**The intrinsic muscles of the mammalian foot / by D.J. Cunningham.**

Journal of Anatomy and Physiology.

# THE INTRINSIC MUSCLES OF THE MAMMALIAN FOOT.

By D. J. Cunningham, M.D., *Senior Demonstrator of Anatomy, University of Edinburgh.*[1] (Plate I.)

In a paper which recently appeared in this *Journal*,[2] I called attention to the fact that the intrinsic muscles of the manus of certain of the Marsupialia might be considered to consist of three groups—*(a)* a palmar group of adductors, *(b)* an intermediate group of flexores breves, and *(c)* a dorsal group of abductors, according to the plane which they occupy as we dissect from the palmar to the dorsal aspect of the hand. Each digit is furnished with three muscles, each of which exercises its own independent action upon it. It derives an adductor from the palmar layer, an abductor from the dorsal layer, and a flexor brevis from the intermediate layer. The medius is an exception to this rule, inasmuch as two of its muscles belong to the dorsal layer.

In making inquiry into the arrangement of the corresponding muscles of the pes, I have extended my investigations over a much wider field than in the case of the manus. Through the kindness of Professor Turner, who placed the stores of the Anatomical Museum of this University at my disposal, I have been

[1] Incorporated with this paper is a description of the intrinsic muscles of the pes of the Cuscus and Thylacine. This is a portion of the Memoir upon the Anatomy of the Marsupialia which I am preparing for the Reports of the "Challenger" Expedition, and is published by permission of the Lords Commissioners of the Treasury.

[2] "Intrinsic Muscles of the Hand of the Thylacine, Cuscus, and Phascogale," *Journ. of Anat. and Phys.* vol. xii.

able to examine a large number of different kinds of mammalian feet, and in this way to arrive at certain conclusions regarding the general disposition of the muscles in question.[1]

I will begin by stating briefly what these conclusions are, and then bring forward the facts upon which they are based.

I. That the typical arrangement of the intrinsic muscles of the pes is the same as in the hand, and that this arrangement is seen to best advantage in the feet of certain of the Marsupialia. In these animals the muscles are disposed in three layers: (1) a *plantar layer* of adductors; (2) an *intermediate layer* of flexores breves; (3) a *dorsal layer* of abductors.[2] Deviations from the typical arrangement of these muscles may take place either by suppression or by fusion of certain of the elements of the different layers. Fusion of the constituents of the intermediate and dorsal layers is extremely common, whilst fusion between the plantar and intermediate muscles is a very rare occurrence.[3]

II. The presence of an opponens muscle is not accounted for in the foregoing disposition of the intrinsic muscles. When present it may be regarded as being derived from one of two sources. Most commonly it is a development from the flexor brevis, but it may also proceed, as in many of the carnivora, from the plantar layer, and thus be associated with the adductors.

III. The last point which I am anxious to prove is, that in many animals the relation of the intrinsic muscles to the metatarsal bones, both as regards their origin and position, corresponds with transitory conditions in the foot of the human embryo.

[1] The term *intrinsic* does not include the extensor brevis digitorum, the flexor brevis digitorum, the accessorius, nor the lumbricals.

[2] The abductors and adductors do not act with reference to a line drawn through the second digit, as in the human foot, but with reference to one drawn through the medius. The only exception to this rule that I have met with in my dissections is the Cuscus, which in this respect resembles man.

[3] Professor Humphry, in his "Memoir upon the Myology of the Orycteropus Capensis" (*Journ. of Anat. and Phys.* May 1868), alludes in a footnote to this typical arrangement, and he singles out the rabbit as affording a good example. In this animal, however, the dorsal and intermediate muscles have undergone partial fusion, and it does not exhibit the disposition so well as the marsupial hand or foot.

I. Let us take up the first of these generalizations, and examine the facts upon which it is founded. We will begin with the Thylacine, a carnivorous marsupial, in which the pes closely resembles that of the dog. The hallux is quite rudimentary, but in connection with the remaining four digits the typical disposition of the intrinsic muscles in three layers is very manifest.

*The Plantar Layer* consists of three muscles, which have as their function the adduction of the toes towards a line drawn through the medius. They are: (1) the adductor indicis; (2) the adductor annularis; (3) the adductor minimi digiti. They all arise in the middle line of the foot from the fibrous structures at the base of the metatarsus, and they diverge from each other so as to reach their respective points of insertion.

