THE PHYLOGENY OF THE PALMAR MUSCULATURE.

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WITH 11 TEXT FIGURES.

Writing in the nineties of the nineteenth century, Leche (1893) introduces his account of the intrinsic muscles of the mammalian hand with the following words: "Da die myologische Literatur noch keine Materialen enthält, welche für eine vergleichende oder auch nur zusammenfassende Darstellung der Handmuskulatur genügt, und da ausserdem die Nomenclatur der verschiedenen Componenten dieser Muskelgruppe ausserordentlich schwankend ist, halte ich es für das Geeignetste eine rein descriptive Darstellung der wichtigeren Befunde bei den verschiedenen Säugethierordnungen zu geben." Although this indictment may not in all its particulars be as pertinent now as it was, there are still remaining for solution many questions concerning the fundamental plan of the mammalian hand muscles and their phylogenetic significance, and the following pages record an attempt to diminish the number of these.

In a previous paper (1903), in which the flexor muscles of the forearm were considered from the phylogenetic standpoint, I showed that the flexor sublimis digitorum had been evolved by the union of certain portions of the antibrachial flexor mass, which primarily terminated at the wrist joint, with the most superficial layer of the intrinsic hand musculature, part of the latter undergoing degeneration to form the terminal portions of the tendons. The profundus tendons, on the other hand, were evolved from a deeper layer of the palmar aponeurosis and the lumbrical muscles represent a layer of palmar muscles which originally arose from that aponeurosis. I did not attempt, however, in that paper, a complete reconstruction of the history of the palmar musculature, and I now propose to correct that omission as far as possible by recording the results of a comparative study of the palmar musculature of the same series of forms as were employed in the earlier paper. These results are based mainly on the study of serial sections.

I. The Palmar Muscles of the Urodelous Amphibia.

The muscles of the Urodele hand are arranged in four layers, for which the terminology employed by Eisler (1895) is quite satisfactory. These layers are (1) a layer of *flexores digitorum breves superficiales* (Fig. 1, *F. B. S.*) arising from the palmar aponeurosis, (2) a layer of *flexores digitorum breves medii* (*F. B. M.*) also arising from the palmar aponeurosis, (3) a layer of *flexores digitorum breves profundi* (*F. B. P.*) arising from the carpals and metacarpals and (4) a layer of *intermetacarpals* (*Im*). A very considerable amount of similarity exists in the arrangement of the various digital slips derived from or composing each of these layers, although departures from the general plan occur in the marginal portions of some of the layers.

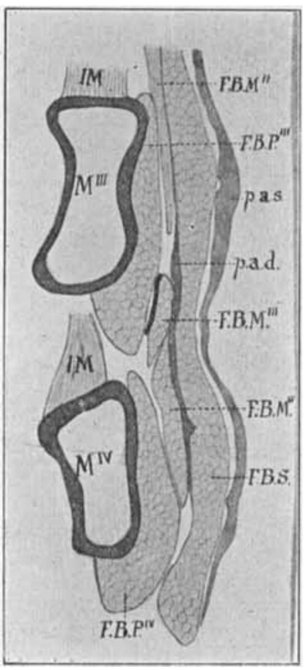

Fig. 1. Transverse section through the third and fourth metacarpals of *Amblystoma tigrinum*. *F. B. P.*, flexor brevis digitorum profundus; *F. B. M.*, flexor brevis medius; *F. B. S.*, flexor brevis superficialis; *I. M.*, intermetacarpalis; M^{iii} and M^{iv}, third and fourth metacarpals; *p. a. s.* and *p. a. d.*, superficial and deep layers of the palmar aponeurosis.

The *flexores digitorum breves superficiales*.—The origin of these muscles in Amblystoma is a curved line whose concavity is directed proximally and which is in the substance of the palmar aponeurosis, dividing this into a superficial and a deeper layer (Fig. 1, *p. a. s.* and *p. a. d.*). The muscular sheet arising from this line soon divides into portions corresponding to the digits, indeed, in some cases the portions are separate from their origin. The general plan for most of the portions may be briefly described as follows, according to what occurs in the third digit (Fig. 2). This portion divides into three slips, (1) a median one (F. S.) which underlies the tendinous prolongation of the palmar aponeurosis to the digit and eventually divides to be inserted into either side of the fibro-cartilage of the metacarpo-phalangeal joint, and (2 and 3) two lateral slips (F. S′.) which also insert into the sides of the metacarpo-phalangeal fibro-cartilage, uniting as they do so with the lateral slips of the flexor digitorum brevis profundus. In the fourth digit the arrangement is essentially the same as in the third, but in the index and minimus only two slips are formed from each portion, the ulnar one being wanting in the index and the radial in the minimus.

From the ulnar border of the muscle an additional portion is separated off which becomes intimately associated with the large ulnar slip of the flexor brevis profundus minimi digiti and forms what may be regarded as an *abductor minimi digiti.* At its origin it is associated with the insertion of the flexor carpi ulnaris, indeed, the fibres of this latter muscle are to a certain extent continued directly into the abductor, additional fibres being added, however, from the ulnar carpal bone.

