THE PHYLOGENY OF THE FOREARM FLEXORS.

BY

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WITH 13 TEXT FIGURES.

Notwithstanding the voluminous literature of descriptive myology, comparatively little has been accomplished toward the determination of the exact homologies of the limb muscles throughout the vertebrate phylum. Something has been done in the way of elucidating a fundamental plan for the mammalian muscles, especially through the efforts of Ruge, Cunningham, Windle, Leche and von Bardeleben, to mention only some of the more recent authors, but even with regard to this group there are still gaps to be filled out and the earlier stages in the phylogeny still require study, notwithstanding Eisler's very important contribution to that side of the story. That author (1895) has made a careful study of the limb muscles of the urodelous amphibia, taking Menopoma as a type, and has attempted to reduce the mammalian condition to a modification of what obtains in that group. Having omitted to consider the reptilia, however, Eisler has missed some important points bearing on the question, and I propose in the following pages to give the results of observations made on both amphibia and reptilia and hope to demonstrate a detailed homology of the arm muscles in these groups and then to extend the homologies to the mammalian muscles.

My attention was primarily directed to the subject through some study which I had made of the perforated flexors of the hand and foot. It has been a general custom to regard these muscles as equivalent and to assume that the primary condition, so far as mammalia are concerned, is represented in the arm and that there has been a secondary recession of the muscle into the foot in the lower limb (cf. Wiedersheim, 1893). On looking into the matter it seemed that the evidence which could be brought forward in support of such a theory was decidedly scant, and I determined to test it by a phylogenetic study, beginning with an attempt to trace the evolution of the flexor sublimis of the arm. This muscle, as a distinct element, being, however, confined to the mammalia, it was evident that in order to obtain a correct appreciation of its significance and a basis for its comparison with the flexor brevis of the foot, it would be necessary to discover what structures, if any, represented the sublimis in the lower vertebrates. Thus the investigation broadened to include a determination of the phylogeny of the entire flexor-pronator mass of the forearm and it is to the results of this portion of the problem that the present paper will be devoted. I hope to consider at some future date the muscles of the leg in a similar manner and so return to the question of the equivalency of the muscles in the two limbs.

A few words are necessary regarding the forms studied and the methods employed. My first intention was to approach the question from the embryological side, and to study the development of the forearm muscles in embryos of *Amblystoma tigrinum*, *Anolis sagræi*,[1] the rabbit and man. I soon discovered, however, that this method would not yield the desired results, for in the mammalian embryos the forearm muscles, when first distinctly recognizable, have practically the adult arrangement. The same result has been obtained by Lewis (1902) in his admirable study of the development of the arm in man, and it would seem that there is a very extensive condensation in the ontogenetic development of the limb muscles in the mammalia. It is probable that the entire phylogenetic history of the forearm muscles of man, for instance, is condensed into the stages during which the muscles are represented by an undifferentiated mesodermic blastema and that, therefore, anomalies of reversion are referable to the possibilities, dependent on past history, latent in this blastema.

The embryological method being then excluded, it was necessary to have recourse to comparative anatomy. Careful dissection revealed much that was of importance, but far more valuable results were obtained from the study of serial sections. From these the topographic relations of the various muscles and their nerve supply could be determined with certainty, and the pictures presented were so much more perfect and striking that I finally relied on the sections rather than on dissections, employing the latter mainly for confirmation.

As types of the urodelous amphibia I studied by both dissections and sections *Amblystoma tigrinum* and by sections only *Plethodon erythronotum*. Of the reptilia I studied *Phrynosoma cornutum*, *Liolepisma laterale*, *Callisaurus draconoides* and *Chrysemys picta*, and of mammalia I examined *Didelphys virginiana* (the material of which I owe to the kindness of Dr. C. F. W. McClure, of Princeton University), the cat,

[1] For material of this form I am indebted to the kindness of my friend, Dr. Henry Orr, of Tulane University.

the mouse and man, employing for my serial sections advanced embryos of these forms instead of adult individuals, simply as a matter of convenience in preparation. I made use of von Ebner's decalcifying solution, embedded in paraffin, cut to a thickness of 20 μ and stained on the slide either with picrolithium carmine or with Delafield's hæmatoxylin followed by van Gieson's picrofuchsin, this latter method giving excellent differentiation of the various tissues.

I. The Forearm Flexors of the Urodelous Amphibia and Lacertilia.

It is well known that the flexor muscles of the forearm of the urodele amphibia may be regarded as consisting of three layers. The most superficial layer consists of muscles arising from the internal condyle of the humerus and extending longitudinally to be inserted either into the carpus or into a strong palmar aponeurosis; the middle layer is made up for the most part of oblique muscles arising from the ulna and passing distally and radially to be inserted into the palmar aponeurosis, one muscle only, the ulno-carpalis, having an almost longitudinal direction and being inserted into the carpus; while the third layer consists of a sheet extending obliquely across between the ulna and radius.

The superficial layer is divided into three or four muscles; (1) the *palmaris superficialis* (Fig. 1, PS), which occupies the median portion of the layer and inserts into the palmar aponeurosis, (2) the ***flexor*** *carpi ulnaris* (F. C. U.), (3) the *flexor antibrachii ulnaris* (*epitrochleo-anconeus*), Eisler, which inserts into the ulna and is more or less perfectly differentiated in different forms, and (4) the ***flexor carpi radialis*** (F. C. R.).

The oblique muscles of the middle layer are divided by the ulnocarpalis into an ulnar and a radial portion, the latter being again more or less distinctly divided into two portions, so that altogether the layer is composed of four muscles. The most ulnar of these and therefore the most superficial may be termed the *palmaris profundus* III (Eisler) (P. P. III); it arises from the ventral surface of the lower part of the ulna and is inserted into the under (dorsal) surface of the palmar aponeurosis. To the radial side of it and separating it at its origin from the palmaris profundus II is the *ulno-carpalis* (U. C.), which, arising from the ulna, descends almost longitudinally to be inserted into the distal row of carpal bones. More radially lies the ***palmaris*** *profundus* II (P. P. II) which resembles closely the palmaris profundus III, arising from the radial side of the lower part of the ulna and inserting into the dorsal surface of the palmar aponeurosis toward its radial edge; and, finally, most radial of all, is the *palmaris profundus* I (P. P. I), which arises from the lower part of the ulna and also from the carpus and may be traced distally and radially to an insertion into the aponeurosis and the base of metacarpale II. As has been already stated the distinction between portions I and II is not always quite evident and there is also a close relationship between I and the muscle of the third layer, the *pronator quadratus* (P. Q.), both being supplied

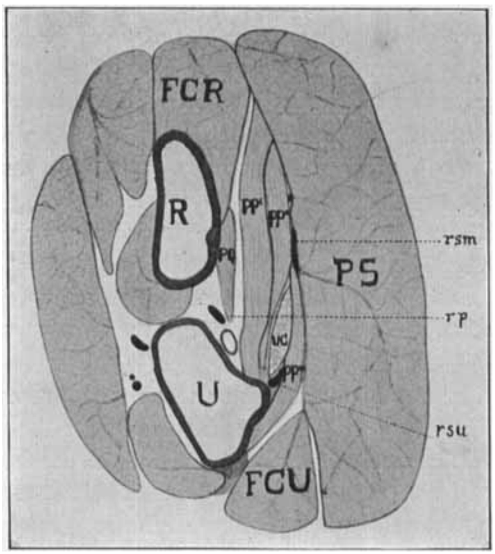


FIG. 1. Transverse section through the lower half of the forearm of *Amblystoma tigrinum*. F. C. R., flexor carpi radialis; F. C. U., flexor carpi ulnaris; PP′-PP‴, first to third portions of palmaris profundus; PQ, pronator quadratus; PS, palmaris superficialis; R, radius; *rp*, ramus profundus; *rsm*, ramus superficialis medialis; *rsu*, ramus superficialis ulnaris; U, ulna; UC, ulno-carpalis.

by the same nerve; portion II has, however, a different nerve supply, receiving branches from the same stem which supplies portion III.

The relations of these muscles as seen in sections may be perceived from Fig. 1, which represents a transverse section through the lower half of the antibrachium of *Amblystoma tigrinum.*

Turning now to the lacertilia one finds a condition which seems at first sight far removed from that obtaining in the amphibia. There is a greater amount of longitudinal division of the muscle layers and a diminution in the amount of the oblique musculature in the middle layer, as well as a tendency for it to associate itself more or less closely with the superficial layer.