*The Intermediate Layer.*—The muscles composing this layer are four in number, and are placed one upon the plantar surface of each metatarsal bone; but further, each muscle consists of two slips which may arise separately or by a common origin from the base of the metatarsal bone with which it is associated. At the root of the toe the two slips embrace the base of the proximal phalanx, and are inserted one into each sesamoid bone, and sometimes also into the extensor tendon as well.

These muscles, then, are true flexores breves when the two slips act in unison. When they act independently of each other, however, they will exercise an abducting or adducting influence according to the slip employed.

*The Dorsal Layer* includes the four dorsal interossei, the abductor minimi digiti, and the abductor ossis metatarsi minimi digiti.

The dorsal interossei cannot be properly studied unless we throw forward both the plantar and intermediate muscles. They are then seen to be prismatic, one-headed muscles, lying in the interosseous spaces, but only reaching for a short distance upwards between the bones; indeed, they are more plantar than dorsal in their relation to the metatarsus. They spring from the bases of the metatarsal bones, and are inserted so as to abduct the toes from a line drawn through the medius. They correspond, therefore, in their insertions with the same muscles in the human hand.

But with this group of muscles we also place the abductor

minimi digiti and the abductor ossis metatarsi minimi digiti, both of which are present in the foot of the Thylacine.

The *abductor minimi digiti* arises from the outer aspect of the tuberosity of the os calcis, and soon ending in a long, slender tendon, it is inserted into the fibular side of the base of the proximal phalanx of the minimus.

The *abductor ossis metatarsi minimi digiti* is more strongly marked than the preceding muscle, and has the usual insertion into the base of the fifth metatarsal bone.

In the Cuscus—one of the phalangers—the position of the hallux at right angles to the long axis of the foot, so as to oppose the other toes, somewhat disconcerts the typical arrangement of the muscles in so far as this digit is concerned. Still, sufficient indications remain to justify the conclusion that its three muscles, viz., the abductor, flexor brevis, and abductor, belong one to each of the three layers that we have laid down as typical.

The *plantar layer* consists of three muscles, viz.: (1) adductor hallucis; (2) adductor minimi digiti; (3) adductor annularis.

The adducting muscles of both manus and pes in all animals show a strong tendency to place themselves obliquely, or even at right angles, to the digit upon which they operate. In this manner they obtain a more powerful adducting influence. In the Thylacine the muscles of both hand and foot seek the middle line for their origin, and from this they radiate to their insertions. Again, in the human foot we see the transversus pedis placing itself at right angles, and the adductor hallucis obliquely, in relation to the great toe. But the most striking examples are to be seen in the hand, and more especially in the foot, of the Cuscus. In the hand the adductors arise from a median fibrous raphe placed over the middle metacarpal bone. In the foot adduction is effected towards a line drawn through the index, and the raphe is placed over the metatarsal bone which corresponds to this digit.

There is no adductor of the medius in the Cuscus, because this digit and the index are enclosed within the same covering of skin, and they have therefore no independent power of movement.

*Adductor hallucis* is the most powerful of the three muscles of

the hallux, and at the same time it is the most complex in its arrangement. It has a double origin—(*a*) from the base of the metatarsal bone of the index and from the tibial side of the proximal half of the fibrous raphe ; (*b*) by a few fibres from the aponeurosis which clothes the dorsal aspect of the first dorsal interosseous muscle. The fleshy fibres soon arrange themselves into three slips which we may distinguish by the terms *plantar*, *intermediate*, and *dorsal*, and by these it is inserted. The plantar slip is attached to the outer of the two sesamoid bones along with the outer head of the flexor brevis hallucis. The intermediate slip ends in a long delicate tendon, and is inserted by this into the fibular side of the minute distal phalanx, and the dorsal portion ends in the extensor tendon.

The *adductor minimi digiti* arises by a wide origin not only from the greater extent of the fibular margin of the raphe, but also from the ligamentous structures at the base of the metatarsus. From this its fibres converge, and it is inserted into the tibial side of the base of the proximal phalanx of the minimus.

