the dorsal surface of the plantaris superficialis lateralis and has, therefore, a plantar position with reference to the plantares profundi (see Fig. 5 of my paper on the crural flexors, 04). The medial plantar retains its deep position as it is traced onwards into the foot, the flexores breves profundi, however, appearing between the nerve and the metatarsals so that the nerve comes to lie between these muscles and the flexor brevis medius str. profundum over the line of the second metatarsal (Fig. 3, *mp*). Over the proximal half of that bone it gives off a branch which is supplied to the various slips of the flexor medius and profundus sets of muscles which are inserted into the hallux, apparently also to the slip of the flexor superficialis which passes to that digit, and is finally distributed to the adjacent sides of the first and second digits. The remainder of the nerve continues its distal course, bending slightly towards the fibular border of the foot so that it comes to lie at first over the second intermetatarsal space and then over the fibular border of the third metatarsal. It gives off a branch to the fibular side of the second digit and toward the head of the third metatarsal it divides into two terminal branches which supply the sides of the third digit. The peculiar condition is thus produced that the muscular distribution of the nerve is confined to the muscles inserting into the hallux, while its cutaneous distribution extends over the three tibial digits.

The lateral plantar behaves quite differently. Beyond the ankle joint it continues its course lying over the fifth metatarsal between the terminal portion of the plantaris superficialis lateralis and the abductor quinti

digiti; but just opposite the insertion of the latter muscle it bends dorsally (Fig. 3, *lp*), passing between the terminal portion of the abductor on the one side and the hallucal long flexor tendon and slip of the flexor brevis superficialis in the other, giving off at the same time two branches. One of these remains superficial and is continued along the medial border of the fifth digit, while the other passes dorsally with the main stem of the nerve and then bends medially to be supplied to all the slips of the flexor brevis medius str. superficiale except that which passes to the hallux. The main stem when it reaches the interval between the flexor brevis medius str. profundum and the flexores breves profundi (Fig. 4) makes an abrupt bend and passes medially as far as the line of the second metatarsal, passing dorsal to the main stem of the medial plantar. Without going into details regarding the various branches given off by the nerve in this deep portion of its course, it may be said that it supplies all the portions of the flexor brevis medius and flexor profundus layers except those which pass to the first digit, and that its cutaneous distribution is limited to the fourth and fifth digits.

This condition is very different from what occurs in Amblystoma, in which the medial plantar has the major supply of the pes. It would seem that there has been a shifting of fibers from the profundus to the fibular superficial stem, so that muscles originally supplied by the former are, in the lacertilia, supplied by the latter, and it is interesting to note that the transference has taken place to a much greater extent in connection with the motor fibers than with the cutaneous ones, so that the sensory supply of the medial plantar extends to digits where muscles are entirely supplied by the lateral plantar.

In making a comparison between the muscles of the urodele and lacertilian it is evident that the nerve supply fails to give any criterion for homology and there is left only the evidence from topographic relations. This, however, yields results which seem conclusive.

The homologies may be briefly stated in the form of a table, no discussion seeming to be necessary except in regard to the flexor brevis medius. In this muscle, as has been noted, there are two layers in the lacertilia, while only one was recognized in the amphibia. There seems little room for doubt, however, that indications of the double layering exist in the urodeles, each slip of the medius in these forms dividing into a more tibial and smaller portion and a larger fibular portion. These lie practically side by side and therefore do not represent exactly the condition in the lacertilia, but nevertheless it seems probable that the tibial

slips are the urodele equivalents of the lacertilian stratum superficiale. If this view be adopted the homologies of the muscles in the two groups may be tabulated as follows:

Urodeles.	*Lacertilia.*
Flexor brevis superficialis	Flexor brevis superficialis stratum superficiale. Flexor brevis superficialis stratum profundum.
Flexor brevis medius fasciculus tibialis.	Flexor brevis medius stratum superficiale.
Flexor brevis medius fasciculus fibularis.	Flexor brevis medius stratum profundum.
Flexores breves profundi.	Flexores breves profundi.
Intermetatarsales.	Ligg. intermetatarsalia.

III. The Plantar Muscles of the Mammalia.

In 1878 Ruge published two important papers dealing with the plantar muscles of the mammalia, one, **78,** being a consideration of the muscles of the human foot from the embryological standpoint, and the second, **78a,** a comparative study of the deeper plantar muscles. In the first paper two important results were recorded, namely, (1) the plantar nature of both the dorsal and plantar interossei, and (2) the primary unity of the adductor hallucis and the transversus pedis. In the second paper, disregarding the superficial muscles and relying upon the doctrine of the immutability of the nerve supply of muscles, the author separates these muscles which are supplied by the medial plantar nerve from those innervated by the lateral plantar, and divides the latter into two groups, one of which the contrahentes, lies to the plantar side of the deep branch of the lateral plantar nerve, while the other, formed by the interossei, lies dorsal to the nerve.

In the same year that Ruge's papers appeared Cunningham, **78a,** published the results of his extensive comparative studies of the plantar muscles, furnishing later, **82,** a more detailed account of his observations. Like Ruge, he disregarded the superficial muscles, but, on the other hand, he declined to accept nerve supply as an absolute criterion for muscle homology, and found in what he termed the "intrinsic" muscles, representatives of the same three layers he had already demonstrated, **78,** in the hand. The most superficial to these layers lies dorsal to the tendons of the long flexor and plantar to the deep branch of the lateral plantar nerve; it is termed the plantar layer of adductors

and corresponds to Ruge's contrahentes. The second and third layers lie dorsal to the nerve and together correspond to Ruge's layer of interossei; the more superficial muscles Cunningham termed the intermediate layer of flexores breves and the deeper one the dorsal layer of abductors.