The *flexores digitorum breves medii* have essentially the same arrangement as do the superficiales. They arise from the dorsal surface of the palmar aponeurosis and are inserted into the fibro-cartilages of the metacarpo-phalangeal joints of each of the four digits. The slips for the medius and annulus arise together and at first form a single muscle, but later on they separate and that for the annulus divides into three slips (Fig. 2, *F. M.*, *F. M'.* and *l*) which become associated with three corresponding slips of the flexor brevis profundus and are inserted with them. The portion for the medius divides into two slips only, comparable to the ulnar and median slips of the annulus, and in the index and minimus only two slips are formed, a radial one being lacking in the index and an ulnar one in the minimus. The insertion in both these digits is, however, in association with the corresponding slips of the flexor brevis profundus.

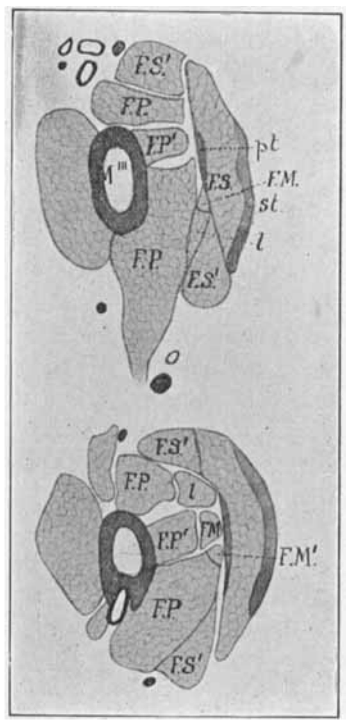

Fig. 2. Transverse section through the third and fourth digits of *Amblystoma tigrinum.* *F. M.*, flexor brevis medius; *F. P.*, flexor brevis profundus; *F. S.*, flexor brevis superficialis; *l*, one of the lateral portions of the flexor brevis medius; *pt*, deep palmar aponeurosis; *st*, superficial palmar aponeurosis.

The *flexores digitorum breves profundi* are four distinct muscles. They arise from the carpal bones and as they are traced distally each is divided into two lateral slips (Fig. 2, *F. P.*) by a median slip which arises from the palmar surface of the metacarpal (*F. P'.*), so that distally three profundus slips may be recognized in each digit. These unite, as has already been stated, with slips from the medii and superficiales to insert into the metacarpo-phalangeal fibro-cartilages. The radial slip of the muscle of the index and the ulnar one of that of the minimus are larger than their fellows and the ulnar slip of the minimus becomes intimately associated with the ulnar portion of the flexor brevis superficialis which has been referred to above as forming the abductor minimi digiti.

The *intermetacarpales,* as their name indicates, extend across between adjacent metacarpal bones (Fig. 1, *Im*). They are consequently three in number and each has a somewhat oblique course across the intermetacarpal interval in which it lies. A muscle takes origin from each side of the fourth metacarpal and extends distally to be inserted, the one into the radial side of the fifth metacarpal, and the other into the ulnar side of the third; the third muscle arises from the radial side of the third metacarpal and is inserted into the ulnar side of the second.

In addition to these muscles, which are the hand muscles proper, there is in the third digit a strictly digital muscle, the *interphalangealis,* which arises from the palmar surface of the distal portion of the proximal phalanx and is inserted into the fibro-cartilage of the proximal interphalangeal joint of the digit.

I have endeavored in this description to be as brief as possible, since, so far as the final object in view, namely, the phylogeny of the mammalian hand muscles, is concerned, a minute account of the amphibian muscles seems unnecessary. What is of importance is a clear perception of their definite arrangement in layers, and a word seems advisable with reference to the relation of these layers to other structures. For unless definite dividing planes marked out by other structures can be recognized it will be a matter of no little difficulty to homologize the layers found in higher forms with those occurring in the group now under discussion.

In this connection one's thoughts naturally turn to the nerves as offering possible guides, and to a certain extent they do. It is not, however, in the details of their distribution to the individual muscles that they are of value in this respect, but rather in their general course and distribution. I do not intend to discuss here the significance of nerve supply in the identification of muscles; I have already in a previous paper (1903) referred to this question. I may say, however, that from what I have observed it seems clear to me that too much importance has been attached to the nerve trunks from which the various individual limb muscles are supplied. Authors have been too apt to assume that what is termed the ulnar nerve, for example, in one form is the exact equivalent of the similarly named nerve in another form, and have concluded either that equivalent muscles may have entirely different innervations or with Gegenbaur (1889), that muscles though similar in all other respects but differing in their innervation are entirely different structures. Gegenbaur bases his conclusion on the assumption that the muscle is the end organ of a motor nerve, and, granting this and granting also that the principal nerve trunks of a limb are throughout exactly equivalent, his conclusion is logical. But there is evidence to show that the second assumption is unwarranted. In other words, the muscle may be regarded as the end organ of the nerve fibre, but that fibre need not in all cases follow the same path to reach its destination; in some cases it may follow the path marked by the ulnar trunk and in another that indicated by the median. The origin and termination of a nerve fibre are in all probability definite in their relations, but the relations of the intervening portion of the fibre may vary greatly. The nerve will follow in general the path of least resistance and this may carry it in one case into one of the larger trunks and in another into a different one, and we may thus have equivalent muscle fibres supplied from different nerve trunks, but yet by equivalent nerve fibres.