The *adductor annularis* is small in comparison with the preceding muscle, but it has the same triangular shape, and it is placed at right angles to the toe upon which it acts. It arises from the fibular border of the distal portion of the raphe, and also from the base of the first phalanx of the index. Crossing the base of the medius, it is inserted into the tibial side of the base of the proximal phalanx of the annularis.

The line towards which these muscles adduct the digits is manifestly one drawn through the index; and this, whilst it corresponds with the human foot, is an exception to the general rule that abduction and adduction are effected with reference to a line drawn through the medius.

*The Intermediate Layer.*—The *flexores breves.*—There are five muscles composing this layer, one to each toe, and they correspond with the same muscles in the Thylacine. Each muscle consists of two slips, and these are inserted one into each sesamoid bone at the base of the digit with which they are associated.

The *flexor brevis hallucis* is one of this group, but owing to the position of the hallux it is somewhat separated from its neigh-

bours. It arises by a single tendinous origin from the under surface of the scaphoid, and dividing into two heads it is inserted by these into the sesamoid bones at the base of the proximal phalanx of the hallux. The tibial insertion is associated with that of the abductor hallucis, and the fibular with that of the plantar part of the adductor hallucis.

The *Dorsal Layer.*—This group includes—(1) abductor hallucis; (2) abductor minimi digiti; (3) abductor ossis metatarsi minimi digiti; (4) the dorsal interossei.

The *abductor hallucis* is a strong muscle which arises from the cartilage of the sole and from a sesamoid bone which glides upon the plantar surface of the scaphoid. Its chief insertion is by fleshy fibres into the tibial sesamoid bone of the hallux, but it is also prolonged onwards by a slender tendon to the distal phalanx, to the tibial side of which it is fixed.

*Abductor minimi digiti* and *abductor ossis metatarsi* should be associated together, as the latter is evidently a development from the first. They both arise from the outer aspect of the os calcis, and they have the usual insertions.

The *dorsal interossei* are placed more in the sole of the foot than the corresponding muscles in the hand. They are one-headed, and show a tendency to fuse with the intermediate flexores breves.

The *first* or *abductor indicis* is the most powerful of the series, and is the only one which has an abducting action. It arises from the internal cuneiform bone, and is inserted into the tibial side of the base of the proximal phalanx of the index and also into the extensor tendon. The index and medius, as we have already seen, have no independent power of movement, and this muscle therefore acts upon both digits. The *second* is either absent or completely amalgamated with the inner head of the flexor brevis of the medius. The reason of this is obvious. The index and medius are enclosed within the same integumental covering, and can only move together. The *third* arises from the ligamentous structures at the base of the metatarsus and ends in a strong tendon which splits into two slips. These diverge from each other, and are inserted one into the fibular side of the base of the proximal phalanx of the medius, and the other into the tibial face of the base of the corresponding phalanx of the

annularis. The *fourth* is attached in precisely the same manner to the adjacent sides of the annularis and minimus.

The two latter muscles, then, can exercise no abducting influence whatever upon the medius and annularis. They can only act so as to approximate the digits into which they are inserted. Associated, however, with the third dorsal interosseous muscle is a small muscular slip lying upon its dorsal aspect and inserted so as to be capable of abducting the medius.

*Opponens minimi digiti* is a strong quadrate muscle placed obliquely in the foot. It arises from the outer margin of the plantar cartilage, and is inserted into the whole length of the fibular margin of the metatarsal bone, and also by a few fibres into the outer aspect of the base of the first phalanx of the minimus.

Of the carnivora I have examined the feet of the domestic dog, the dingo, the cat, the puma, the leopard, the lion, the otter, and the badger. In the two last the foot is pentadactylous, whilst in the others it is tetradactylous—the hallux being rudimentary.

Let us in the first instance direct our attention to the tetradactylous carnivora. In these the metatarsal bones are placed in such close apposition that the intrinsic muscles of the pes are situated almost entirely upon the plantar aspect of the metatarsus. In the dog (fig. 5), indeed, it is with difficulty that the point of a knife can be introduced into the interosseous spaces. In the cat, puma, leopard (fig. 6), and lion, whilst the bones are in actual contact towards the tarsus yet they open out towards their phalangeal extremities, and in the narrow eliptical spaces thus formed, the thin, sharp edges of the dorsal interossei may be seen reaching half-way up the interosseous spaces.