Taking the condition found in *Phrynosoma cornutum* as typical, the arrangement of the muscles at about the middle of the forearm is as shown in Fig. 2. Starting from the ulnar side there is first the flexor carpi ulnaris (F. C. U. and F. C. U.'), consisting of two distinct slips; traced distally these fuse to form a single tendon which inserts into the ulnar side of the carpus, while proximally they separate more

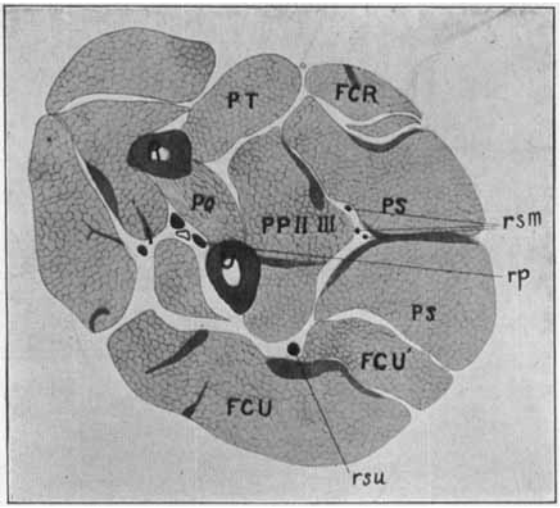


FIG. 2. Transverse section through the middle of the forearm of *Phrynosoma cornutum*. F. C. R., flexor carpi radialis; F. C. U. and F. C. U'., lateral and medial portions of the flexor carpi ulnaris; PP II, III, deep portions of the palmaris communis; PQ, pronator quadratus; PS, superficial portions of the palmaris communis; P.T., pronator teres; R, radius; *rp*, ramus profundus; *rsm*, ramus superficialis medialis; *rsu*, ramus superficialis ulnaris; U, ulna.

and more, their origins from the internal condyle being separated by the epitrochleo-anconeus, whose insertion into the ulna lies above the level of the section figured.

The median portion of the arm is occupied by a strong mass which forms the *flexor digitorum profundus* (auct.), although it would be better to use the term flexor communis digitorum employed by Stannius, or, better still, palmaris communis if we are to regard it as a single muscle. In reality it consists of five distinct portions, only four of which are seen in Fig. 2. Two of these four (P. S.) are superficial, occupying the interval between the more median head of the flexor carpi ulnaris and the flexor carpi radialis (F. C. R.), and the other two (P. P. II and III) are deeper, one resting immediately upon the ventral surface of the ulna, while the other lies ventral to the pronator quadratus (P. Q.) and the radius. The fifth portion (Fig. 3, P. P. I) is short and is an oblique muscle arising from the ventral surface of the ulnar side of the carpus. All five portions insert distally into the palmar aponeurosis, which, in the majority of the forms studied, contains a strong volar cartilage. Proximally the superficial portions take origin from the internal condyle, while the deeper portions arise from the ulna or, in the case of the fifth portion, from the ulnar side of the carpus.

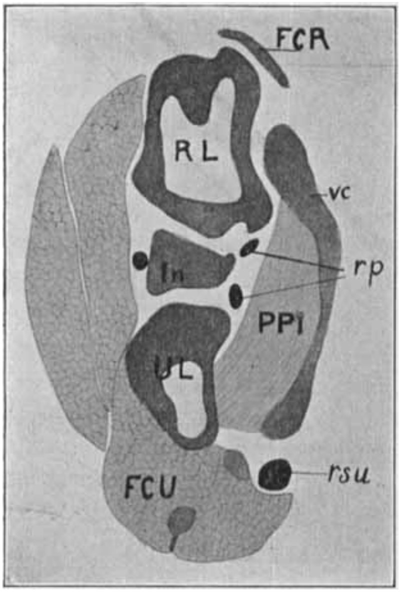


FIG. 3. Transverse section through the wrist of *Liolepisma laterale*. F. C. R., flexor carpi radialis; F. C. U., flexor carpi ulnaris; In, intermedium; PP I, first part of deep portion of the palmaris communis; RL, radiale; *rp*, ramus profundus; *rsu*, ramus superficialis ulnaris; UL, ulnar; *vc*, volar cartilage.

On the radial side of the arm are two muscles, a more superficial flexor carpi radialis (F. C. R.) and a deeper *pronator radii teres* (P. T.) both of which arise from the internal condyle of the humerus, the former having its insertion into the radial side of the carpus and into the base of metacarpale I, while the latter inserts into the lower part of the radial side of the radius.

Finally, constituting the deepest layer, there is a pronator quadratus (P. Q.), extending between the radius and ulna, and in the proximal part of the arm a *pronator accessorius* (Mivart), which arises from the internal condyle and is inserted into the radius.

Before proceeding to a comparison of the individual muscles of the amphibia and reptilia a description of the nerves of the forearm in the two groups will be necessary. For they present a remarkable similarity in their arrangement and will serve as guides in the determination of some of the more obscure homologies.

In the amphibia the flexor muscles of the forearm are supplied by a large trunk which enters from the brachium towards the radial side and constitutes what has been termed the *N. brachialis longus inferior.*

It passes obliquely inwards between the flexor carpi radialis and the radius and soon divides into a superficial and a deep branch. The *ramus profundus* (Fig. 1, *rp*) passes behind the pronator quadratus, which it supplies, and descends the arm in that position to the lower edge of the muscle, where it comes to lie immediately below, *i. e.* dorsal to the palmaris profundus I to which it sends fibres.

The superficial branch passes toward the median line of the arm ventral to the pronator quadratus, and divides into two branches after giving a twig to the flexor carpi ulnaris and to the epitrochleo-anconeus. The two branches may be termed the *ramus ulnaris* (*rsu*) and the *r. medialis* (*rsm*). The former gives off a second branch to the flexor carpi ulnaris and passes obliquely across the ventral surface of the ulno-carpalis, which it supplies, and then descends the arm upon the ulnar side of that muscle. In Amblystoma it lies in the lower part of the forearm between the ulno-carpalis and the palmaris profundus III, and, as it nears the carpus, it bends ulnarwards between the latter muscle and the ulna and comes to lie superficially upon the ulnar side of the arm. In Plethodon, however, in which the origin of the palmaris profundus III does not extend so high upon the arm, the nerve begins to bend ulnarward before it reaches the origin of the muscle and consequently possesses somewhat different relations to it than it does in Amblystoma.

The medial ramus breaks up into a number of branches which ramify in the substance of the palmaris superficialis, one, however, descending a short distance to give off a branch to the palmaris profundus II and also to the palmaris profundus III.

The supply of the various amphibian muscles may be tabulated, then, as follows:

Epitrochleo-anconeus Flexor carpi ulnaris Ulno-carpalis	R. superficialis ulnaris.
Palmaris superficialis Palmaris profundus II Palmaris profundus III	R. superficialis medialis.
Palmaris profundus I Pronator quadratus Flexor carpi radialis	R. profundus.

In the reptilia the main nerve stem for the flexor muscles of the forearm enters from above upon the radial side and, as in the amphibia, may be termed the N. brachialis longus inferior. It early divides into two stems, a ramus profundus and a R. superficialis, whose general relations are practically identical with those found in the amphibia.

The R. profundus (Fig. 2, *rp*) bends mesially and dorsally, curving around the radius, and comes to lie dorsal to the pronator quadratus, in which position it descends the arm. It supplies the pronator quadratus and also the pronator accessorius and the flexor carpi radialis, and at the lower border of the quadratus it passes ventrally so as to lie upon the ventral surface of the carpus (Fig. 3, *rp*), giving off a branch to the oblique portion of the palmaris communis.

The R. superficialis divides, as in the amphibia, into a R. medialis (Fig. 2, *rsm*) and a R. ulnaris (*rsu*). The latter passes obliquely across the arm between the superficial and deep layers of the palmaris communis, reaching the ulna at the lower edge of the insertion of the epitrochleo-anconeus, which muscle it supplies, also sending twigs to the lateral head of the flexor carpi ulnaris. It then continues down the arm, lying to the ulnar side of the deep portions of the palmaris communis and so passes into the manus.

The R. medialis follows at first the course of the ulnaris until it reaches approximately the median line of the arm, when it gives off branches to the more median head of the flexor carpi ulnaris. Early in its course it gives a branch to the pronator radii teres. It passes down the arm between the superficial and deep portions of the palmaris communis, both of which it supplies and in which it is finally lost.

Tabulating the muscles according to their nerve supply the arrangement is as follows:

Epitrochleo-anconeus Flexor carpi ulnaris (lateral head)	R. superficialis ulnaris.
Palmaris communis (superficial portions) Palmaris communis (deep portions II & III) Flexor carpi ulnaris (median head) Pronator radii teres	R. superficialis medialis.
Palmaris communis (oblique portion) Pronator quadratus Pronator accessorius Flexor carpi radialis	R. profundus.

We are now in a position to make a comparison of the individual amphibian and reptilian muscles. On the ulnar side the epitrochleo-anconeus has become more distinctly separated from the flexor carpi ulnaris in the reptilia, and with the latter muscle a portion of the palmaris superficialis has associated itself to form the medial head, while the rest of the palmaris superficialis, represented by the superficial portions of the palmaris communis, shows a tendency to divide into two portions.

The palmares profundi II and III are represented by the deep portions of the palmaris communis shown in Fig. 2. They have, however, undergone a very important modification by the extension of their origin proximally upon the bones of the forearm, so that they have acquired a more longitudinal direction, a condition which is associated with a reduction of the width of the volar cartilage into which they are inserted as compared with the amphibian palmar aponeurosis. The proximal extension has occurred chiefly in connection with portion II of the muscle and with it there has been a certain amount of extension of its origin radialwards. The palmaris profundus I has retained its original oblique direction and also its primary origin from the lower end of the ulna and the ulnar carpal bones, and has thereby been brought into somewhat different relations to the other portions of the profundus than obtained in the amphibia. In a section through the distal part of the forearm of Amblystoma the profundus I appears as the most radial of the profundus muscles, while in the reptilia it seems to be the most ulnar. The identification of the muscle in the two groups rests mainly on its nerve supply and, if this be accepted as a sufficient criterion, an explanation is to be sought for the apparent difference in its position. I believe that this can be found in the change in the direction of the second and third portions of the profundus and the migration of their origins proximally, the profundus I being thereby permitted to occupy exclusively the lower part of the ulna and the ulnar side of the carpus, and since its insertion in the reptilia is into the dorsal surface of the volar cartilage, while the other portions of the profundus insert into its proximal border, there is no obstacle in the way of a conversion of the arrangement seen in the amphibia into what occurs in the reptilia.