In the urodeles and lacertilia I have shown that three (or four) layers are distinctly recognizable dorsal to the long flexor tendons or their homologue, and for this reason Cunningham's arrangement of the deep muscles is preferable to that of Ruge. His dorsal layer of abductors is in part equivalent to what have been described in the preceding pages of this paper as the intermetatarsales; his intermediate layer is similarly equivalent in general to my flexores breves profundi; while his plantar layer of adductors corresponds to my flexor brevis medius str. profundum. But by the exclusion of the superficial layers—indeed of everything superficial to and connected with the long flexor tendons, both Cunningham and Ruge fall into error in the assignment to their "intrinsic" or deep muscles of certain structures which are derivatives of the superficial layer. There are in the foot two superficial layers of muscles which are just as properly termed intrinsic as are the adductors and interossei, and in what follows I shall recognize the same layers as have been described in the foot of the lower forms, giving special names to certain of the marginal muscles when this seems desirable.

The *flexor brevis superficialis.* In the mammalia studied the flexor brevis superficialis was represented by both the strata described in the lacertilia. In the *superficial stratum* of the lacertilia there was a distinct tendency for the muscle slip for the hallux to separate from the rest of the layer; this becomes more pronounced in the mammals, in which the slip becomes practically an independent muscle. Furthermore, we must include in this layer certain marginal muscles of the foot, which may be termed abductors.

Considering first the main portion of the muscle, it arises in the opossum from the plantar surface of the strong tendon of the flexor fibularis cruris, a short distance above the ankle joint, and partly also from the tendon of the flexor tibialis at about opposite the ankle joint, and is distributed by four slips (Figs. 5 and 6, fbs_s), to the second, third, fourth, and fifth digits, each slip dividing into two tendons, between which passes a tendon of the long flexor. In the cat and mouse the fibers arise from the aponeurosis into which the long flexors insert. The difference, however, is more apparent than real, since, as has already been pointed out, McMurrich, 04, both the aponeurosis and the tendons of the long flexors represent portions of an original plantar aponeurosis.

The well developed slip of the flexor brevis superficialis which passed to the hallux in the lacertilia is represented in the opossum by two closely associated muscles. One of these, which may be termed the *abductor hallucis* (Fig. 5, *ah*), arises from the dorsal surface of the tarsal spur, over the base of the first metatarsal, and is inserted into the first phalanx in close proximity to the medial metatarso-phalangeal sesamoid cartilage; the other, which may be designated the *flexor brevis superficialis hallucis* (Fig. 5, *fbs'*), arises in part from the dorsal surface of the tarsal spur, but more extensively from the sheath which encloses the tendon of the long flexor, the main portion of the flexor brevis superficialis and the medial plantar nerve, and is inserted into the medial metatarso-phalangeal sesamoid cartilage.

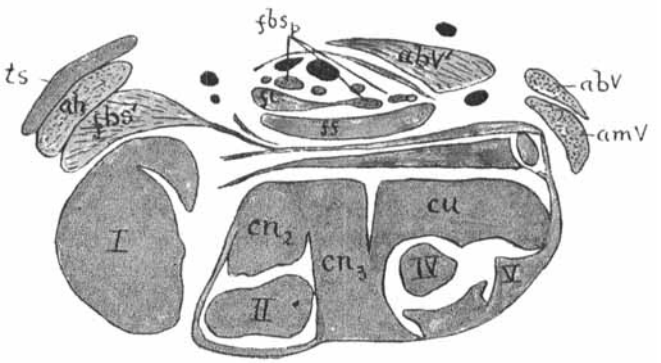


FIG. 5. Transverse section through the junction of tarsus and metatarsus in the opossum. *abV* and *abV'* = abductor quinti digiti; *ah* = abductor hallucis; *amV* = abductor ossis metatarsi quinti digiti; cn_2 and cn_3 = second and third cuneiforms; *cu* = cuboid; *fbs'* = hallucal slip of flexor brevis superficialis; fbs_p = flexor brevis superficialis str. profundum; *ff* = tendon of flexor fibularis; *ft* = tendon of flexor tibialis; *ts* = tarsal spur; *I*, *II*, *IV*, and *V* = metatarsals.

These two muscles, although closely associated, are separated by a distinct sheet of connective tissue, and their fibers have a markedly different direction, so that in sections they are readily distinguishable. Considerable differences of opinion have been expressed as to their significance. Coues, **72**, failed to recognize the abductor as distinct from the more lateral slip, which he describes as a portion of the flexor brevis hallucis; Ruge, **78a**, who fails to recognize two muscles, terming the combination the abductor hallucis; while Cunningham, **82**, who does recognize the abductor, refers it to his dorsal layer (*i. e.*, the intermetatarsal layer), while the flexor superficialis hallucis he assigns as part of the flexor

brevis hallucis to his intermediate layer (*i. e.*, the flexores breves profundi layer). The fact that both muscles are supplied by the medial plantar nerve and their apparent equivalency to the strong hallucal slip of the lacertilian flexor brevis superficialis lead me to regard Cunningham's assignments as incorrect; they are due to the erroneous conception of the intrinsic muscles adopted by Cunningham.