Owing to the crowding of the muscles into the sole, the clear definition between the three typical layers is to a great extent lost. None of the muscles are suppressed, but fusion has taken place between several which we have hitherto seen as separate and distinct factors.

*Plantar Layer.*—In all cases the adducting muscles remain as a distinct plantar layer, and they are arranged so as to adduct towards a line drawn through the medius. Generally they a

two in number, viz.: (1) adductor minimi digiti (fig. 2, *a.m.*); (2) adductor indicis (fig. 2, *a.i.*). Occasionally a third is to be found in the dog—an adductor annularis; but this is feebly developed, and always more or less fused with the tibial head of the flexor brevis of that toe. This seems to indicate that in the other animals this muscle is lost not by suppression but by fusion.

Associated with the plantar layer is the opponens minimi digiti (fig. 2, *o.m.*). It is a narrow band of fibres which arises in common with the adductor minimi digiti, and is inserted into the plantar face of the distal third of the shaft of the fifth metatarsal bone.

*Dorsal and Intermediate Layers* (fig. 2).—It is in the dorsal and intermediate layers of muscles that we find the greatest deviation from our type. The flexores breves ($f.^2$ to $f.^5$) and dorsal interossei ($d.^1$ to $d.^4$) owing to the more or less complete obliteration of the interosseous spaces have undergone a partial amalgamation; still there are traces left of a character sufficiently patent to enable the dissector to determine the complex nature of the muscles with which he has to deal. As a general rule, the fusion is complete towards the middle of the metatarsal bone, whilst towards the origin and insertion of the muscles more or less perfect separation can be effected. The mode of insertion of these muscles cannot be regarded as affording a true means by which they can be distinguished from each other. The dorsal interossei, it is true, are invariably inserted into the extensor tendon; but on the other hand, the flexores breves are not in all cases inserted into the sesamoid bones alone. One of the two slips is frequently inserted into the extensor tendon as well.

The fused flexores breves and dorsal interossei constitute a series of muscles which are frequently described as being bicipital, whilst in reality they are tricipital, and in the case of the medius quadricipital.

The dorsal interossei are disposed so as to abduct the toes from a line drawn through the medius. In no case do they arise from the shafts of the metatarsal bones.

It is interesting to trace the different degrees of fusion which exist between the outer head of the flexor brevis minimi digiti

and the abductor minimi digiti in the different animals. In the dog the fusion is complete, and there is little or no trace of an abductor to be found; in the lion the abductor arises from the os calcis, and constitutes a separate muscle as far as the base of the fifth metatarsal bone, but here it becomes partially amalgamated with the outer head of the flexor brevis; in the puma, cat, and leopard (fig. 2, *ab.*), the abductor remains distinct throughout.

Passing now to the pentadactylous carnivora, we find that the otter (fig. 1) and badger in the disposition of the intrinsic muscles of the pes approach very closely to the typical arrangement. The muscles are all placed in the sole, but still they remain separated from each other, and the three layers can be distinguished without any difficulty. The plantigrade character of a foot has apparently no effect in regulating the relation which exists between the intrinsic muscles and the metatarsus. In the badger the plantar position of these muscles is quite as well marked as it is in the otter and other digitigrade carnivora.

The squirrel, hedgehog, and rabbit closely resemble the tetradactylous carnivora in the general arrangement of their intrinsic pedal muscles. The adductors constitute a distinct plantar layer, whilst the flexores breves and dorsal interossei are more or less completely fused. In the course of my dissections, however, I have met with two very aberrant forms which require a more extended notice. I refer to the Dasypus sexcinctus (fig. 3) and the Bathyergus capensis (fig. 4).