One muscle of the amphibian forearm I have not been able to recognize in the reptilia. This is the ulno-carpalis. The ramus ulnaris of the superficial branch of the inferior brachial nerve passes across the ventral surface of this muscle and descends the arm upon its ulnar surface and in the reptilia the corresponding nerve has the same relations to the second part of the palmaris profundus, using that designation for the portion of the palmaris communis which has been identified with the amphibian profundus II. Arguing from this topographic relation, it seems possible that the muscle has been incorporated in the reptilian profundus II. Such a condition would, however, necessitate a decided alteration of the insertion of the ulno-carpalis, which must have shifted from the carpus to the palmar aponeurosis and, furthermore, I find no branches of the ramus ulnaris, which supplies the amphibian muscle, entering the substance of the reptilian palmaris profundus. While I hesitate to express a conviction that the muscle is unrepresented in the reptilia, the weight of evidence seems to me to point that way.

The flexor carpi radialis seems to be equivalent in the two groups, while the pronator radii teres seems to correspond to the radial portion of the amphibian palmaris superficialis. In Liolepisma the nerve which passes to the flexor carpi radialis arises from the N. brachialis inferior longus before its division into the deep and superficial rami, but it is more nearly associated with that portion of the nerve which becomes the R. profundus and I have therefore associated it with that ramus. The branch to the pronator teres, on the other hand, was the first branch from the R. superficialis medialis and there is, accordingly, good reason for believing that the pronator teres and the flexor carpi ulnaris are quite distinct structures.

The reptilian pronator accessorius is supplied, like the pronator quadratus, from the R. profundus and I see no reason for doubting the conclusion of Fürbringer (1870), that it represents the upper portion of the amphibian quadratus.

The homologies of the amphibian and reptilian muscles as described above may be tabulated thus:

Amphibia.	Reptilia.
Ulno-carpalis	?
Epitrochleo-anconeus	Epitrochleo-anconeus
Flexor carpi ulnaris	Flexor carpi ulnaris (lateral head)
Palmaris superficialis	Flexor carpi ulnaris (medial head) Palmaris communis (superficial portions) Pronator radii teres
Palmaris profundus III Palmaris profundus II	Palmaris communis (longitudinal deep portions)
Palmaris profundus I	Palmaris communis (oblique deep portions)
Pronator quadratus	Pronator quadratus Pronator accessorius
Flexor carpi radialis	Flexor carpi radialis

II. The Forearm Flexors of the Mammalia.

In the amphibia and reptilia it is evident that the forearm muscles proper end at the wrist joint, their action upon the digits being through their insertion into the palmar aponeurosis, from which the palmar muscles arise. In the mammalia it is customary to regard the long digital flexors as extending from their antibrachial origins to the phalanges, and in comparing them on this basis with the corresponding muscles of the lower groups, it is necessary to assume that there has been either an extension of the origin of certain palmar muscles proximally, or a shifting of the insertion of antibrachial muscles distally, or, perhaps, a combination of both these processes. My results show that such a way of regarding the long flexors is erroneous and that if we are to obtain correct homologies we must compare only the antibrachial portions of the mammalian flexors with antibrachial muscles of the amphibia and reptilia, the palmar portions being comparable to palmar structures, tendons or muscles. My reason for this conclusion will be given in a subsequent section of this paper, but in what follows here attention will be directed solely to the strictly antibrachial portions of the mammalian flexors.

I regret greatly that I have not been able to include a monotreme in the material studied, for, to judge from the descriptions to which I have access, they present most interesting resemblances to the conditions obtaining in the reptilia. The tendency toward an indistinctness in the separation of the superficial and deep layers of the forearm flexors seen in the reptilia is apparently carried further in the monotremes, there being recognizable in them, as distinct muscles, only a flexor carpi radialis, a pronator radii teres, a flexor communis digitorum, an epitrochleo-anconeus and a flexor carpi ulnaris, the last in Echidna being united with the flexor communis to about the middle of the forearm. Dissections have failed so far to reveal any division of the flexor communis into constituent elements such as may be recognized in other mammals, and it would be interesting to determine whether or not such a division could be recognized in sections. Lacking information on this important point I must perforce take, as my starting point for a consideration of the mammalian muscles, a condition in which a differentiation of the flexor communis has occurred, a condition a little in advance of what is found in the monotremes and yet a little below what is found in such a mammal as the opossum, in that it fails to show any differentiation of the antibrachial portion of the flexor sublimis. I take such a condition for comparison with the lower forms rather than one in which the forearm portion of the sublimis is differentiated, because this muscle is peculiar to the mammalian series and possesses within that series a somewhat complicated development which may more conveniently be considered later on.

The arrangement of the muscles in the somewhat hypothetical condition may be supposed to be as follows. Superficially upon the ulnar side of the forearm is the flexor carpi ulnaris (Fig. 4, F. C. U.) arising by two heads, one from the internal condyle of the humerus and the other from the olecranon process, and inserting below into the ulnar side of the carpus. In close proximity to this muscle is the epitrochleo-anconeus, also arising from the condyle of the humerus and inserting into the olecranon process.

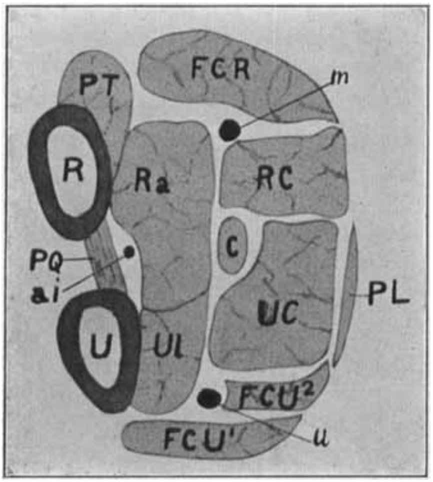


FIG. 4. Transverse section through the forearm of an hypothetical mammal. *ai*, anterior interosseus nerve; C, centralis; F. C. R., flexor carpi radialis; F. C. U.[1] and F. C. U.[2], lateral and medial portions of the flexor carpi ulnaris; *m*, median nerve; PL, palmaris longus; PQ, pronator quadratus; PT, pronator teres; R, radius; Ra, radialis; RC, condylo-radialis; U, ulna; *u*, ulna nerve; UC, condylo-ulnaris; Ul, ulnaris.

Upon the radial side there is a flexor carpi radialis (F. C. R.), extending from the internal condyle to the base of one or more of the radial metacarpals, and a pronator radii teres, again from the condyle and inserting a varying distance down the outer surface of the radius.

The median portion of the arm is occupied by (1) a palmaris longus (P. L.), extending from the internal condyle to the palmar aponeurosis, and (2) a large mass, composed of several more or less distinct portions and which may be termed the flexor communis digitorum. The constitution of this muscle has been admirably elucidated by Windle (1890), and I propose to follow closely his description of it, based as it is upon a profound and critical analysis of its various components. My observations have confirmed his for the most part, the only modification which I shall make being the omission for the present of a sublimis component. I do this because, as I hope to show later, the sublimis is far from being an equivalent muscle throughout the mammalian series, a view which differs fundamentally from that apparently held by Windle.

Omitting the sublimis, then, as a distinct component, there are recognizable in the flexor communis digitorum five components. Three of these, named by Windle, the *condylo-radialis* (Fig. 4, R. C.), the *condylo-ulnaris* (U. C.) and the *centralis* (C.), have their origin from the internal condyle of the humerus; the fourth and fifth components, the *radialis* (*Ra*) and the *ulnaris* (*Ul*), on the other hand arise from the bones from which they derive their names. All the five components unite in a common tendon.

Finally, as one of the mammalian muscles there is to be mentioned the pronator quadratus, which extends across between the distal twothirds of the radius and ulna, its upper border occasionally, however, reaching almost the proximal ends of the bones.

If, now, we attempt to employ the nerve supply of these muscles as a guide to their homologies in the lower vertebrates, we are at once met with the difficulty that the arrangement of the nerves in the mammalia is very different from what was characteristic for the lower forms. In place of the single nervus brachialis inferior longus entering the forearm to supply all its flexor muscles, there are two such nerves, the ulnar and the median. In a general way the ulnar corresponds to the R. superficialis ulnaris of the lower forms and the median to both the R. Profundus and the R. superficialis radialis, but the homology cannot be carried into detail. Indeed, from what I have observed in the forms I have studied, I am inclined to believe that the median and ulnar nerves are not perfectly equivalent throughout the mammalian series, the ulnar, for instance, in one case containing fibres which in another case are included in the median. That such may be the case has already been pointed out by von Bardeleben (1891), who finds in the mammalia a plexus formation between the median and ulnar in the proximal part of the forearm, and Kohlbrugge (1897),[2] arguing from the differences he finds in the nerve-supply of apparently homologous forearm muscles in different mammals, goes so far as to maintain that the median and ulnar nerves are not to be regarded as definite and invariably equivalent nerves, but merely as paths which may conduct elements of different origins.