In the mouse, and to a greater extent in the cat, there is a reduction of the hallucal muscles owing to the reduction of the digit. In the mouse a muscle, supplied by the medial plantar nerve, arises from the navicular bone and is directed medially and distally to be inserted into the tibial side of the first phalanx of the hallux. It represents the hallucal slip of the flexor brevis superficialis, and in two out of three individuals studied was a single muscle. In a third individual, however, it had two heads, one from the navicular and the other, much smaller, from the tibial sesamoid bone which Baur, **85**, has identified with the tibiale. The two heads eventually fuse, but it seems not improbable that the smaller one represents the abductor hallucis.

In the cat the only representative of a superficial hallucal flexor seems to be the muscle named scapho-cuneiformis by Reighard and Jennings, **01**. It arises from the navicular bone and from the calcaneo-cuneiform ligament and, in the individual studied, could be distinctly traced to the base of the rudimentary metatarsal. Reighard and Jennings describe it as inserting into the lateral surface of the first cuneiform; the difference may be due to my preparations having been made from an advanced fetus. The muscle is supplied by a branch from the medial plantar nerve.

The fifth digit, in addition to a slip from the main mass of the flexor brevis superficialis, receives certain other superficial muscles which must be assigned to that layer. In the opossum there are three such muscles. One, for which Cunningham's, **82**, name *abductor ossis metatarsi quinti digiti* (Fig. 5, *amV*), may be adopted, has its origin from the lateral surface of the tuberosity of the calcaneus and passes distally, over the quadratus plantæ to be inserted into the lateral surface of the base of the fifth metatarsal. A second muscle (Fig. 5, *abV*), arises from the calcaneus in close proximity to the preceding and over the base of the fifth metatarsal is continued into a slender tendon, which inserts into the lateral surface of the base of the proximal phalanx of the digit; while the third muscle (Figs. 5 and 6, *abV'*), takes its origin from the plantar surface of the sheath enclosing the long flexor tendons and passes distally and laterally to unite with the tendon of the second muscle near its

insertion. These last two muscles, Cunningham, **82**, describes as a two-headed abductor quinti digiti. All three muscles are supplied by branches from the lateral plantar nerve.

Ruge, **78a**, describes the same three muscles, but Coues, **72**, failed to find the abductor ossis metatarsi, the arrangement described by him being similar to that observed by Ruge in *Didelphys cancrivorus*. Furthermore, Coues terms the oblique head of the abductor the flexor brevis minimi digiti, an objectionable term for it on account of its leading to a confusion both with the slip which passes to the minimus from the main mass of the flexor brevis superficialis and with the homologue of the muscle known by the same name in human anatomy (see p. 430). While Cunningham's terminology for the muscles is acceptable, it may be noted that here, as in the case of the abductor hallucis, he is in error in referring them to his dorsal layer.

In the lists which Cunningham, **82**, gives of the muscles of his dorsal layer as they occur in the large number of mammals he studied, it will be noticed that while the three muscles occur in several marsupials, in other forms they are reduced to two and in others to one. When two exist they are a single-headed abductor and an abductor ossis metatarsi; and when but one occurs it may be either an abductor or an abductor ossis metatarsi. The cat belongs to that group of forms in which there are two muscles, an abductor ossis metatarsi (the calcaneo-metatarsalis of Reighard and Jennings, **01**), passing from the side of the tuberosity of the calcaneus to the base of the fifth metatarsal, and an abductor (the abductor medius quinti digiti of Reighard and Jennings), arising from the plantar aponeurosis over the abductor ossis metatarsi and inserting into the lateral metatarso-phalangeal sesamoid bone. The mouse, on the other hand, possesses only an abductor ossis metatarsi. The muscles of both forms are supplied by branches from the lateral plantar nerve.

The *flexor brevis superficialis stratum profundum* is represented in all the mammalia studied by muscle fibers which are distinctly separated from those of the stratum superficiale and take their origin from the plantar surface of the long flexor tendon shortly before it divides into its slips for the digits. In the opossum the muscle forms a practically continuous sheet, covering the entire width of the tendon, and divides distally into four slips (Figs. 5 and 6, fbs_p), one of which passes to each of the tendons of the main mass of the stratum superficiale. In the cat (Fig. 7, fbs_p) and mouse the stratum is represented by only two slips which unite with the superficial tendons for the third and fourth digits. Those occurring in the cat have been described by Reighard and Jen-

nings, 01, as lumbricales, but they cannot properly be regarded as belonging to that group of muscles.

The *flexor brevis medius stratum superficiale.* This layer is represented in the mammals in part by the lumbricales. In the opossum these are four in number (Fig. 6, fbm_s), arising from the tendon of the flexor fibularis just as it divides into the tendons for the four lateral digits. Three of the muscles consequently arise in the angle between the four diverging tendons and the fourth from the tibial side of the tendon to the index. The muscles pass to the tibial side of the base of the proximal phalanx of the second, third, fourth, and fifth digits. In the mouse there are also four lumbricals arising in the angles formed by the split-