The foot of the former (fig. 3) is of peculiar interest from the fact that, except in the case of the hallux and minimus, there is a complete suppression of the intermediate flexores and the dorsal interossei. The plantar adducting muscles, however, are well represented. They are four in number, viz.: (1) adductor hallucis (*a.h.*); (2) adductor minimi digiti (*a.m.*); (3) adductor indicis (*a.i.*); (4) adductor annularis (*a.a.*). They adduct the toes towards a line drawn through the medius. Only two members of the intermediate group are to be found, viz., the flexor brevis hallucis (*f.*$^{1}$*t. f.*$^{1}$*f.*) and the flexor brevis minimi digiti (*f.*$^{5}$). The former is well developed, and has the usual bicipital character, although the tibial head is to a

certain extent fused with the abductor hallucis (*ab.h.*). The flexor brevis minimi digiti (*f.*[5]) is an extremely minute and single slip of muscular fibres, and can have little or no action upon the digit into which it is inserted. The dorsal group is composed of three muscles, viz.: the abductor hallucis (*ab.h.*), the abductor minimi digiti (*ab.*), and the abductor ossis metatarsi minimi digiti (*a.o.*).

The *abductor hallucis*, as we have seen, is to a certain extent fused with the tibial head of the flexor brevis. They soon separate, however, and the abductor is inserted by a long narrow tendon into the tibial side of the ungual phalanx of the hallux.

The *abductor minimi digiti* and *abductor ossis metatarsi* arise from the os calcis. The former is inserted by a long tendon into the fibular side of the distal phalanx of the minimus, whilst the latter is inserted into the base of the metatarsal bone of the same digit.

But the most remarkable feature in the pes of the Dasypus sexcinctus is that the place of the absent muscles is taken by fibrous bands (*f.b.*) which have precisely the same disposition and connections as those muscles of which they are the substitutes.[1]

A more extended account of the myology of the pes of this animal may be found (26th vol. *Lin. Trans.*) in an able memoir by Mr J. C. Galton. I cannot agree with Mr Galton, however, in the terms which he has applied to certain of the muscles. He looks upon the muscle which stretches between the os calcis and the base of the fifth metatarsal bone as being the abductor minimi digiti, and the muscle passing from the os calcis to the ungual phalanx of the minimus as being the flexor brevis. There can be little doubt that these mucles represent those after which I have named them, viz., the abductor ossis metatarsi and the abductor minimi digiti. The minute fasciculus (to which, by the way, he has affixed no name) is the true flexor brevis minimi digiti.

But, again, he is of opinion that the adductor minimi digiti is

[1] In the Ornithorhynchus a tendency to the same result is to be seen. The muscles have the typical arrangement, but the intermediate flexores and dorsal interossei are feebly developed, and the former show a considerable admixture of fibrous tissue with the muscular fibres.

the opponens. Such a conclusion I consider to be altogether untenable, as it is the very essence of an opponens that it should be inserted into the metatarsal bone, whilst this muscle is inserted into the distal phalanx.

The peculiarity of arrangement in the pedal muscles of the Bathyergus (fig. 4) simply consists in a total absence of the plantar adducting muscles, and also of the dorsal abducting muscles. The intermediate flexores breves, however, are well developed—each consisting of two strong slips ($f.^1$ to $f.^5$).

Whether the plantar and dorsal muscles are absent from suppression or fusion with the flexors, it is impossible to make out. If it be due to the latter cause, there are certainly no traces of the fusion to be discovered.

The quadrumana must next claim our attention. Of these I chose for dissection the foot of a large monkey with a powerful opposable hallux, and also the foot of a lemur.

The adducting apparatus is remarkably powerful, and further, it is plantar in position. An interesting point in connection with these muscles, is the presence of a transversus pedis, or transverse adductor hallucis, almost blended with the true adductor hallucis. This bears upon the development of these muscles in the human foot. Dr Ruge of Heidelberg[1] has recently proved that the transversus pedis at an early stage of development of the human embryo lies in apposition with the true adductor, and that its transverse position in the adult is due to its travelling forwards towards the heads of the metatarsals. In the adult monkey, then, it is interesting to find the two muscles blended the one into the other.

The flexores breves and the dorsal interossei are partially fused as in the carnivora.

We are now evidently approaching the human foot, as the flexores of the index, medius and annularis are small and insignificant in size in comparision with the same muscles in other animals. Again, the dorsal interossei are bipenniform, arising from the shafts of the metatarsals and occuping the entire interosseous spaces.

In some of the smaller monkeys the interosseous muscles,

[1] "Processes in the Development of the Muscles of the Human Foot," by George Ruge, *Morphologisches Jahrbuch* (1878).

whilst they occupy the intermetatarsal spaces, are one-headed, and arise entirely from the base of the metatarsus.