I may say that in the arm of the human embryo I employed in the present study, a strong branch was given off from the median at the level of the branching of the brachial artery and, following the course of the ulnar artery, it passed obliquely inward between the sublimis and profundus muscles to join and become completely incorporated in the ulnar nerve. Krause and Telgmann (1868) mentioned this condition as of occasional occurrence in man and state that it is almost constant in apes.

But while we cannot employ the nerve supply as a certain basis for the homologies of the mammalian muscles, yet it may yield accessory evidence if we can determine the general plan of the rearrangement of the nerve fibres, which has taken place. I believe the rearrangement may be pictured as being along the following lines:

[2] I regret that I have not been able to consult this paper. The statement made concerning it is based on the review of the paper by von Bardeleben in the Ergebnisse für Anatomie und Entwicklungsgeschichte, Bd. IX, 1899.

The separation of the N. brachialis inferior longus into its forearm branches has, in the intermediate forms between the reptilia (or amphibia) and mammalia, receded up the arm until in the mammalia it occurs practically at the brachial plexus. During the recession a very considerable change in the relative position of the R. profundus has occurred, since it has left its deep situation and come forwarl to join the greater part of the R. superficialis radialis, forming a stem, the median, which lies ventral to the deeper muscles and has on the whole a radial position.

That portion of the original profundus, however, which supplies forearm muscles remains more or less distinct from the median and forms the anterior interosseous nerve which passes to its destination anterior to the pronator quadratus.

The ramus superficialis medialis, which, even in the lower forms, splits into numerous branches soon after its entrance into the forearm, probably associates itself partly with the R. profundus to form the median and partly joins the R. superficialis ulnaris to form the ulnar, and it is in the relative amounts of it which enters into the composition of each of these nerves that variation occurs in the mammalia.

Bearing in mind, then, that we probably have in the mammalian anterior interosseous nerve the representative of the portion of the R. profundus which is supplied to the forearm, the portion of that nerve destined for the hand being included in the main stem of the median, and considering also the topographic relations of the deep portions of the flexor communis digitorum supplied by it, it seems that we are justified in identifying these portions of the communis with the portion of the reptilian palmaris profundus which is supplied by the R. profundus; in other words the radialis and ulnaris portions of the flexor communis are together almost equivalent to portion I of the palmaris profundus. But not entirely so, since as a rule the ulnar portion of the ulnaris also receives some twigs from the ulnar nerve, and the portions of the muscle so supplied probably represent another portion of the deep muscles of the lower forms, but exactly which, it is difficult to state with certainty. There seem to be two possibilities worthy of consideration; either (1) the twigs for the ulnar nerve, which enter the muscle, represent a portion of the R. ulnaris, in which case it is necessary to turn to the amphibia to find a homologue for the muscle fibres in the ulno-carpalis, or (2) the twigs represent a portion of the R. superficialis medialis which has associated itself with the R. ulnaris, and in this case the muscle fibres would represent either the second or third portion or both these portions of the palmaris profundus. I am not prepared to say which of these possibilities is correct, although I am much more inclined to favor the second than the first.

However that may be, I feel confident that in the radialis and ulnaris portions of the flexor communis digitorum we have the representatives of the palmaris profundus and that these muscles are the only representatives of the profundus. The remaining portions of the flexor communis, together with the palmaris longus, represent the palmaris superficialis, and it is interesting to note that the mammalian muscles have the same relations to the elbow joint, so far as their general origin is concerned, as those of their reptilian prototypes; there has been, in other words no skipping across the joint of the profundus group of muscles.

For the remaining muscles the homologies are less complicated. The flexor carpi radialis is equivalent throughout all the forms under consideration; the pronator radii teres, which in the majority of mammals lacks the coronoid head, seems undoubtedly equivalent to the reptilian muscle of the same name; this is also true for the epitrochleo-anconeus, which, it may be remarked, is, as Leche (1898) has suggested, a member of the flexor group and not one of the extensor series with which it has usually been classified. The flexor carpi ulnaris presents a slight difficulty, it being a question whether it represents the compound muscle so named in the reptilia, or merely the lateral head of that muscle. The double origin of the mammalian muscle, which is usual, seems to indicate that it is the equivalent of the entire reptilian muscle, in which case we have further evidence that a portion of the R. superficialis medialis is included in the mammalian ulnar nerve.

Tabulating the homologies stated above we get the following results:

Amphibia.	Reptilia.	Mammalia
Ulno-carpalis	?	?
Epitrochleo-anconeus	Epitrochleo-anconeus	Epitrochleo-anconeus
Flexor carpi ulnaris	Flexor carpi ulnaris (lateral head)	Flexor carpi ulnaris (lateral head)
Palmaris superficialis	Flexor carpi ulnaris, (medial head)	Flexor carpi ulnaris (medial head)
	Palmaris superficialis	Palmaris longus; Portio condylo-radialis; Portio condylo-ulnaris; Portio centralis
	Pronator radii teres	Pronator radii teres
Palmaris profundus III; Palmaris profundus II	Palmaris profundus II, III	Portio ulnaris; Portio radialis
Palmaris profundus I	Palmaris profundus I	
Pronator quadratus	Pronator quadratus; Pronator accessorius	Pronator quadratus
Flexor carpi radialis	Flexor carpi radialis	Flexor carpi radialis

The results which I have recorded above differ materially from those obtained by Eisler (1895) from the comparison of the mammalian muscles with those of an amphibian. His homologies may be stated briefly as follows: The superficial palmar of the amphibia is represented by the palmaris longus, having become very much reduced in size correlatively with a marked increase in the size of the deep palmars. Of these the palmaris profundus II, gradually extending its origin proximally and radially, becomes transformed into the flexores digitorum profundus and longus pollicis; the palmaris profundus III similarly migrates proximally upon the ulna and eventually, passing over the elbow joint, reaches the internal condyle of the humerus and becomes the flexor digitorum sublimis; while the profundus I is normally unrepresented in the mammalian forearm, but occasionally appears as the anomalous radio-carpeus of Fano (the flexor carpi radialis brevis seu profundus of Wood).

It seems to me that these results are open to criticism along three general lines. In the first place the omission of all consideration of the reptilia has placed Eisler at a disadvantage in having no bridge over the enormous gap which undoubtedly exists between the urodelous amphibia and the mammalia. Even if we accept an amphibian ancestry for the mammalia, it seems probable that the ancestors were much more reptilian in character than are any of the existing urodeles and, furthermore, not only must the mammalian musculature be referred back to the amphibian but so must the reptilian. Accordingly we may expect to find in the reptilian muscles, if not direct evidence of the phylogeny of the mammalian conditions, at all events indications of the lines along which it proceeded and, it seems to me, this expectation has been fully borne out by the results described in the preceding pages. There is certainly much more general similarity in the arrangement of the reptilian and mammalian forearm musculature than in that of the amphibia and mammalia.

In the second place Eisler has failed to take into consideration the evidence derived from the nerve supply of the amphibian musculature. It may not be possible as yet to institute a certain homology between the amphibian and mammalian forearm nerves, but I believe that I have shown a sufficient general equivalency to warrant the acceptance of the nerve supply as important corroborative evidence. The identification, therefore, of the palmaris profundus II with its nerve supply from the R. superficialis medialis with the mammalian flexor profundus supplied by fibres which represent the R. profundus, seems very doubtful, unless the evidence from other sources is more than ordinarily convincing, and that it is so has not, I believe, been demonstrated.

Thirdly, the homologies proposed by Eisler demand a very considerable modification in the topographic relationship of the muscles. A muscle, the profundus III for example, which is clearly a portion of the deep layer in the amphibia, becomes, in the mammalia, the superficial flexor sublimis, altering its topographic relations to the principal nerves of the arm. Such an alteration is of course possible, but its probability is greatly diminished if an homology can be found which does not demand it, and I have shown that there is such an homology. Indeed, the superficial and deep layers of the amphibian forearm musculature are clearly recognizable in both the reptilia and the mammalia, and there seems no reason for manufacturing homologies which require their confusion. Furthermore, it seems to me that an homology which demands an extensive migration of muscle masses across joints should be viewed with suspicion, and such a migration is demanded by Eisler's identification of the palmaris profundus III with the flexor sublimis. With the enormous reduction which he supposes to have occurred in the palmaris superficialis, room is afforded upon the internal condyle for such a migration, but as has just been indicated and as will be shown later there is evidence to show that this reduction has not occurred. Hence, independently of the *a priori* objections to a migration of a profundus muscle across a joint, there is, in the present case, an additional objection on the ground that the muscle would have found the territory for which it was striving already preëmpted.

Finally, a word concerning the identification of the palmaris profundus I with the anomalous flexor radialis brevis. I have had an opportunity for studying this muscle in a subject dissected last winter in the Anatomical Laboratory of this University, and from its general relations I should be strongly inclined to regard it as a portion of the flexor carpi radialis, though I cannot exclude the possibility of its derivation from the pronator quadratus. In either event, however, I agree fully with Le Double (1897) in assigning it to the group of progressive anomalies: "Il est la conséquence du morcellement plus complet de la masse flexo-pronatrice, et non un 'remnant' de cette masse, pour me servir d'une expression du professeur Humphry."