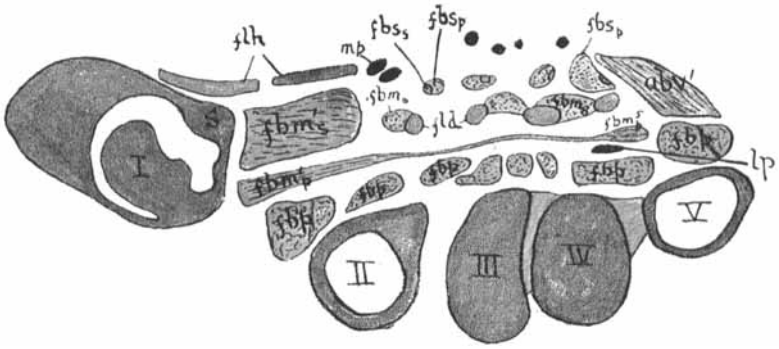


FIG. 6. Transverse section through the foot of the opossum. abV' = abductor quinti digiti; fbm_p = flexor brevis medius str. profundum; fbm_s = flexor brevis medius str. superficiale; fbp = flexor brevis profundus; fbs_p = flexor brevis superficialis str. profundum; fbs_s = flexor brevis superficialis str. superficiale; fld = tendon of flexor longus digitorum; flh = tendon of flexor longus hallucis; lp = lateral plantar nerve; mp = medial plantar nerve; s = metatarso-phalangeal sesamoid cartilage of hallux; I-V = metatarsals.

ting of the long flexor tendon and passing to the same digits as in the opossum, while in the cat there are only three muscles in the group, that for the second digit being lacking.

In the opossum and mouse the muscle to the second digit is supplied by a branch of the medial plantar nerve, while the other three are supplied by the lateral plantar. In the cat all the muscles of the set are supplied by the lateral plantar, the muscle to the second digit being, as stated, wanting.

In the lacertilia a large muscle belonging to the superficial layer of the flexor brevis medius passes to the hallux, and in the opossum what I believe to be the same muscle (Fig. 6, fbm'_s) occurs. It arises in close association with the hallucal portion of the flexor brevis superficialis,

from the medial surface of the sheath enclosing the long flexor tendons, and also from the base of the second metatarsal. It passes distally parallel with the hallucal slip of the flexor brevis superficialis, the long flexor tendon for the hallux lying between the two muscles, and is inserted into the lateral surface of the base of the first phalanx, a sesamoid cartilage being developed in its tendon. It is supplied by the deep branch of the lateral plantar nerve. In the cat and the mouse the muscle does not occur, unless it be represented in the mouse by a few scattered muscle fibers which occur in new born animals between the hallucal slips of the flexor brevis superficialis and the flexor brevis medius str. profundum.

This is the muscle which Coues, **72**, and Cunningham, **82**, describe as the lateral head of the flexor brevis hallucis associating it with the hallucal slip of the flexor brevis superficialis, the latter author referring both slips to his intermediate layer (*i. e.*, the flexor brevis profundus). Ruge, **78a**, on the other hand, regards the muscle as distinct from the flexor brevis superficialis slip and refers it to his layer of contrahentes (*i. e.*, to the flexor brevis medius str. profundum). I shall have occasion to consider this muscle or rather its human equivalent in connection with the human flexor brevis hallucis and shall remark concerning it here only that it occupies a plane ventral (*i. e.*, plantar) to that of the hallucal portion of the flexor brevis medius str. profundum (Fig. 6) and that this fact, together with its innervation from the lateral plantar nerve and the relations of what is apparently the corresponding muscle in the lacertilia, lead me to consider it a portion of the superficial layer of the flexor brevis medius.

The *flexor brevis medius stratum profundum* is formed by what are usually known as the adductors or, as they have been termed by Ruge, **78a**, following Bischoff, **70**, the contrahentes. In the opossum they are four in number. The two muscles which pass respectively to the hallux and minimus (Fig. 6, $fbm_p^{1\,5}$) are large fan-shaped structures which arise from a median tendinous raphe extending from the base of the third metatarsal to the base of the proximal phalanx of the third digit, the fibers converging from this raphe on the one side to the base of the proximal phalanx of the hallux and on the other to the base of the proximal phalanx of the minimus. The other two muscles are almost concealed by those just described, beneath which they lie, taking their origin from the dorsal surface of the tendinous raphe and passing distally to be inserted, the one into the fibular side of the base of the second digit and the other into the tibial side of the base of the fourth digit. All four muscles are supplied by branches from the deep branch of the lateral plantar nerve.

In the mouse the layer is represented by only three muscles, that to the fourth digit being wanting. They arise from the strong fibrous sheath which invests the peroneus longus and insert into the fibular side of the bases of the proximal phalanges of the first and second digits and into the tibial side of the corresponding phalanx of the minimus. In the cat the reduction in number is carried one step farther, in that the muscles pass to only two digits, namely the index and minimus (Fig. 7, $fbm_p^{2\,5}$), but the latter digit receives two slips, one of which is inserted into the tibial side of the base of the proximal phalanx, while the other inserts into the tibial side of the metatarsal near its head and forms what has been termed the *opponens minimi digiti*. In both forms all the muscles are supplied from the lateral plantar nerve.

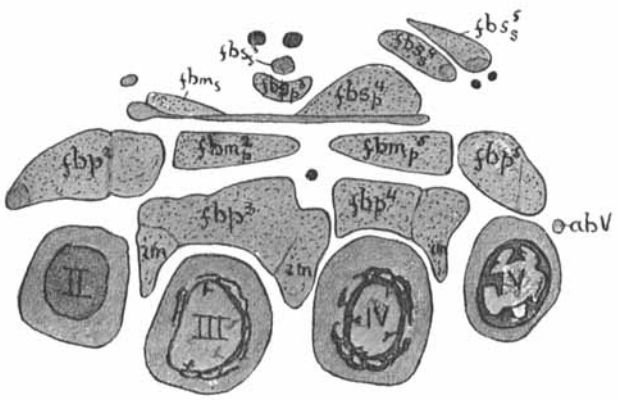


FIG. 7. Transverse section through the foot of the cat. abV = abductor quinti digiti; fbm_p = flexor brevis medius str. profundum; fbm_s = flexor brevis medius str. superficiale; fbp = flexor brevis profundus; fbs_p = flexor brevis superficialis str. profundum; fbs = flexor brevis superficialis, str. superficiale; im = intermetatarsalis; II-V = metatarsal bones.