In the lemur there is an oppenens minimi digiti.

We come now to the human foot; and if we have proved our point, the homologies of its intrinsic muscles are simple.

The adductor hallucis, transversus pedis, and the three plantar interossei are the representatives of the plantar layer in other animals. The flexor brevis minimi digiti and the flexor brevis hallucis are the only representatives of the intermediate series of flexores breves; and lastly, the abductor hallucis, the abductor minimi digiti, and the dorsal interossei constitute the dorsal layer.

It is true that the representatives of the three layers have lost their relative planes in the foot; but this is due partly to the arched condition of the metatarsus, whereby the short flexors, from their relation to the piers of the arch, have been thrown downwards, and partly to the suppression of the flexores breves in connection with the index, medius, and annularis, whereby the plantar interossei muscles have sunk deeply into the sole.

II. The question now arises: if the intrinsic muscles of the foot are laid down in three layers, to which of these does the opponens muscle belong?

It is necessary, however, before we inquire into this point, that we should have a clear understanding what the muscles are to which the term "opponens" should be applied. We need not look to its function for a true definition, for many of the opponens muscles have little or no opposing action. It is clearly the insertion which must be taken as the distinguishing feature, and we may define the term as being one which may be properly applied to any intrinsic muscle which is inserted into the shaft of a metatarsal bone.

An opponens hallucis is of very rare occurrence. It is found in some few cases, however, as, for example, in the ourang.[1] The opponens minimi digiti pedis is very common, and often very strongly marked. It may be regarded as belonging in some instances to the adducting or plantar layer, and in others to the intermediate or flexor layer. Thus Ruge of Heidelberg has conclusively shown that in the human foot (when present)

[1] St George Mivart in his *Lessons in Elementary Anatomy*.

it is a special development of the flexor brevis minimi digiti. In the lemur and phalanging marsupials it apparently has the same derivation.

On the other hand, many of the digitigrade carnivora afford a beautiful example of its association with the plantar layer. We have already seen it in the dog, cat, puma, leopard (fig. 2, *o.m.*), lion, and otter (fig. 1, *o.m.*), arising in common with the adductor minimi digiti.

III. The last point which we have to consider is one of great interest—viz., that the relation of the intrinsic muscles of the foot to the metatarsus in many animals corresponds to transitory conditions in the foot of the human embryo.

I have on more than one occasion in the course of this paper referred to the very important researches by Ruge of Heidelberg into the development of the muscles of the human foot.

In his memoir upon this subject, Ruge shows that the interossei muscles in the foot of the early embryo are plantar in position, and that the upward growth of the dorsal interossei and the formation of the interosseous spaces take place as a subsequent and gradual step. In three of the diagrams which illustrate the text, he gives representations of sections through the metatarsus at three different periods of development. In the first the metatarsal bones, with the exception of the first two, are in close apposition, and in consequence all the interossei muscles, excepting the first dorsal, are plantar in position. The second diagram is from a foot somewhat more advanced. It shows that as development progresses the metatarsal bones separate from each other, and that simultaneously with this the dorsal interossei begin to shoot up between them like wedges. The third illustration gives a view of the relative position of the muscles and metatarsal bones as they are to be seen in the adult. The bones are widely apart from each other, and the muscles have reached the dorsum of the foot.

Among the lower mammals, the dog, in its adult condition, corresponds exactly with the first stage of the human embryo in the relation of its intrinsic pedal muscles to the metatarsus. The metatarsal bones are closely compressed together (fig. 5), and the muscles are entirely plantar in position.

The large majority of mammals never reach beyond the second stage of the foot of the human embryo in this respect. Let us take as an example the foot of the leopard (fig. 6). In this animal the metatarsal bones, whilst they are closely applied to each other towards the tarsus, open out slightly from each other towards their phalangeal extremities; and in the intervals between them the sharp edges of the dorsal interossei may be seen reaching half-way up the interosseous spaces ($d.^2$ to $d.^4$).

Comparatively few animals correspond with the third stage of the human foot; still, certain monkeys approach very closely to man in this respect.