III. The Antibrachial Flexors in Man and the Evolution of the Flexor Sublimis.

The flexor muscles of the forearm in man present certain departures from the condition which has been considered fundamental for the mammalia, the more important of these departures concerning the pronator radii teres and the flexor communis digitorum. The peculiarity in the pronator consists in its possession of a coronoid head in addition to the condylar one, the median nerve passing into the forearm between the two heads. This condition, so far as I am aware, occurs only in man and in the anthropoid apes, and in these forms it is associated with a marked reduction in the size of the pronator quadratus. There seems to be no doubt but that Macalister (1868) was right in regarding the deep head as something quite distinct from the pronator teres proper, and I believe we may go further than Macalister when he says in his earlier paper that it is to be regarded as "the germ of a superior transverse muscle, the upper equivalent and co-ordinate of the pronator quadratus below." In its highest degree of development in the mammalia this latter muscle occupies the entire length of the forearm, and in Perameles and some species of Halmaturus, in the dog and the hyæna, its proximal portions are united with the pronator teres (Leche). In man and the anthropoids, as Macalister points out in his later paper (1869), we seem to have other instances of a similar fusion, in association with which there has been, however, a degeneration of a considerable portion of the quadratus, only its proximal and distal portions persisting.

In the case of the flexor digitorum communis the modifications are much more complicated. The most striking peculiarity of the human flexor is its separation into a large flexor sublimis seu perforatus and a flexor profundus seu perforans, and, furthermore, the separation of the profundus into the profundus of anthropotomy and the flexor longus pollicis.

That the occurrence of a flexor longus pollicis is due to a differentiation of a portion of the profundus, to be more precise of a portion or all of the portio radialis, seems beyond question. It is a muscle which has not infrequently been described as absent in the lower forms, or in other cases, its absence has been accounted for by a fusion with the profundus. To my mind neither of these expressions fits the case; the latter one implies that it is an independent typical constituent of the mammalian flexors which in certain cases has disappeared by fusion with the neighboring muscle, while the former implies that it is unrepresented. The occurrence of the muscle in a comparatively small number of the mammalia, *e. g.* in certain carnivores, Hylobates and man, indicates by no means indistinctly its secondary nature, and it certainly seems improbable that it could appear sporadically, as it does, without having some representative in the arms of forms nearly allied to those which possess it. If it be a separated portion of the profundus, then it has a representative throughout the entire mammalian series, probably even in forms which lack a pollex, for the relation of the profundus is not primarily to the individual digits but to a common tendon, a point which will be elucidated in the succeeding part of this paper.

Independently of the decided difference in the views of Eisler and myself as to the homologue of this muscle in the amphibia, it seems to me that Eisler is wide of the mark in attempting to discover an indication of its independent existence in the lower forms, as he does in the partial separation of the profundus II into two portions. Its independence from the mammalian profundus is too recent phylogenetically to warrant a hope of an absolute identification of it in the amphibia. Its separation occurs only within the mammalian phylum and, indeed, only in certain of the more highly specialized members of that phylum. I can see no reason for supposing that the occurrence of the muscle in the dog and the hyæna has any phylogenetic relation to its occurrence in man; it seems rather to have been developed, i. e. separated from the profundus independently in the two cases.

The palmaris longus is a muscle which may well be regarded as typical of the mammalia, though its absence in the monotremes, that is to say its lack of separation from the flexor communis implies that its differentiation has occurred within the limits of the phylum. The available evidence seems to point to its having been the first separation from the common flexor, and its distinctness from the other components does not seem to be equal in different forms. In other words it is doubtful if the muscle is an absolutely equivalent structure throughout the mammalian series, but this, as well as the question as to the nature of the palmar fascia to which it is attached, can be more satisfactorily discussed later.

The sublimis, like the palmaris longus, has been differentiated from the flexor communis digitorum within the limits of the mammalian phylum and is not an equivalent muscle throughout the group, since it contains a greater portion of the flexor communis in man and the higher forms than it does in the lower. It is hardly necessary to remark that the identification of the sublimis with the flexor brevis digitorum (perforatus) of the reptilia, which has so frequently been made, is incorrect.

The comparison of the sublimis in different mammals must rest upon the recognition of its relations to Windle's five portions of the flexor communis and these relations are as yet unknown in the majority of the mammalia. I shall, accordingly, first describe what I have found in the forms which I have studied, namely in the opossum, the cat, the mouse and man, and employ the table contained in Windle's paper only after I have established the probable line of differentiation.

In a section through the upper part of the arm of an opossum (Fig. 5) the five portions of the flexor communis are clearly recognizable, the condylo-ulnaris (C. U.), lying beneath the medial head of the flexor carpi ulnaris (F. C. U[2]) and the palmaris longus (PL) and ventral to the ulnaris (*Ul*), the condylo-radialis (CR) lying to the radial side of the palmaris and the condylo-ulnaris, while between it and the radialis is the slender centralis (C), which corresponds to the "slender little spindle of muscle, quite distinct from the rest," described by Coues (1872), whose identification of it with the flexor longus pollicis is manifestly erroneous. Tracing the various portions down the arm, it is found that

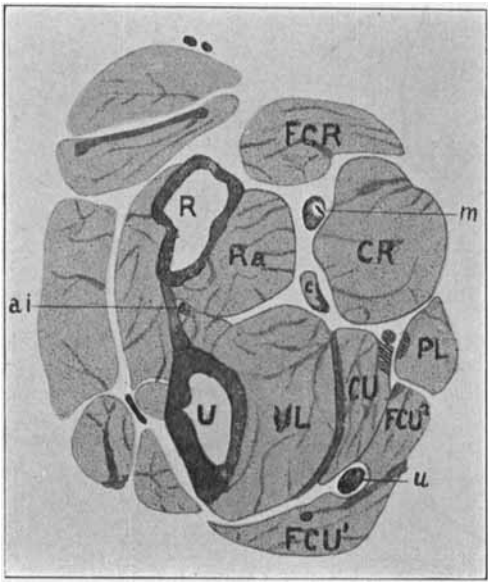


Fig. 5. Transverse section through the forearm of the Opossum. *ai*, anterior interosseus nerve; C, centralis; CR, condylo-radialis; CU, condylo-ulnaris; F. C. R., flexor carpi radialis; F. C. U.[1] and F. C. U.[2], lateral and medial portions of the flexor carpi ulnaris; *m*, median nerve; PL, palmaris longus; R, radius; Ra, radialis; U, ulna; *u*, ulnar nerve; UL, ulnaris. The shaded areas represent the flexor sublimis digitorum.

the condylo-ulnaris decreases in size rather rapidly, its fibres passing into a flat tendon which lies on the surface of the muscle in contact with the ulnaris. A portion of the muscle, represented approximately by the portion which is shaded in Fig. 5, may, however, be traced onward to the wrist where it passes into a tendon lying to the ulnar side of and superficial to the large tendon which is formed by the fusion of the main condylo-ulnar tendon with the other four portions of the flexor communis. Later the superficial condylo-ulnar tendon divides into three slips, which pass to the second, third and fourth digits and are three of the tendons of the flexor digitorum sublimis.

On tracing the palmaris longus distally it is found to develop upon its deep surface a slender tendon, represented by the shaded portion in Fig. 5, and toward the wrist the rest of the muscle passes into a flat tendon which is lost in the palmar fascia. The slender tendon can be traced onward into the hand below, *i. e.* dorsal to the flat tendon and the palmar

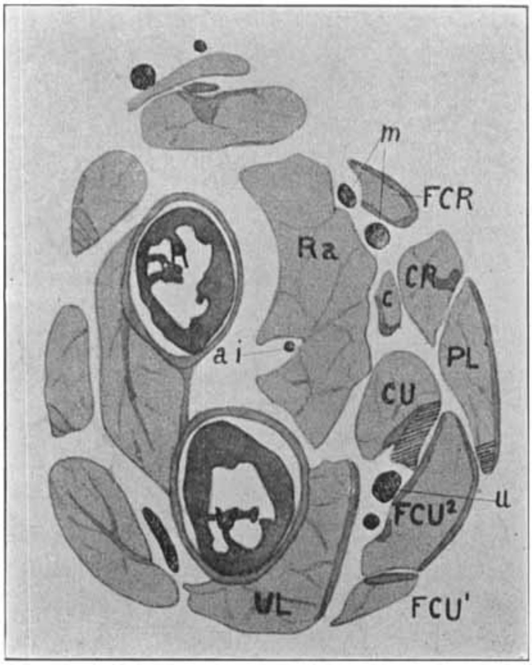


Fig. 6. Transverse section through the forearm of an embryo cat of 7 cm. Lettering the same as in the preceding figure.

fascia, and, verging toward the ulnar side of the hand, it becomes the sublimis tendon to the minimus. This origin of a portion of the sublimis from the palmaris differs from the account given by Coues, the only description of the myology of the opossum I have been able to consult; this author, as well as Windle, derives all four tendons from the condylo-ulnaris. The origin of the minimal tendon from the palmaris was found both in my sections and dissection and, as will be seen, is in harmony with what occurs in other forms in which the sublimis is in a low state of differentiation.