The *flexores breves profundi* and the *intermetatarsales* are so intimately associated in all the forms studied that they may be considered together. Compared with the lacertilia it is noticeable that the intermetatarsales are represented by muscles, instead of ligaments, and that there is a very different arrangement of the flexores profundi with reference to the various digits. Instead of a general inclination of the slips from the fibular to the tibial side one finds that in the mammalia they are almost directly longitudinal in their course and that certain of them are so fused with the intermetatarsales as to be distinguishable from them only by intervening fibrous bands, in some cases by a more or less pronounced difference in the direction of their fibers and by their more plantar position.

In the opossum there occurs in the interval between the first and second metatarsals a muscle (Fig. 6) which arises from the base of the first metatarsal and passes distally to be inserted into the tibial metatarso-phalangeal sesamoid cartilage of the second digit. In cross sections near its origin the muscle is distinctly seen to be composed of two portions, separated from one another by a tendinous partition, and the fibers on either side of the partition have a distinctly different direction. How far the presence of the partition and the difference in direction may be relied upon as an indication of a fusion of two primarily distinct muscles is uncertain, especially since towards their insertion the two portions fuse so as to be indistinguishable. I am inclined to believe, however, on the basis of comparison with lower forms, that in this case the peculiarities do indicate a fusion and that the muscle really represents a flexor brevis profundus hallucis and an intermetatarsalis I.

Passing fibularly one finds over the second metatarsal two muscles again separated by a tendinous partition and also showing a very different direction of their fibers. These are evidently the flexores breves profundi II and they insert into the two sesamoid bones over the metatarso-phalangeal joint of their digit, the more tibial one coming into relation with the combined flexor profundus I and intermetatarsalis I. Over the third metatarsal the arrangement is more complicated. Proximally one finds two muscle bundles lying side by side and separated by a tendinous partition, but as one passes distally additional fibers, with a slightly different direction, become added upon either side, so that eventually four muscle bundles may be recognized over the bone (Fig. 6). The two lateral ones extend dorsally between the third and the adjacent metatarsals, while the two median ones, which are considerably smaller than the others, are confined to the plantar surface of the metatarsal. Eventually the plantar and lateral muscles of one side of the median line separate from the corresponding bundles of the other side, so that two pairs of muscles become recognizable which insert into the tibial and fibular metatarso-phalangeal sesamoid cartilages of the third digit. The two median bundles I take to be the flexores breves profundi III, while the lateral bundles are the intermetatarsales II and III.

In the case of the fourth digit a determination of the arrangement is somewhat difficult, but just as muscles pass from the hallux to the second digit, so muscles from the minimus pass to the fourth digit, and it will therefore be convenient to consider the two digits together. In sections taken near the bases of the metatarsals two indistinctly separated bundles are to be seen over the third intermetatarsal space and a third one lies

partly over the fourth space and partly over the tibial border of the fifth metatarsal. The two more tibial bundles, which probably represent but a single muscle, take their origin from the sheath of the peroneus longus tendon, while the fibular one seems rather to come from the base of the fifth metatarsal. Additional fibers are added to the fibular muscle from an origin on the tibial surface of the fifth metatarsal. These fibers are easily recognizable from their decidedly oblique direction, and it seems probable that they represent a distinct muscle, namely, the intermetatarsalis IV. Eventually the two more tibial bundles insert into the tibial metatarso-phalangeal sesamoid, while the fibular muscle, together with the intermetatarsalis IV terminates on the fibular sesamoid.

Over the plantar surface of the fifth metatarsal two muscles, which arise from the sheath of the peroneus longus tendon, occur. They are separated by a distinct tendinous partition, and, as they are traced distally, separate to be inserted into the two sesamoid cartilages of the metatarso-phalangeal joint.

Finally, I find beneath the hallucal slip of the flexor brevis medius str. superficiale and between that muscle and the conjoined flexor brevis profundus I and intermetatarsalis I a small bundle of muscle fibers, which may possibly represent an additional slip of the flexor brevis profundus layer. It is so rudimentary, however, that it is impossible to assign to it an origin or an insertion; it is distinctly separate from the combined intermetatarsal and flexor profundus I and its fibers have a direction almost at right angles to those of the flexor brevis medius str. superficiale above it. No equivalent of the muscle occurs either in the mouse or the cat, in both of which the hallux is considerably reduced as compared with that of the opossum.

In the mouse the arrangement of the flexor brevis profundus is very similar to that of the opossum, except that the various slips are much more intimately fused and consequently much more difficult to recognize. Over the base of the first metatarsal there is a mass of muscular tissue in which no indications of a composite nature could be detected. It passes to the tibial metatarso-phalangeal sesamoid of the second digit and seems therefore to correspond to the combined intermetatarsal and flexor profundus I of the opossum. Over the second metatarsal are two muscle slips separated only by a tendinous partition. They both insert into the fibular metatarso-phalangeal sesamoid of the digit, the arrangement differing in this respect from that of the opossum. The muscles of the third digit are arranged as in the opossum, though much more extensively fused. The mass which they form curves dorsally around each surface of the metatarsal and the lateral parts of the crescent so formed

are separated from the central portion by a tendinous partition. The entire mass eventually separates into two portions which insert respectively into the tibial and fibular metatarso-phalangeal sesamoids of the digit and seem to represent the two flexores breves profundi III together with the intermetatarsales II and III. In the fourth digit also there is much fusion of slips. A relatively large bundle passes from the fifth metatarsal to the fibular sesamoid of the digit, representing the fourth intermetatarsal, but whether it also includes a portion of the flexor profundus IV remains uncertain. The main mass of the flexor profundus V passes to the fibular sesamoid of its digit, but it gives off a slip which unites with the adductor slip for the digit and appears to represent the tibial portion of the flexor profundus V.