But the lines of least resistance which the main nerve trunks will tend to follow are to a marked extent definite, being largely associated in the limbs with the arrangement of the muscles in layers. Consequently, unless there be sufficient reasons to the contrary, the position of the main nerve stems may be taken as guides for the homology of certain of the muscle layers, especially in the amphibia and reptilia, in which there is great similarity in the arrangement of the main nerve trunks. It is of importance, therefore, to indicate the general arrangement of the principal nerves with reference to the muscle layers in the amphibia.

The nerves of the amphibian forearm are three in number, a ramus profundus, a ramus superficialis ulnaris and a ramus superficialis medialis. Of these the last is confined entirely to the forearm so far as its muscular distribution is concerned, the other two being continued into the hand. The ramus profundus at the wrist rests directly upon the carpal bones and as it is traced distally curves to lie between the flexor brevis profundus III and the flexor brevis medius II, later on breaking up into a number of branches which supply the muscular slips associated with the second and third digits and with the radial side of the fourth. The ramus superficialis ulnaris at its entrance into the hand also lies directly upon the volar surface of the carpus and is continued onward between the ulnar slips of the flexor brevis profundus and flexor brevis medius, eventually breaking up into branches for the muscles inserted into the fifth digit and the ulnar side of the fourth.

The position of the main stems of the two nerves is therefore in the interval between the flexores breves profundi and the flexores breves medii, and there are consequently in the Urodeles two layers of muscles superficial (volar) to the nerves, namely, the flexor brevis medius and the flexor brevis superficialis, and two dorsal to them, namely, the flexor brevis profundus and the intermetacarpales.

For the separation of the layers of each of these pairs no assistance is obtainable from the nerves, but in the case of the volar pair the separation is clearly indicated by the deeper layer of the palmar aponeurosis, while the position and direction of the intermetacarpales render them readily distinguishable from the flexores breves profundi.

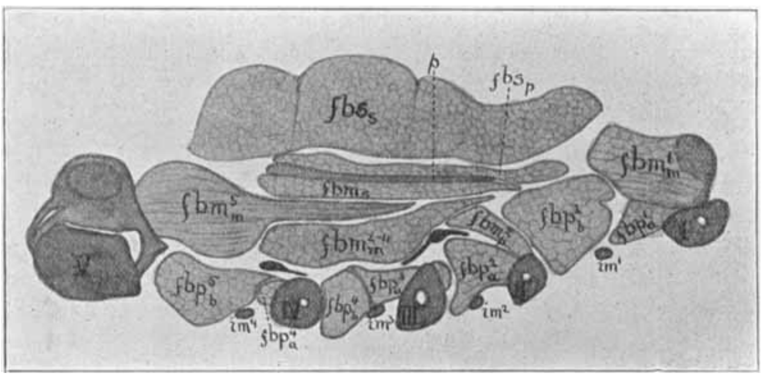

FIG. 3. Transverse section through the hand of *Liolepisma laterale*. fbm_s, superficial layer of the flexor brevis medius; fbm_m, middle layer of the flexor brevis medius; fbm_p, deep layer of the flexor brevis medius; fbp_a, muscles of the flexor brevis profundus which insert into their own digits; fbp_b, muscles of the flexor brevi profundus which insert into adjacent digits; *im*, ligaments representing the intermetacarpales; *p*, palmar aponeurosis which gives rise to the deep tendons to the digits.

II. The Muscles of the Reptilian Hand.

I have studied the hand muscles of the lacertilia from serial sections of *Liolepisma laterale* and *Callisaurus draconoides* and also by dissection of a fully grown specimen of *Iguana tuberculata* Gray, opportunity for the examination of the last having been afforded by the courtesy of my colleague, Professor J. E. Reighard. The dissection of the iguana proved to be of very great assistance in elucidating the extremely complicated appearances presented by the transverse sections of the other species, since, owing to the development of intersecting tendinous bands in certain of the layers, whereby they had the appearance of being composed of a number of distinct slips, and, further, owing to the lack of distinct layers of fascia separating some of the layers, it was by no means easy to recognize the true significance of some of the muscles.

As pointed out in my paper on the forearm flexors (1903), the superficial aponeurosis which covers the flexor brevis superficialis in the amphibia is wanting throughout the greater part of its extent in the reptilia, so that the muscle is exposed completely on the removal of the integument. On the other hand, one finds a strong aponeurosis beneath the flexor superficialis (Fig. 3, *p*), arising from the distal edge of the volar cartilage or ossification (Figs. 4 and 5, *vc*) and passing distally to become the profundus tendons. This beyond question is comparable to the aponeurosis which separates the middle and superficial layers in the amphibia and may therefore serve as one of the orientation planes for the comparison of the muscles in the two groups, the position of the palmar nerves, which is quite as distinct and definite as in the amphibia, marking a second plane. The muscle tissue lying between these two planes may be compared with the amphibian flexor brevis medius, that immediately dorsal to the nerve layer to the amphibian flexor profundus, and, finally, more dorsally still the equivalents of the intermetacarpals should be found.