In the cat the condylo-ulnaris is not distinctly separated from the ulnaris in the upper part of the arm and it contains a tendon imbedded in its substance which is continuous with a tendon on the ventral surface of the ulnaris. Apparently a portion of the condylo-ulnaris inserts into the ulnaris tendon and this unites with the other four portions to form the profundus tendons as in the opossum, but the rest of the muscle, the shaded portion in Fig. 6, can be clearly seen to divide near the wrist into a smaller radial and a larger ulnar portion which remain distinct from the ulnaris and in each of which a tendon develops. The tendon belonging to the larger portion eventually divides into two slips which form the sublimis tendons for the third and fourth digits, the tendon for the smaller portion of the muscle passing to the second digit. The fourth tendon, that for the fifth digit, is formed by a slip from the palmaris longus, the relations of the sublimis being very similar to what obtained in the opossum, though the amount contributed to it by the condylo-ulnaris is somewhat greater in the cat.

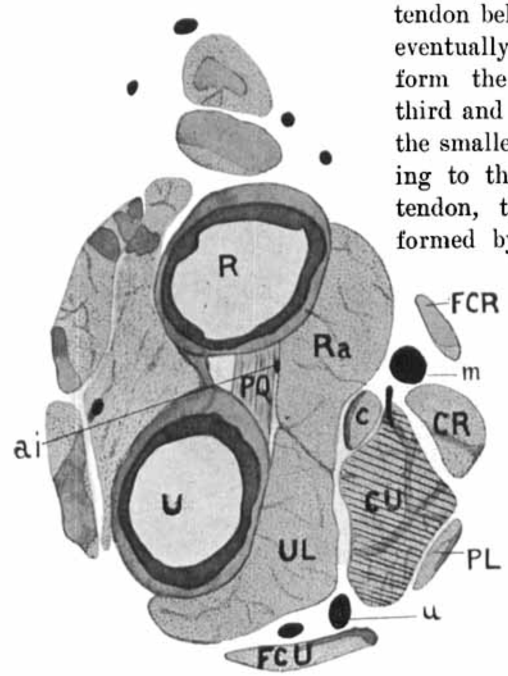


FIG. 7. Transverse section through the forearm of a new-born mouse. Lettering as in Fig. 5.

In the mouse the conditions are somewhat different, however. As usual the five portions of the flexor mass and the palmaris longus can be recognized (Fig. 7) and tracing them downward it can be seen that the ulnaris, radialis, centralis and condylo-radialis all unite together to form a profundus tendon. But the condylo-ulnaris remains quite separate from the rest and at the wrist divides into three portions which, becoming tendons, pass as the perforated tendons to the second, third and fourth digits, there being in this form, or at all events in the single individual I studied, no sublimis tendon to the fifth digit and hence no contribution to the sublimis from the palmaris longus.

These three forms afford a very definite clue to the relations of the sublimis to the flexor communis. It is principally associated with the condylo-ulnaris, the portion to the fifth digit, however, being derived from the palmaris longus. In the opossum but a small portion of the condylo-ulnaris is devoted to the formation of the sublimis, the contribution is distinctly greater in the cat and the entire muscle is taken up into it in the mouse.

Having then some indication of the line which the differentiation of the sublimis follows, we may now turn to the table given by Windle (1890) and inquire whether it reveals any further differentiation along the same line. And first of all we may consider his account of the the arrangement in the rat. The condylo-ulnaris is stated to be absent in this form, while the other four portions of the flexor mass are recognizable, and the sublimis is indicated as being an independent muscle. This may with propriety be interpreted, on the basis of what I have found in the mouse, that the condylo-ulnaris has been completely taken up into the sublimis, and, applying the same interpretation to other forms tabulated by Windle, we find that the same condition obtains in the majority of the rodentia. Proceeding to higher forms we find that in *Cebus capucinus* the condylo-ulnaris is again wanting and that, furthermore, the sublimis is closely associated with the condylo-radialis, that is to say, the sublimis not only includes the whole of the condylo-ulnaris but also receives a contribution from the condylo-radialis. The same condition occurs also in *Cynocephalus maimon,* with the addition that in this form the centralis has also disappeared, having, I imagine, been taken up into the sublimis. This disappearance of the centralis is also noted for several other monkeys, although in these no mention is made of any association of the condylo-radialis with the sublimis, and, finally, in the orang, it is stated that not only are the condylo-ulnaris and centralis wanting, but this is also the case with the condylo-radialis, the sublimis at the same time having a radial origin.

The condition in the orang is essentially the same as in man and we may now see what a study of sections of a human arm reveals, my preparations being made from an embryo of 4.5 cm. Instead of being absent in part all the five portions of the flexor mass can be readily distinguished (Fig. 8), and on tracing them downward it is found that the condylo-ulnaris, the condylo-radialis and the centralis unite together to form the flexor sublimis; the ulnaris is the flexor profundus and the radialis the flexor longus pollicis. In other words instead of the three condylar portions of the flexor communis being absent or only occasionally present as anomalies in man, they are always present and are incorporated in the flexor sublimis. Windle maintains that the condylo-radialis is represented by the second or ulnar head of the flexor longus pollicis; this I doubt. There is no question but that, in the arm I studied, the entire mass of the condylo-radialis passed into the flexor sublimis, and the ulnar head of the radialis, *i. e.* the longus pollicis, is readily accounted for by the fact that that portion not infrequently takes its origin from the ulna as well as from the radius.

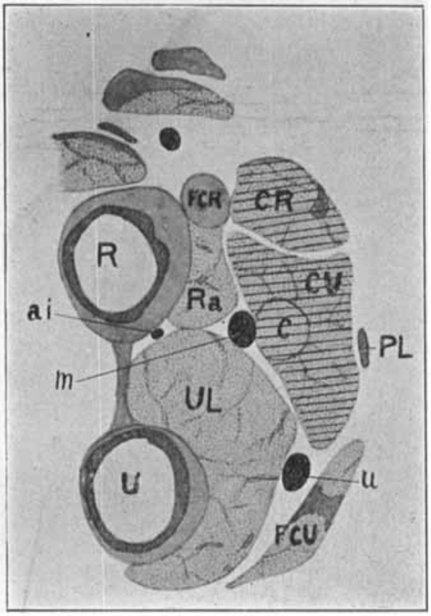


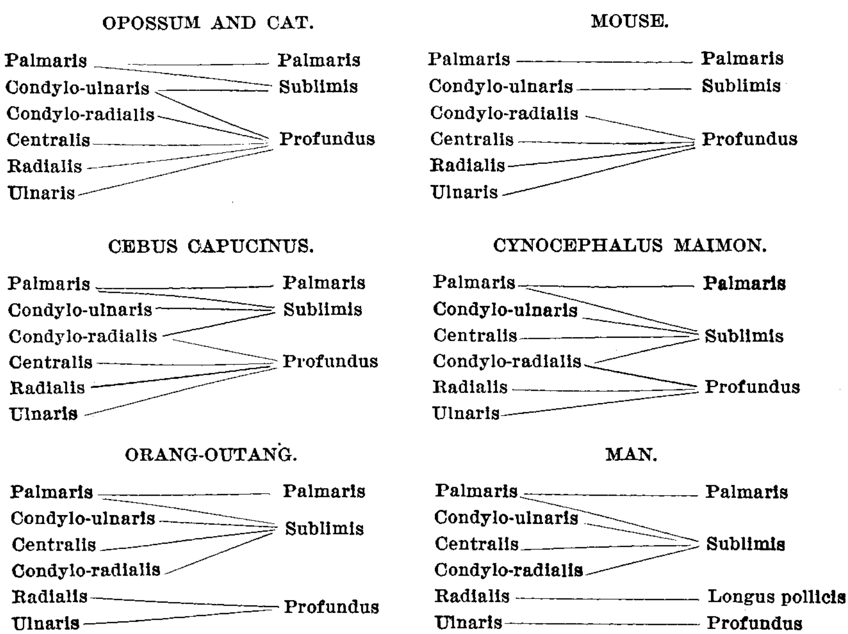
FIG. 8. Transverse section through the forearm of a human embryo of 4.5 cm. Lettering as in Fig. 5.

The various portions of the sublimis possess an interesting relation to the digits. The tendons for the two ulnar fingers come from the condylo-ulnaris; that for the medius is formed entirely from the condylo-radialis and in the arm lies to the radial side of the tendon for the index, crossing obliquely over that tendon upon its palmar surface at the wrist; the index tendon is formed mainly from the centralis, though I could not be certain that it did not also include some portions of the condylo-ulnaris.

The history of the sublimis, then, seems to be as follows: In the mammalian prototypes the arrangement of the forearm flexors was somewhat as is now found in the monotremes, there being a single flexor mass without any marked differentiation of a superficial and a deep portion. The single tendon formed from this mass divided at the wrist into a superficial set of sublimis tendons and a deep set representing the profundus, but the muscle mass of the forearm showed no such separation. Its first differentiation consisted in the separation of a palmaris longus, which became attached to the minimal sublimis tendon as well as to the palmar fascia, and a portion of the condylo-ulnaris separated and became continuous with the other three sublimis tendons. Later the entire condylo-ulnaris was brought into connection with the sublimis and the portion of the palmaris which joined the ulnar tendon separated from that muscle and became incorporated in the condylo-ulnaris. In higher forms the centralis also united with the sublimis tendons as well as a portion of the condylo-radialis and, finally, in the anthropoids and in man, all the superficial or condylar portions of the original flexor communis separated to join the sublimis tendons, leaving only the ulnaris and radialis attached to the profundus tendon. In brief, starting with a condition in which there is no definite distinction between a superficial and a deep layer of antibrachial flexors, there has been a gradually increasing separation of the superficial layer, until, finally, we have in the flexor sublimis *plus* the palmaris longus the exact homologue of the palmaris superficialis of the reptilia.