In the cat, owing to the reduction of the hallux, no representatives of the flexor brevis profundus I nor of the intermetatarsalis I exist. Otherwise the arrangement resembles closely that of the mouse. In the second digit only the two slips of the flexor brevis profundus (Fig. 7, *fbp*^{2}), occur, and these pass to the two metatarso-phalangeal sesamoids of the digit. Both slips of the flexor profundus V are well developed.

A comparison of the mammalian plantar muscles as described above with those of the lacertilia may be made as follows:

Lacertilia.	*Mammalia.*
Flexor brevis superficialis str. superficiale.	Flexor brevis superficialis str. superficiale. Abductor hallucis.
Abductor V.	Abductor ossis metatarsi V. Abductor V.
Flexor brevis superficialis str. profundum.	Flexor brevis superficialis str. profundum.
Flexor brevis medius str. superficiale.	Lumbricales. Hallucal slip of flexor brevis medius str. superficiale.
Flexor brevis medius str. profundum.	Adductors.
Flexor brevis profundus intermetatarsales.	Interossei.

IV. The Plantar Muscles in Man.

It remains now to consider the plantar muscles of the human foot in the light of the conclusions reached in the preceding pages, and in doing so the nomenclature employed in human anatomy may be followed.

The *flexor brevis digitorum* presents little difficulty. It is clearly homologous with the main mass of the flexor brevis superficialis str. superficiale, and certain of the peculiarities it presents are explicable on the basis of the phylogenetic history of that muscle. Thus the frequent origin of the slip for the minimus from the plantar surface of the tendon of the long flexor is clearly a reminiscence of the significance of the tendon as a portion of the plantar aponeurosis, and it merely obscures the true relationship to regard the slip having such an origin as something distinct from what is usually regarded as the normal slip.

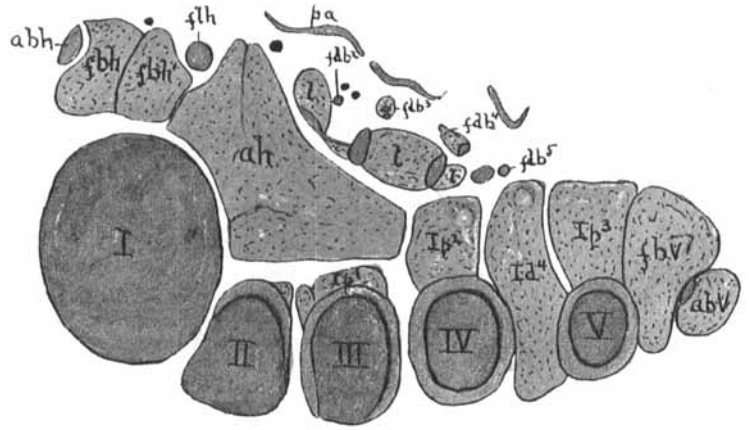


FIG. 8. Transverse section through the foot of a human fetus of 9 cm. *abh* = abductor hallucis; *abV* = abductor quinti digiti; *ah* = adductor hallucis; *fbh* and *fbh'* = medial and lateral heads of flexor brevis hallucis; *fbV* = flexor brevis quinti digiti; *fdb* = flexor brevis digitorum; *flh* = tendon of flexor longus hallucis; *Id* = dorsal interosseus; *Ip* = plantar interosseus; *l* = lumbricalis; *I-V* = metatarsal bones.

The stratum profundum of the flexor brevis superficialis is so evident a constituent of the plantar musculature both in the lacertilia and mammalia, that its occurrence in the human foot seemed more than likely. An examination of sections of a foot from a fetus of 9 cm. revealed what I take to be its representative. Before the flexor brevis begins to divide into its terminal slip, tendons appear imbedded in the center of the muscle mass, and of these, in the foot in question, there were four, notwithstanding the fact that the tendon for the fifth digit, as is so often the case, was derived from the tendon of the long flexor. The muscle fibers surrounding the most medial tendon gradually separated from the rest to form the slip to the second digit, and those sur-

rounding the most lateral tendon similarly separate to form the slip for the fourth digit. The fibers surrounding the two remaining tendons arrange themselves in two bundles, one lying immediately above the other, which, with their tendons, eventually unite to form the slip for the third digit (Fig. 8, *fdb* ^{3}). I take the more dorsal of the two bundles to represent the flexor brevis superficialis str. profundum; the slip to the third digit being the only portion of it persisting.

The flexor brevis digitorum has been taken to be the exact equivalent of the flexor sublimis digitorum of the arm, and on that basis has been regarded as primarily a crural muscle which has secondarily descended into the foot. If the homologies traced in the preceding pages be correct, there are no grounds for assuming a descent of the muscle from the crural region. It is from the beginning an intrinsic muscle of the foot.