But there is also a relation between the human embryo and many of the adult animals in the mode of origin of the dorsal interossei. Ruge points out that in the early embryo these muscles are one-headed, and that it is only in a later stage that they acquire their bipenniform character and their origin from the metatarsal shafts. How similar is this to what we have seen to be the permanent condition in the great majority of mammals[1] (fig. 1, $d.^1$ to $d.^4$).

The plate which accompanies this paper is the work of Mr J. Dunlop Dunlop, and I am greatly indebted to him for the careful and accurate manner in which he has delineated the various objects.

---

## Explanation of Plate I.

Fig. 1. *Left Pes of the Otter* (plantar aspect), showing the intrinsic pedal muscles.

| | |
|---|---|
| (*a.h.*) Adductor hallucis. | Plantar Group of Muscles. |
| (*a.i.*) Adductor indicis. | |
| (*a.m.*) Adductor minimi digiti. | |
| (*o.m.*) Opponens minimi digiti. | |

[1] It is curious to find in an animal so low as the duck-bill platypus a closer approach to man in the mode of origin of its dorsal interossei muscles than in any of the other animals we have examined, with the exception of the quadrumana. The second and third dorsal interossei muscles in the pes of this animal are distinctly bipenniform, and arise from the shafts of the metatarsal bones. The first and fourth muscles are one-headed, and arise only from the base of the metatarsus.

These muscles are represented detached from their origins, and thrown forwards.

($f.^1$) Flexor brevis hallucis.
($f.^2$) Flexor brevis indicis.
($f.^3$) Flexor brevis medii.
($f.^4$) Flexor brevis annularis.
($f.^5t.$) Tibial head of the flexor brevis minimi digiti.
($f.^5f.$) Fibular head of the flexor brevis minimi digiti.

} Intermediate Group of Muscles.

The flexor brevis hallucis is represented by a single head; the other muscles of this group are seen to be bicipital.

($d.^1$ to $d.^4$) The four dorsal interossei muscles.
($a.o.$) Abductor ossis metatarsi minimi digiti.

} Dorsal Group of Muscles.

The abductor minimi digiti is absent as a distinct muscle. It is fused with the outer head of the flexor brevis ($f.^5f.$), and this is the reason why this slip is so large, and takes origin higher up in the foot than its neighbour ($f.^5t.$). An abductor hallucis is sometimes present as a distinct slip, but it was absent in the foot from which the drawing was taken.

Fig. 2. *Left Pes of Leopard* (reduced—plantar aspect). The plantar layer of muscles has been thrown forwards.

($a.i.$) Adductor indicis.
($a.m.$) Adductor minimi digiti.
($o.m.$) Opponens minimi digiti.

The dorsal and intermediate muscles are observed to be partially fused.

($f.^2$ to $f.^5$) The flexores breves.
($d.^1$ to $d.^4$) The dorsal interossei.
($ab.$) Abductor minimi digiti.
($a.o.$) Abductor ossis metatarsi.
($h.$) Rudimentary hallux.

Fig. 3. *Left Pes of Dasypus sexcinctus* (plantar aspect).

($a.h.$) Adductor hallucis.
($a.i.$) Adductor indicis.
($a.a.$) Adductor annularis.
($a.m.$) Adductor minimi digiti.

---

($f.^1t.$) Tibial head of flexor brevis hallucis.
($f.^1f.$) Fibular head of flexor brevis hallucis.
($f.^5$) Flexor brevis minimi digiti.

---

($ab.h.$) Abductor hallucis.
($ab.$) Abductor minimi digiti.
($a.o.$) Abductor ossis metatarsi.
($f.b.$) Fibrous bands representing the suppressed muscles.

Fig. 4. *Left Pes of Bathyergus capensis* (plantar aspect).

(*f.*[1] *to f.*[5]) The flexores breves.

The abducting and adducting muscles are absent.

Fig. 5. *Left Pes of Dingo* (dorsal aspect).—The close apposition of the metatarsal bones is seen.

Fig. 6. *Left Pes of Leopard* (dorsal aspect—reduced).—Shows that, whilst the metatarsal bones are closely applied towards the tarsus, they open out from each other towards their phalangeal extremities.

(*d.*[2] *to d.*[4]) Second, third, and fourth dorsal interosseous muscles.