After what has been already said it is perhaps hardly necessary to point out that my views as to the significance of such anomalies as the occurrence of a distinct centralis in man are quite different from those expressed by Windle. For I do not believe its occurrence is the appearance of a muscle usually absent, but, on the contrary, the muscle is always present as a constituent of the sublimis and its recognition as a distinct structure is due to its failure to unite with the other components of that muscle. Indeed, it seems highly probable, that we are in error in stating, as is usually done, that the palmaris longus is not infrequently absent in man; we should rather say that in many cases it becomes completely incorporated with the sublimis, just as a portion of it, as represented in the lower forms, does normally.

The progressive development of the sublimis in the mammalia, together with the homologies of the flexor muscles in various forms, may be shown as follows:



IV. The Extension of the Long Flexors into the Hand.

We come now to the concluding chapter in the history of the flexors of the forearm. It has been shown that they are primarily confined to the forearm, acting on the digits only by the intervention of the palmar aponeurosis and the palmar muscles which arise from it, and it remains to be seen how the direct connection with the digits which they possess in the mammalia has been brought about.

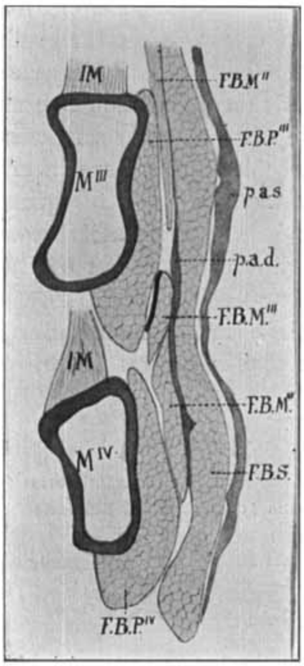


Fig. 9.

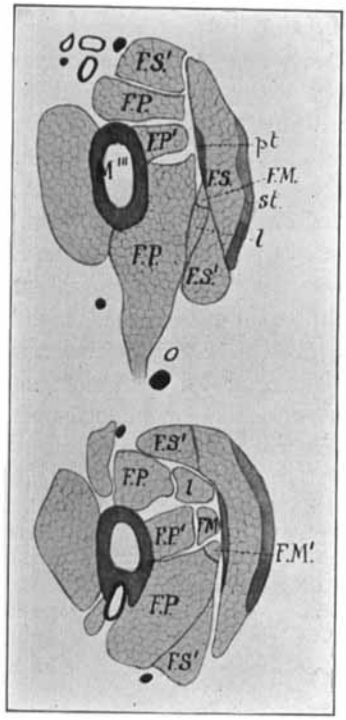


Fig. 10.

Fig. 9. Transverse section through the third and fourth metacarpals of *Amblystoma tigrinum*. F. B. P., flexor brevis digitorum profundus; F. B. M., flexor brevis medius; F. B. S., flexor brevis superficialis; I. M., intermeta-carpalis; M^{III} and M^{IV}, third and fourth metacarpals; *p. a. s.*, and *p. a. d.*, superficial and deep layers of the palmar aponeurosis.

Fig. 10. Transverse section through the second and third digits of *Amblystoma tigrinum*. F. P., and F. P.′, flexor brevis digitorum profundus; F. M., median portion of flexor brevis medius; F. M.′, portion of flexor brevis medius which unites with the flexor profundus; F. S., median portion of flexor brevis superficialis; F. S.′, portions of the flexor superficialis which unites with the flexor profundus; *l*, lumbricalis; *i. e.*, lateral portion of the flexor medius; *pt*, profundus tendon; *st*, superficial tendon.

To do this it is necessary to return to the amphibia and consider the relations of the palmar and forearm muscles to the palmar aponeurosis.

In Amblystoma, for example, as a series of sections is traced distally, one finds some distance above the wrist a layer of fascia making its appearance upon the palmar surface of the palmaris superficialis. This is the palmar aponeurosis, and it is into the deep (i.e. the dorsal) surface of this that the superficialis inserts. More distally the aponeurosis receives the insertion of the palmares profundi, also upon its deep surface, and immediately distal to this insertion one finds some muscle bundles making their appearance in the substance, as it were, of the aponeurosis. These bundles represent the proximal portion of the origin of the *flexores digitorum breves superficiales* (Eisler), and in more distal section they increase in number and form a continuous sheet (Fig. 9, F. B. S.), which divides the palmar aponeurosis into two layers, a more superficial one (*p. a. s.*) lying ventral to the flexores and a deeper one (*p. a. d.*) dorsal to them. The muscle sheet soon divides longitudinally into three portions, the more lateral parts, destined for the second and fifth digits, separating for a median part destined for the third and fourth fingers. On account of the divergence of the second and fifth digits from the median line a series of sections transverse to the axis of the forearm will, when continued into the hand, cut these digits obliquely, so that the relations of their muscles cannot be as readily perceived as those of the third and fourth digits; for the present, therefore, attention will be directed solely to the arrangement of the muscles and aponeuroses belonging to these latter digits.

Immediately beneath the deep layer of the palmar aponeurosis and arising from its deep surface are the *flexores digitorum breves medii* (Eisler) (F. B. M.), while below these again and resting directly upon the palmar surfaces of the metacarpal bones from which they arise are the flexores digitorum breves profundi (F. B. P.). Finally, stretching across between the metacarpals are the *intermetacarpales* (I. M.). The flexores superficiales and medii are the muscles which especially interest us just now and they may be briefly described as follows, so far as the portions which pass to the third and fourth digits are concerned. At the junction of the proximal and distal halves of the metacarpals the superficialis sheet divides into two portions corresponding to the two digits, and at about the same time a longitudinal division of the superficial layer of the palmar aponeurosis occurs, a strong slip of it being contained distally upon the palmar surface of each superficialis slip (Fig. 10), while beneath each superficialis slip a thickening appears in the deep layer of the aponeurosis. More distally the lateral portions of each superficialis slip separate (Fig. 10, F. S.') and pass dorsally to fuse with the corresponding flexor brevis profundus (F. P.), while the remaining median portion later on divides into slips, which may be traced distally to their insertion into either side of a strong fibro-cartilaginous nodule occurring at the metacarpo-phalangeal joint.

In the meantime the deep layer of the palmar aponeurosis has divided longitudinally into slips or tendons, which are the continuations of the thickenings already mentioned as occurring in it, and one of these tendons lies immediately below the median portion of each flexor superficialis slip passing to the digits under consideration (Fig. 10, *pt*). When the final division of the muscle slips occurs, the tendons derived from the deep layer of the aponeurosis pass ventrally between the two terminal slips of the muscle and unite with the superficial tendons, passing on with them to be inserted into the base of the terminal phalanges.

The flexores medii, compared with the superficiales, are small muscles. As they are traced distally that for the fourth digit (Fig. 9, F. B. M.^{IV}) lies over the palmar surface of the fourth metacarpal, being separated from it by the corresponding flexor profundus (F. B. P.^{IV}), while that for the third digit (F. B. M.‴), much smaller than the other, lies rather to the ulnar side of its metacarpal. The muscle of the fourth digit divides longitudinally into three slips (Fig. 10, F. M., F. M.^{I} and *l*), that upon the ulnar side uniting with the subjacent flexor profundus IV, while the median and radial slips insert into the metacarpo-phalangeal fibro-cartilage, the median one entering into close relationship with the underlying median portion of the flexor profundus (F. P.′). The muscle of the third digit, owing to its more ulnar position with reference to the axis of the digit, lacks a radial slip, dividing into only two portions (F. M. and *l*), the more radial of which corresponds to the median part of the fourth muscle and like it unites somewhat closely with the underlying portion of the flexor profundus, while the ulnar portion inserts independently into the ulnar side of the metacarpo-phalangeal fibro-cartilage.

The points to which attention needs to be especially directed for our present purpose are (1) the splitting of the palmar aponeurosis into two layers by the origin of the flexores breves superficiales, (2) the formation of tendons by the deep layer of the aponeurosis, which, after the division of the flexores superficiales into their terminal slips, pass up between them to join the tendons from the superficial layer of the aponeurosis, and (3) the origin of the flexores breves medii from the under surface of the deep layer of the aponeurosis.

Turning now to the reptilia one is at once struck by the fact that there is no strong aponeurotic layer covering the surface of the flexor brevis superficialis (flexor sublimis seu perforatus Auct.) (Fig. 11, F. B. S.).

On the other hand a very strong aponeurosis (*vc*), frequently partly transformed into cartilage, is present *beneath* the flexor superficialis, giving origin to this muscle from its palmar surface and receiving the insertion of the forearm muscles as described on a preceding page.

We may for convenience confine our attention mainly to the muscles associated with the three middle digits, for the same reason that led us to disregard the lateral digits in the amphibia.