The *abductor hallucis* (Fig. 8, *abh*), and *abductor quinti digiti* (*abV*) likewise require but brief consideration. There seems no doubt but that they are equivalents of the correspondingly named muscles in the lower mammals and are therefore derivatives of the primary superficial plantar layer.

In the case of the *flexor brevis hallucis*, however, the matter is more complicated. The conception of it as a single muscle, so constantly found in text-books, probably dates back to Albinus, **34**, by whom it was thus described, and is sufficiently satisfactory to the anatomist who studies muscles through physiological spectacles. So soon as a morphological basis is sought for the classification of muscles, this one loses its simplicity. Cruveilhier, **77**, reserves the name flexor hallucis brevis for the more medial portion of the muscle, regarding the lateral portion as a part of the adductor, and in this he has been followed by Flemming, **87**, and Gegenbaur, **92**, as well as by Ruge, **78a**, in his comparative studies. Cunningham, **82**, however, regards the two heads as representing the hallucal portions of his intermediate layer, the layer to which the plantar interossei belong and which, in typical cases consists of a pair of muscles for each digit.

From my own studies I am compelled to dissent from the interpretation which Cunningham gives to the muscle and to side with Cruveilhier and Flemming in regarding it as composed of two distinct portions which belong to different layers. My reasons for this belief are based largely upon the results obtained from the studies recorded in the preceding pages, which seem to point to the morphological independence of the two heads of the muscle. But confirmation of this view is

afforded by the frequency with which, throughout the mammalia, as described by Cunningham, 82, the lateral head disappears, leaving the medial head as the sole representative of the muscle, and also by the fact pointed out by Ruge, 78, and which I can confirm, that the tendon of the flexor longus hallucis throughout the greater part of its relationship with the muscle rests *upon* and not to the medial side of the lateral head (Fig. 8). For if the medial head, as there is every reason to believe, is a portion of the flexor brevis superficialis, then a muscle lying dorsal to the long flexor tendon cannot be regarded as belonging to the same layer that it does.

In accepting this view I differ, however, from Cruveilhier and Flemming as to the morphological significance of the lateral head. The medial head (Fig. 8, *fbh*), as just stated, is undoubtedly a portion of the flexor brevis superficialis, but instead of referring the lateral head to the adductor layer, *i. e.*, to the flexor brevis medius str. profundum I would assign it to the flexor brevis medius str. superficiale, *i. e.*, to the layer from which the lumbricals are derived. This conclusion is based upon the comparative series shown by the lacertilia, the opossum and man, in all of which the same muscle is recognizable and in the first named group is evidently a portion of the flexor brevis medius str. superficiale. The muscle, then, may be regarded as the lumbrical of the hallux.[1]

Flemming, 87, attaches considerable importance to the nerve supply of the lateral head being from the lateral plantar, while that of the medial head is from the medial plantar. In so describing the supply he follows the account given in most of the continental anatomies. Cunningham, 87, however, takes exception to this, stating that not only in the human foot but in those of all the mammals he studied, with one exception, the supply of both heads was from the medial plantar and my own observations on one adult and two fetal human feet give the same result. The nerve supply, however, cannot be taken as a criterion in this matter, especially if the lateral head of the muscle be regarded as belonging to the lumbrical layer; for the lumbrical of the second digit is normally supplied by the medial plantar and, furthermore,

[1] It seems probable that the corresponding medial head of the flexor brevis pollicis has the same significance. In an earlier paper, 03, I referred it to the adductor set, but the arrangement in the foot throws new light upon the question. Young, 79, has identified in the Rock kangaroo a muscle, distinct from the flexor brevis pollicis, as a pollical lumbrical, but its isolated occurrence makes it questionable whether it can properly be regarded as such, rather than as an anomaly.

Brooks', 87, observations on the innervation of the lumbricals show that a confusion of the constituents of the two plantar nerves may occur, similar to that which may obtain between the ulnar and median in the hand.

A word concerning the origin of the flexor brevis hallucis may not be out of place. In certain English text-books, Morris, 3d Ed., and Cunningham for example, it is stated to arise in part from the cuboid bone. This may possibly represent its physiological origin, but it certainly gives a very incorrect idea of its morphological relations. It is very clear from the study of fetal preparations that the muscle has its origin primarily from the first cuneiform and secondarily from a dense lamella of connective tissue which forms a sheath for the tendon of the flexor longus hallucis and proximally is continuous with a dense fascia covering the tendon of the peroneus longus and also with a strong ligament which extends from the navicular to the third cuneiform. It is through its connection with the peroneal sheath that the muscle reaches

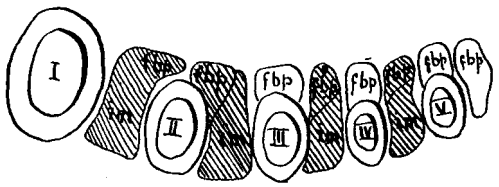


FIG. 9. Diagram to show the constitution of the interossei in the human foot. *fbp* = flexor brevis profundus; *im* = intermetatarsal; *I-V* = metatarsal bones.

the cuboid, but it is a mistake to suppose that this bone forms part of its true morphological origin.

The *lumbricales* are, as in the hand, clearly representatives of the flexor brevis medius stratum superficiale of the lower forms. And, similarly, both portions of the *adductor hallucis* are portions of the flexor brevis medius str. profundum, Ruge's, 78, observations on the development of the caput transversum, apart from comparative studies, showing its embryological relations to the caput obliquum. Meckel's, 32, identification of the caput transversum as a lumbrical is unsupported by either embryological or comparative evidence.