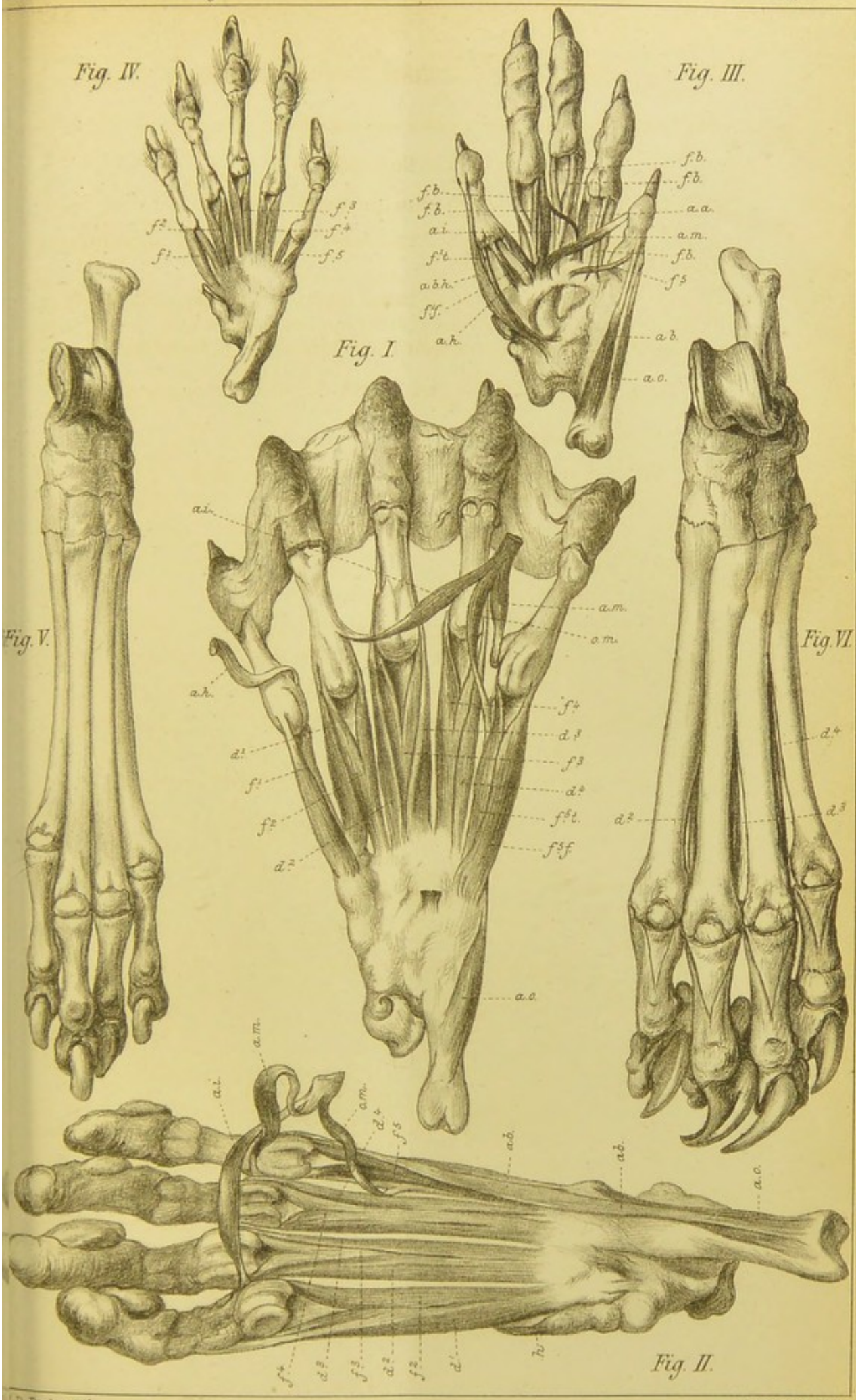
Fig. IV.
Fig. III.
Fig. I.
Fig. V.
Fig. VI.
Fig. II.
f.b.
a.a.
a.i.
a.m.
f.l.
a.b.h.
f.f.
a.h.
a.b.
a.c.
o.m.
d.4
d.3
d.2
f.s.l.
f.s.f.