Working on this basis one at once observes that the superficial and middle layers are much more complicated than in the amphibia. It will be remembered that in that group the lateral parts of each portion of the flexor brevis superficialis unite toward their insertion with the profundus slips and that a similar fusion of the slips of the medius and profundus occurs. This condition becomes in one sense emphasized in the reptilia in that slips separate from both the superficialis and medius to form distinct muscles and, indeed, distinct muscle strata, which unite with subjacent layers at their insertions, and it is accordingly possible to recognize in the flexor superficialis a *stratum superficiale* (Fig. 3, fbs_s) and a *stratum profundum* (fbs_p), and in the flexor medius a *stratum profundum* (fbm_p) distinct from the rest of the layer. But this is not all, for on the development of the profundus tendons in the reptilia from the deep layer of the palmar aponeurosis, the superficial portions of the flexor medius, as I have already pointed out (1903), remain in association with these tendons, forming the equivalents of the mammalian lumbricales, and we thus have a *stratum superficiale* (fbm_s) as well as a deep one separated from the flexor medius, which may, accordingly, be described as consisting of three strata. Thus the reptilian layers compared with those of the amphibia are as follows:

Amphibia.	Reptilia.
Fl. brevis superficialis	Fl. brevis superficialis stratum superficiale.
	Fl. brevis superficialis stratum profundum.
Fl. brevis medius	Fl. brevis medii stratum superficiale.
	Fl. brevis medii stratum medium.
	Fl. brevis medii stratum profundum.
Fl. brevis profundus	Fl. brevis profundus.
Intermetacarpales	Intermetacarpales.

The *flexor digitorum brevis superficialis.*—The *stratum superficiale* is a strong muscle arising from the surface of the volar cartilage and

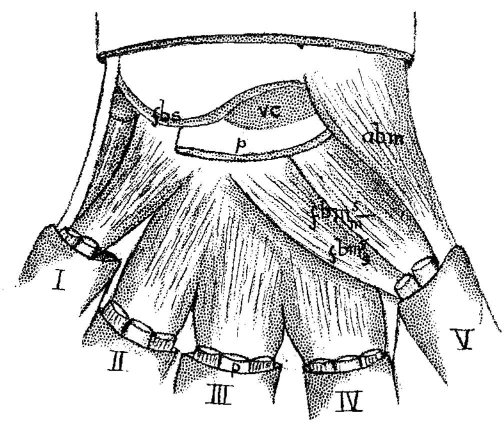

FIG. 4. The stratum medium of the flexor brevis medius of *Iguana*. fbm^5_m, portion to the fifth digit; fbm_s^5, portion of the stratum superficiale to the fifth digit; *fbs*, line of origin of the flexor brevis superficialis; *abm*, abductor minimi digiti; *p*, the deep palmar aponeurosis and the profundus tendons; *vc*, volar cartilage.

aponeurosis, the line of the origin (Fig. 4, *fbs*) being somewhat curved, with its convexity directed distally and prolonged much more proximally at its ulnar extremity than at the radial. Traced distally it divides into six portions, one for each of the four radial digits and two for the minimus. The portions for the second, third and fourth digits when traced distally are found to divide each into two slips which diverge to fade out in the fibrous tissue covering the sides of the metacarpo-phalangeal joint, allowing the profundus tendon to pass between them and become superficial. The portion to the pollex, however, does not divide into two slips, but passes entirely to the outer side of the joint, the profundus tendon becoming superficial to its ulnar side, while in one of the portions to the minimus, although two terminal slips are recognizable, the ulnar one is very small, the main insertion of the muscle being into the radial side of the digit. It may be noted also that in Iguana this fifth portion at its origin overlaps somewhat the fourth portion, an arrangement which is, however, by no means so pronounced in Callisaurus or Liolepisma.

The second portion which passes to the fifth digit (Figs. 4 and 5, *ab. m.*) may well be termed the *abductor minimi digiti.* It is throughout its extent quite separate from the rest of the superficial sheet, except immediately at its origin which is from the ulnar prolongation of the line from which the rest of the flexor superficialis arises. In the Iguana the muscle wraps itself around the fifth metacarpal to a con-

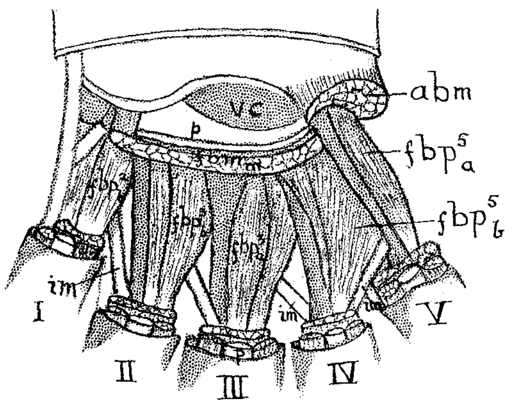

FIG. 5. The flexores breves profundi and intermetacarpales of *Iguana*. *abm*, abductor minimi digiti; fbp_a, direct and fbp_b, oblique muscles of the flexor profundus; *im*, intermetacarpales; fbm_m, line of origin of the stratum medium of the flexor brevis medius; *p*, deep palmar aponeurosis which gives origin to the profundus tendons; *vc*, volar cartilage.

siderable extent, but in Callisaurus this is not so evident, the muscle lying rather to the ulnar side of the bone, but in both it is inserted into the ulnar side of the proximal phalanx of the digit. The muscle is more or less closely related to one of the slips of the flexor brevis profundus (Fig. 5, fbp_a^5) and might on this account be regarded as possibly a portion of that layer rather than of the superficialis. I shall postpone a discussion of this possibility until the profundus layer has been described.