Traced distally the central portion of the superficialis sheet divides into three portions (Fig. 11, F. B. S.), which pass to the three digits we are considering, and underneath each portion there is a strong tendon which is a distal continuation of the volar cartilage. Shortly before reaching the metacarpo-phalangeal joint each portion of the superficialis splits into two slips, which separate so as to lie one on each side of the strong tendon just mentioned and gradually fade out into the fascia covering that tendon.

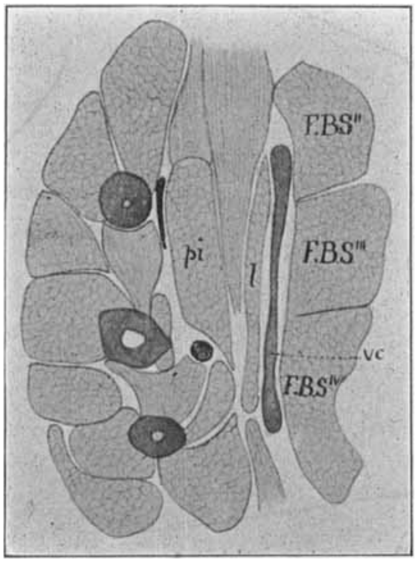


FIG. 11. Transverse section through the palm of *Liolepisma laterale*. F. B. S., flexor brevis digitorum superficialis; *l*, lumbricalis; *i. e.*, superficial layer of the flexor brevis medius; *pi*, palmar adductors; *t. e.*, deep layer of the flexor brevis medius; *vc*, volar cartilage.

The muscles which correspond to the amphibian flexores breves medii reach a much greater development than in the lower group and are arranged in two distinct layers, the superficial one (Fig. 11, *l*) lying immediately beneath the volar cartilage, from which it takes origin, while the deeper one (*pi*) is in relation with the underlying metacarpal bones. This latter layer does not concern us at present and will be left for consideration on another occasion. The superficial layer when traced distally divides into four portions which pass to the II-V digits, there being no portion for the pollex. Each portion lies beneath the corresponding portion of the flexor superficialis, being separated from it by the strong tendon derived from the volar cartilage. More distally each of the portions corresponding to digits II-IV divides into two slips which come to lie on either side of the corresponding strong tendon and are finally inserted into opposite sides of the base of the metacarpo-phalangeal fibrocartilage of the digit to which they belong.

In the case of the fifth digit the conditions are slightly different, in that the superficial sheet of the flexor medius does not extend laterally beyond its radial border, and hence, when the division of the sheet into separate slips takes place, that for the minimus lies upon the radial side of its digit and does not divide into two terminal slips as do the others, but inserts entirely into the radial side of the arthrodial fibrocartilage. The arrangement of these muscle-slips is shown diagrammatically in Fig. 12.

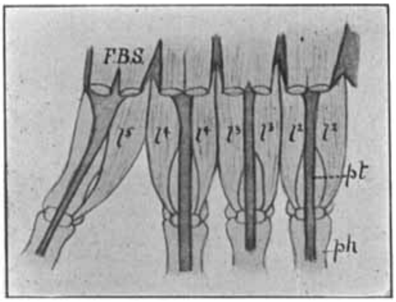


FIG. 12. Partly diagrammatic representation of the arrangement of the lumbricales (*l*), in *Liolepisma laterale*. F. B. S., flexor brevis superficialis; *ph*, phalanx; *pt*, profundus tendon.

If now we proceed to compare these arrangements with those seen in the amphibia we arrive at the following conclusions. The portion of the superficial layer of the amphibian palmar aponeurosis, which covers the flexor brevis superficialis, has disappeared in the reptilia or is represented in the flexor, if one prefers to state it that way. The more proximal portions of the aponeurosis, however, are represented by the volar cartilage, and the strong tendons which are continued distally toward the fingers from the volar cartilage are, in their proximal portions, the representatives of the tendons formed from the deep layer of the amphibian aponeurosis. Beyond the point of the bifurcation of the slips of the flexor superficialis these tendons in the amphibia fuse with the tendons

FIG. 13. Diagram showing the mode of formation of the profundus tendon. F. B. S., flexor brevis superficialis; F. B. M., flexor brevis medius; P. A., palmar aponeurosis. The stippled portion of the aponeurosis disappears in the reptilia.

from the superficial layer of the aponeurosis, and it is probable that in the reptilia the tendons from the same point are equivalent to those of the amphibia. The annexed diagram (Fig. 13) will give, I trust, a sufficiently clear idea of the arrangement in the two groups, the portion of the amphibian aponeurosis which has disappeared in the reptilia being indicated by the stippling.

From the reptilian arrangement as interpreted above to the mammalian the passage is easy. The tendons which are continued distally from the volar cartilage to the digits clearly correspond to the mammalian profundus tendons and the superficial layer of the flexor brevis medius is, I believe, equivalent to the mammalian *lumbricales.* The deep layer of the medius, however, entering as it does into relation with the flexores breves profundi and the metacarpals, is probably represented in the mammalia by the palmar adductors, an homology which I hope to consider in detail in a later paper. It is interesting to compare the arrangement of the lumbricales in Echidna as described by Westling (1889)[3] with that which I have found in the superficial layer of the flexor brevis medius of the reptilia.

The reptilian equivalents of the sublimis tendons are indicated, I believe, by the condition found in the monotremes and in certain marsupials. In Ornithorhynchus a muscle has been described as the flexor digitorum sublimis (Smith, Westling), which has essentially the same relations as the flexor brevis superficialis of the reptilia, and in Thylacinus and Phascogale (Cunningham, 1882), this muscle is represented by four minute tendons which arise from the strong tendon of the flexor communis digitorum. The communis tendon I take to be practically the homologue of the reptilian aponeurosis in which the volar cartilage is developed and the small tendons which arise from its surface are therefore equivalent to four of the slips of the flexor brevis superficialis of the reptilia, which have undergone, as so frequently happens, transformation into connective tissue (see von Bardeleben and Bland Sutton).

The identification of the tendon of the flexor communis with the reptilian palmar aponeurosis is not, however, quite exact, for there exists in the mammalia a palmar fascia which covers the sublimis tendons and receives the insertion of the palmaris longus. This muscle is a portion of the condylar flexor mass of the forearm and is, as has already been seen, closely related to the sublimis, containing, in the lower mammals, elements which in higher forms are included in that muscle. This being the case it must be supposed that the original insertion of the palmaris was with the rest of the flexor mass into the palmar aponeurosis, and that with the separation of the palmaris there has also been a separation of a palmar layer of the aponeurosis to form the mammalian palmar fascia. The relations of the superficial thenar and hypothenar muscles to the fascia support this view of its origin, since these muscles are persisting portions of the flexor brevis digitorum superficialis. The correct equivalent, accordingly, of the reptilian palmar aponeurosis in the mammalia is the tendon of the flexor communis *plus* the palmar fascia, but it should be pointed out that there is a strong probability, that the distal

[3] I have not been able to consult this paper, but the figure which bears on this point is reproduced by Leche in the Mammalia of Bronn's Thierreich.

portions of the mammalian fascia may represent the portion of the amphibian palmar aponeurosis which has disappeared in the reptilia I have studied.

The phylogenetic history of the mammalian long flexors, which has been traced in the preceding pages, may be briefly stated as follows: In the primary condition the entire flexor mass of the forearm terminates at the wrist, a certain portion of it inserting into the bones of the forearm and carpus and the rest into a strong palmar aponeurosis. From the latter two sets of muscles take origin, (1) from its substance the flexores breves superficiales, and (2) from its deep surface the flexores breves medii. By the mode of origin of the first of these the palmar aponeurosis is divided distally into two layers, a more superficial one which is prolonged distally into strong tendons which insert into the bones of the terminal phalanges, and a deep one also prolonged into tendons which pass between the terminal steps of the flexores superficiales to unite with the superficial tendons. This is the amphibian stage.

In the second or reptilian stage the portion of the superficial layer of the palmar aponeurosis which covers the flexores breves superficiales disappears and the action of the forearm flexors which insert into the aponeurosis is distributed to the digits entirely through the tendons of the deep layer, which, together with the persisting terminal portions of the superficial tendons, may be recognized as the equivalent of the mammalian profundus tendons. The portions of the two layers of the forearm flexors which act on the aponeurosis fuse more or less completely, the flexores breves superficiales retain their amphibian relations, while the flexores medii divide into two layers, the more superficial of which represents the lumbrical muscles of the mammalia.

In the last or mammalian stage the flexores breves superficiales become transformed more or less completely into the tendons of the flexor sublimis, and as the scale is ascended, a gradually increasing amount of the superficial portion of the flexor communis separates to become continuous with these tendons, until, in man, the entire condylar portion of the muscle, except so much as is represented by the palmaris longus, is taken up into the flexor sublimis.

In the cases of the first and fifth digits some departures from the processes outlined above occur, but these may be more conveniently discussed in connection with the history of the other hand muscles in a later paper.

The results recorded above as to the relations of the sublimis tendons to the forearm muscles agree in general with those arrivel at by Eisler, but I have succeeded, I believe, in tracing with greater exactness the processes by which the final arrangement has been acquired. Eisler has failed to perceive the true relations of the profundus tendons to the amphibian palmar aponeurosis, relations which it would be difficult to discover without the aid of sections. He has, however, recognized the relations of the flexores breves superficiales to the sublimis and the probable end to end union of the two muscles, an arrangement which, as he points out, throws clear light on many of the anomalies occurring in connection with the human sublimis.

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