The *interossei* resemble closely those of the hand, whose phylogeny I have already, 03, considered. They represent a combination of the flexores breves profundi and the intermetatarsales, and their constitution may be understood from the accompanying diagram (Fig. 9). Considering first the three central digits; each possesses two slips of the flexor brevis profundus. Both slips of the second digit unite with

the first and second intermetatarsals forming the first and second dorsal interossei, which insert into the proximal phalanx of that digit. The medial slip of the third digit forms the first plantar interosseous, while the lateral slip unites with the third intermetatarsal to form the third dorsal interosseous; the medial slip of the fourth digit forms the second plantar interosseous, while its lateral slip unites with the fourth intermetatarsal to form the fourth dorsal interosseous.

In the fifth digit both slips of the flexor brevis profundus retain their separate individualities, the medial one forming the third plantar interosseous, while the lateral one is the muscle known as the *flexor brevis quinti digiti*.

I have found nothing in my preparations that I could regard as a hallucal flexor profundus, although on comparative grounds such muscles should be expected. There is a probability, judging from what occurs in the opossum, that the first dorsal interosseous contains an element representing a hallucal flexor profundus, just as is the case in the hand, but of this I have not been able to obtain definite evidence. The so-called interosseous primus volaris of Wood, **67**, does not appear to belong to the interosseous set of muscles; its position towards the medial surface of the hallux and its relations with the abductor are opposed to such an assignment of it. It seems rather to be a slip of the flexor brevis hallucis which has retained its primary origin from the first cuneiform, instead of shifting to the plantar aponeuroses with the rest of the muscle. So too the portion of the oblique head of the adductor hallucis, which Henle, **71**, regards as the equivalent of the interosseus primus volaris of the hand, is rather to be regarded as a portion of the flexor brevis medius str. profundum.

In the preparations I have studied there is no distinct *opponens hallucis,* nor is the *opponens quinti digiti* represented as a distinct muscle. I am unable to determine the significance of the former muscle, whether it be a derivative of the adductor or the flexor brevis hallucis, but viewing the possibilities as they appear in my preparations I am inclined to look to the adductor for its origin (cf. Brooks, **87**). In a fetus of 9 cm. I find that a portion of the flexor brevis quinti digiti inserts upon the upper part of the fifth metatarsal, a fact which seems to point to the derivation of the opponens quinti digiti from the flexor brevis. In this opinion I am in accord with Ruge, **78**. It is certainly a very different structure from the so-called opponens quinti digiti of the cat (see p. 426).

Many difficulties are encountered in the working out of the detailed

homologies of the human plantar muscles, and the final determination of some of them requires more extensive material than has been at my disposal. But one point is, I believe, conclusively settled, and that is the arrangement of the human plantar muscles in a series of layers which are homologous with those found in both the reptilia and the amphibia. This point established gives a broader basis for comparison than the study of individual muscles can afford, and, it is to be hoped, will lead to a full understanding of the morphology of the plantar muscles. The identifications described above may be represented in tabular form as follows:

Lacertilia.	*Man.*
Flexor brevis superficialis str. superficiale.	Flexor brevis digitorum. Medial head of flexor brevis hallucis. Abductor hallucis. Abductor quinti digiti.
Flexor brevis superficialis str. profundum.	Portion of slip of flexor brevis digitorum to 3d digit.
Flexor brevis medius str. superficiale.	Lateral head of flexor brevis hallucis. Lumbricales.
Flexor brevis medius str. profundum.	Adductor hallucis. Opponens hallucis?
Flexor brevis profundus. Intermetatarsales.	Flexor brevis quinti digiti. Opponens quinti digiti. Interossei.

Summary.

1. The plantar muscles in the urodele amphibia are arranged in four layers and are all intrinsic to the foot, arising either from the plantar aponeurosis or from the bones of the foot.

2. In the lacertilia the number of layers becomes increased to six by the division of the superficial and middle layers so that in each of them there is a stratum superficiale and a stratum profundum.

3. The plantar aponeurosis has also differentiated into two layers, the deeper of which forms the plantar portion of the tendons of the long flexors.

4. In the mammalia the six layers found in the lacertilia persist.

5. The marginal portions of the flexor brevis superficialis early separate from the main mass of the muscle and form the abductors of the hallux and minimus.

6. The mammalian flexor brevis hallucis is a compound muscle; its medial head is derived from the flexor brevis superficialis and its lateral head from the flexor brevis medius stratum superficiale.

7. The flexor brevis superficialis stratum profundum is represented in the human foot by a muscle bundle and tendon which unites with the slip of the flexor brevis digitorum passing to the third digit.

8. The flexor brevis digitorum is not a crural muscle which has secondarily descended into the planta. It is from the beginning an intrinsic muscle of the foot.

9. The flexor brevis quinti digiti is not equivalent to any portion of the flexor brevis hallucis, but is a portion of the flexor brevis profundus layer.

10. The oblique and transverse heads of the adductor pollicis are primarily parts of a single muscle and are portions of the flexor brevis medius stratum profundum.

11. The opponens hallucis is probably a derivative of the oblique head of the adductor hallucis; the opponens quinti digiti is a portion of the flexor brevis quinti digiti and therefore a portion of the flexor brevis profundus.

12. The dorsal interossei are formed by the fusion of portions of the flexor brevis profundus with the intermetatarsales, the plantar interossei being formed by the remaining portions of the flexor brevis profundus.

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January 11, 1907.

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