The *stratum profundum* of the superficial flexor I did not succeed in tracing perfectly in Iguana, a large slip passing to the fourth digit and a smaller one to the third being the only portions observed. In Callisaurus and Liolepisma, however, it was readily distinguished in sections as a thin layer (Fig. 3, fbs_p) which separated from the dorsal surface of the str. superficiale almost opposite the junction of the proximal and distal halves of the metacarpals and passed distally to each of the three middle digits, lying dorsal to the slips of the superficial stratum and becoming closely associated with the slips of the stratum superficiale of the middle flexor near their insertion.

The portion pertaining to the second digit is quite slender and lies entirely upon the ulnar side of the digit; that for the third digit is stronger, however, and forms two slips passing one to either side of the digit, and the portion for the fourth digit also divides into two terminal slips between which a thin band of small-fibred muscular tissue extends forming, when the slips unite with the subjacent slips of the flexor medius, a complete sheath for the profundus tendon.

It seems probable that a representative of this stratum also occurs in connection with the first digit, a portion of the flexor superficialis coming into relation near its insertion with the pollical portion of the flexor medius; it was not, however, quite distinctly separated from the general mass of the superficiale. In the case of the fifth digit the existence of a stratum profundum slip was much more evident, but on account of its intimate association with the minimal slip of the flexor profundus it will be more convenient to consider it later in connection with that muscle.

The *flexor digitorum brevis medius.*—The *stratum superficiale* of the flexor medius arises from the dorsal surface of the palmar aponeurosis just where it divides to form the profundus tendons; the portion for the fifth digit forms an exception to this statement, since it arises rather from the surface of the stratum medium. The stratum consists of four thin band-like portions which pass to the four ulnar digits, there being no portion for the pollex. The portion for the index is very narrow and is completely concealed by the profundus tendon; in Iguana it passes to the ulnar side of the digit, but in Liolepisma it divides into two terminal slips which insert into either side of the base of the proximal phalanx. The portions for the medius and annulus are broader and each divides into two terminal slips which insert into either side of the digit, the annular portion being associated throughout a considerable part of its course with the corresponding portion of the deep stratum of the flexor brevis superficialis.

The portion for the minimus (Fig. 4, fbm_s^5) differs somewhat from the other three, as already stated, in arising from the thin fascia covering the volar surface of the stratum medium. It has a very oblique direction, its origin being over the proximal portions of the second and third metacarpals, so that in its course to its digit it crosses obliquely over the medial and annular portions of the stratum medium. It is inserted into the radial side of its digit.

The *stratum medium* (Fig. 4) is the thickest layer of the flexor medius, almost equalling the flexor superficialis in its development. It is divided by tendinous bands lying in the sagittal plane into a number of parts, several of which pass to each digit. The general mass sends a portion to each digit, that to the minimus (Fig. 4, fbm_m^5) having an oblique direction, and overlapping at its origin the portions which pass to the fourth and part of that of the third digit.

The *stratum profundum* consists of three distinct portions which arise in the fascia covering the dorsal surface of the stratum medium and pass to the radial side of the medius, index (Fig. 3, fbm_p^2) and pollex. At their origin these muscles lie distinctly in a plane palmar to that occupied by the main nerve trunks, but more distally the nerves come to lie in the same plane as the muscles, so that from sections cutting the distal parts of the muscles it would be difficult to say whether they belonged to the flexor medius or the flexor profundus. Their relations at their origins, however, clearly show their true significance.

The muscle which passes to the third digit has its origin over the ulnar edge of the third metacarpal, so that in its course to its insertion it passes somewhat obliquely toward the radial side. The same is also true for the other two muscles, that for the index arising over the ulnar border of the second metacarpal and that for the pollex over the middle line of the first metacarpal, its obliquity, however, being more pronounced than that of the other two muscles owing to its being inserted into about the middle of the radial surface of the metacarpal, instead of passing to the neighborhood of the metacarpo-phalangeal joint.

The *flexor digitorum brevis profundus.*—The flexor profundus presents some interesting peculiarities in the arrangement of its constituent muscles (Fig. 5). In the amphibia it consisted of three slips, a median and two lateral, for each digit; in the reptilia almost the same condition obtains, but the median slip, except in the case of the minimus, is greatly reduced and is associated with one of the lateral slips and, furthermore, each radial lateral slip of the four ulnar digits, instead of being inserted into the digit from which it arises, passes obliquely across an intermetacarpal interval to be inserted into the ulnar side of the adjacent digit.

In the pollex I find but one muscle that I can certainly refer to this layer (Fig. 3, fbp_a^1). It arises from the first metacarpal and inserts into the metacarpo-phalangeal cartilage of the same digit. There is a possibility that the muscle to the pollex which I have referred to the stratum profundum of the middle flexor may really belong to the flexor profundus series, but its general relations seem rather with the medius.

The index possesses two muscles of the profundus set. One of these (Figs. 3 and 5, fbp^{2}_{b}) arises from the radial side of the base of the second metacarpal and inserts into the ulnar side of the metacarpo-phalangeal cartilage of the first digit. In Callisaurus this muscle consists of two fairly distinct portions, one of which has an origin both more distal and more upon the volar surface of the metacarpal than the other and probably represents the middle slip of the amphibian muscle. The second muscle (fbp^{2}_{a}) is more slender than its fellow and arises from the ulnar side of the metacarpal and inserts into the ulnar side of the metacarpo-phalangeal cartilage of the second digit.

In the third and fourth digits the arrangement is similar; the muscles which arise from the radial side of the corresponding metacarpals (fbp^{3}_{b} and fbp^{4}_{b}) apparently include a median slip as well as a radial and extend to the ulnar side of the second and third digits respectively, while two other muscles (fbp^{3}_{a} and fbp^{4}_{a}) arising from the ulnar and volar surfaces of the metacarpals pass to the ulnar side of the proximal phalanx of their own digits.

In the fifth digit the muscle which passes across to the fourth digit (fbp^{5}_{b}) is relatively strong and is readily recognizable, but that which passes directly to the proximal phalanx (Fig. 5, fbp^{5}_{a}) is not so easily distinguishable, being more or less concealed by and associated with the part of the flexor brevis superficialis which constitutes the abductor minimi digiti. In Iguana and Callisaurus the profundus brevis muscle was quite distinct from the abductor though completely covered by it, in Iguana, indeed, almost enclosed by it (Fig 5). In Liolepisma, however, I was not able to separate the two muscles, which present relations recalling those found in Amblystoma. One would naturally be inclined to regard the amphibian arrangement as the more primitive one and that found in Callisaurus and Iguana as derived by a separation of an originally simple muscle into two portions, but although I have not been able to exclude this possibility yet I am more inclined to believe that the distinctness of the two muscles is really the more primitive and that the arrangement which occurs in Amblystoma and Liolepisma is the derived one.

My reasons for this view are based partly upon the relationship which the portion of the amphibian muscle bears to the flexor carpi ulnaris. This muscle belongs to the superficial layer of the forearm musculature, and in Amblystoma is partly directly continuous with the abductor. Furthermore, the continuity of the line of origin of the abductor with that of the flexor brevis superficialis and its origin in part from the ulnar margin of the palmar aponeurosis are facts of no little importance. The distinctness of the abductor except at its origin from the rest of the flexor superficialis need have but little weight, since even in the amphibia a distinct separation of the lateral portions of the palmaris superficialis as the flexores carpi ulnaris and radialis is already in existence, and the continuity of the flexor carpi ulnaris with the abductor might well contribute to a separation of the latter. Nor does a fusion of a portion of the flexor brevis superficialis with a muscle belonging to the flexor profundus seem improbable, since there is typically such a fusion in the amphibian hand in the cases of the various slips to the digits.

Accepting then the superficial nature of the abductor we find in the reptilia an interesting rearrangement of the muscles which constitute the flexor brevis profundus as compared with the condition in the amphibia. The portion to each digit is practically reduced to two slips and, what is more important, one of these slips assumes an oblique direction, passing across an intermetacarpal space to be inserted into the digit adjacent to that from which it arises. I emphasize this arrangement of the profundus slips since it has important bearings upon the arrangement assumed by the corresponding muscles in the mammalia.

The *Intermetacarpales.*—These muscles (Figs. 3 and 5, *Im*) have entirely lost their muscular structure and have been converted into strong tendinous bands which extend obliquely across the various intermetacarpal spaces. The three radial tendons are directed ulnarly and distally, being attached at one extremity to about the middle of the ulnar side of the first, second and third metacarpals and passing to the radial side of the distal extremity of the second, third and fourth metacarpals respectively, The fourth tendon, however, has exactly the reverse arrangement, passing from the radial side of the fifth metacarpal distally to the distal end of the fourth, and, furthermore, it becomes intimately associated with the ulnar (distal) edge of the radial profundus slip of the fifth digit.

The arrangement of the nerve trunks in the reptilian hand is essentially the same as in the amphibian and does not require any detailed description.

In the preceding account I have refrained from applying to the individual muscles terms borrowed from mammalian myology, because the differentiation and association of the various layers has not proceeded to such a degree as to allow of an accurate application of such terms. I have already, in my previous paper (1903), shown that the use of the term flexor sublimis digitorum in reptilian myology is incorrect, and that the same is true of the terms interossei volares and interossei dorsales, these muscles as we recognize them in the mammalia not yet being differentiated, I shall show later on. The arrangement in layers in the amphibia and reptilia is the important matter for the present study and it is to this that I have endeavored to draw especial attention in my description.

III. The Muscles of the Mammalian Hand.

In this chapter I propose to consider the muscles of the mammalian hand from the standpoint of their arrangement in layers, so as to obtain a general comparison with the condition occurring in the reptilia and amphibia, and, furthermore, I shall confine my remarks to what is found in the opossum (*Didelphys virginiana*), the cat and the mouse, reserving for a final chapter a detailed consideration of the muscles of the human hand.

Cunningham in his admirable studies of the myology of the Challenger marsupials (1878 and 1882) furnished a most important standpoint for the proper understanding of the fundamental plan of the mammalian hand musculature in recognizing its arrangement in a number of definite layers. He confines his attention to what he terms the "intrinsic" muscles of the hand, limiting that term so as to include only "those muscles which remain after the removal of the flexor and extensor tendons." In this intrinsic musculature he recognizes three layers: (1) a palmar layer consisting of the adductors, (2) an intermediate layer and (3) a dorsal layer containing the dorsal interossei and the abductores pollicis and minimi digiti.

This conception seems to me to be faulty in three particulars. It may well serve as a plan for the mammalian hand muscles, if we limit our study to that group, but to obtain a correct understanding of the mammalian muscles we must formulate for them a fundamental plan which correlates them with the musculature of lower groups of vertebrates, and this cannot be satisfactorily accomplished if we limit the term "intrinsic" as Cunningham has done. For, as I endeavored to show in my earlier paper (1903), all the muscles of the hand are primarily "intrinsic," *i. e.*, confined to the limits of the hand, and not only must the muscles which Cunningham has discussed be included in our fundamental plan, but also the lumbricales and the tendons of the flexor sublimis which are representatives of the flexor brevis superficialis. Instead, therefore, of recognizing but three layers in the mammalian hand we must, I believe, admit at least five. These five layers I would correlate with the reptilian layers as follows:

Reptilia.	Mammalia.
Fl. brevis superfic. str. superfic. Fl. brevis superfic. str. prof.	Flexor brevis superficialis.
Fl. brevis medii str. superfic.	Lumbricales.
Fl. brevis medii str. medius. Fl. brevis medii str. prof.	Adductores.
Fl. brevis profundus	Fl. brevis profundus.
Intermetacarpales	Intermetacarpales.

I say I would recognize "at least" five layers, since there is a possibility, though it seems to be remote, that representatives of both the middle and deep strata of the flexor brevis medius may be present; this point may, however, be more satisfactorily discussed later on.

The other two exceptions that I would take to Cunningham's scheme concern his distribution of the individual muscles to the different layers. By failing to recognize the most superficial layer he has included certain marginal muscles which, I believe, properly belong to it, in his intermediate layer, *i. e.*, in the flexor brevis profundus, and others in his dorsal layer. Furthermore, his dorsal layer includes also muscles equivalent to portions of the flexor brevis profundus of the reptilian hand, there being in the mammalia an intimate association of certain slips of the flexor brevis profundus with the intermetacarpales to form the dorsal interossei. These questions again can be more satisfactorily discussed later.

The planes of separation of the mammalian layers are essentially the same as in the lower vertebrates. Although a marked rearrangement of the main nerve stems has occurred in the higher group (see my previous paper, 1903), yet, I believe, we are justified in assuming that the plane occupied by the deep branch of the ulnar nerve corresponds with that occupied by the nerve stems in the reptilia and, consequently, the two layers situated dorsal to this plane correspond to the similarly situated layers of the reptilia. Again, I have shown, I trust satisfactorily, that the tendons of the flexor profundus digitorum represent the deeper layer of the amphibian palmar aponeurosis and the profundus tendons of the reptilia and thus serve to separate, to a certain extent at least, the superficial and middle layers.

The *flexor digitorum brevis superficialis.*—In my paper on the phylogeny of the forearm flexors I showed that the flexor brevis superficialis of the reptilia and amphibia was represented in the mammalia partly by the terminal portions of the tendons of the flexor sublimis digitorum. Since, however, this muscle sends no tendon to the pollex, we may well expect to find some special representative of the superficial flexor in the radial side of the mammalian hand, and, furthermore, it is not unlikely that portions of the ulnar border of the sheet may have persisted and even slips of its more median portion.

That this likelihood is reality can, I think, be readily perceived by the study of a series of mammalian hands. In the opossum there is superficially in the ulnar part of the hand, in addition to the sublimis

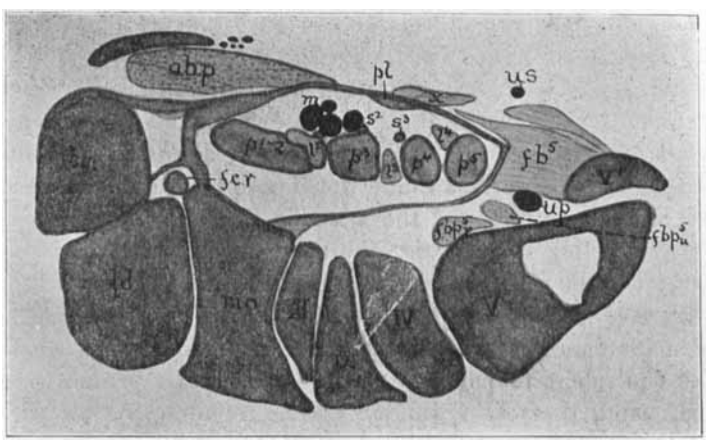

FIG. 6. Transverse section through the wrist of the opossum. *abp*, abductor pollicis; fb^5, flexor brevis minimi digiti; fbp^5_r and fbp^5_u, radial and ulnar slips of the flexor brevis profundus; *fcr*, flexor carpi radialis; l^{2-4}, lumbricales; *m*, median nerve; *ma*, os magnum; p^{1-5}, tendons of the flexor profundus digitorum; *pl*, palmaris longus; *s*, radial sesamoid; s^{2-3}, tendons of the flexor sublimis digitorum; *td*, trapezoid; *tm*, trapezium; *u*, unciform; *us* and *up*, superficial and deep branches of the ulnar nerve; *x*, remnant of the flexor brevis superficialis.

tendon, a well marked mass of muscle tissue, consisting of several more or less distinct slips arising partly from the sheath of the long tendons and partly from the hook of the unciform. A portion of this muscle tissue passes superficial to the superficial branch of the ulnar nerve to be lost in the fascia covering the abductor minimi digiti, and may well be regarded as representing the *palmaris brevis* of other mammals. The greater bulk of the mass (Fig. 6, fb^5), however, passes between the superficial (*us*) and deep (*up*) branches of the nerve to be inserted into the outer part of the cartilage which covers the volar surface of the metacarpo-phalangeal joint, and this and its representatives in other mammals I shall speak of as the *flexor brevis minimi digiti,* reserving until later the question as to the propriety of the use of that name.

A third portion (Fig. 6, *x*) is recognizable as a rather small slip arising from the volar surface of the sheath for the long tendons (the anterior annular ligament) close to the ulnar side of the tendon of the palmaris longus (*pl*), passing thence obliquely ulnarwards to fade out in the sheath of the tendon of the flexor profundus digitorum to the minimus. I found that the sublimis tendon of the fifth digit separates in the opossum from the palmaris longus and it seems not impossible that the slip now under consideration may represent an undegenerated portion of the flexor brevis superficialis from which that tendon has been differentiated. The probability of such an interpretation of the slip is strengthened by the fact that a small amount of muscle tissue persisted in the specimen I studied by sections (an embryo of 6.5 cm.) on either side of the sublimis tendons of the third (Fig. 7, *x*) and second digits. The presence of these slips seems to furnish strong confirmation of the views I have maintained as to the morphological significance of the sublimis tendons, the opossum in respect to the persistence of these slips as in so many others furnishing indications of a connecting link between the reptilia and the higher mammalia, in which, so far as my experience and information go, this median portion of the flexor brevis superficialis is entirely unrepresented by muscle tissue.

In addition to the muscles so far named there is a well developed *abductor minimi digiti,* whose origin is contiguous to that of the flexor brevis minimi digiti though extending a little farther proximally and whose insertion is into the ulnar side of the base of the proximal phalanx.

The muscles of the hand of the opossum have been studied with special reference to their arrangement in layers by Young (1879) and Brooks (1886*bis*) who adopt essentially Cunningham's plan. In the identification of the individual muscles of the little finger there are certain discrepancies between these two authors, and my results, while agreeing in the main with those obtained by Brooks, differ somewhat even from his. Thus what Young has termed the abductor minimi digiti is, as Brooks has pointed out, the flexor brevis, while Young's opponens is the true abductor. Young failed to observe the slip which I have regarded as a muscular portion of the flexor sublimis, though Brooks figures it and speaks of it as the flexor brevis digitorum manus. Neither author makes mention of the palmaris brevis which might readily be overlooked in dissections on account of its thinness and its relation to the fascia.

On the radial side the flexor brevis superficialis is somewhat more strongly represented than on the ulnar. The large muscle mass which forms the thenar eminence may be regarded as consisting of three portions, recognizable both in dissections and sections: (1) a portion formed by a band (Fig. 6, *abp*) which arises from the dorsal surface of the crescentic sesamoid cartilage of the radial side of the wrist (*s*), (2) a larger and broader portion arising from the volar surface of the annular ligament, its origin extending ulnarly to the line of the profundus tendon for the index and (3) a portion (Fig. 7, fbp_r^1) which arises from the radial side of the sheath for the long flexor tendons

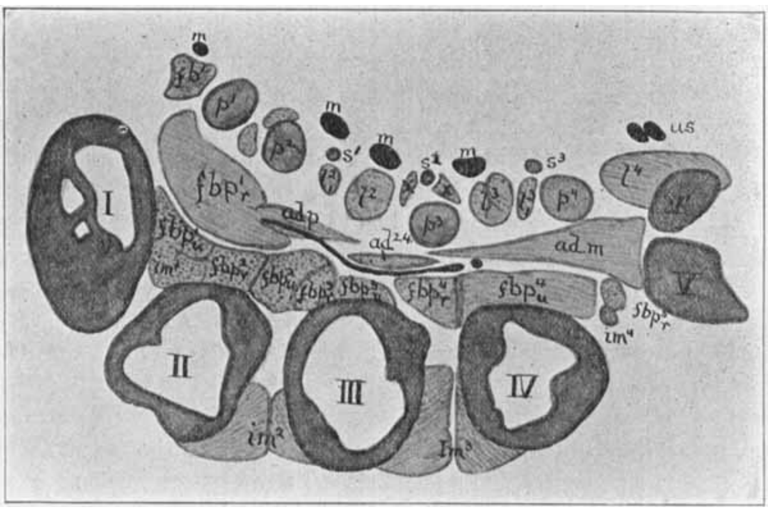

FIG. 7. Transverse section through the hand of the opossum. ad^{2-4}, adductors of the second and fourth digits; *adm*, adductor minimi digiti; *adp*, adductor pollicis; fb^1, flexor brevis pollicis; fbp_r, and fbp_u, radial and ulnar slips of the flexores breves profundi; *im*, intermetacarpales; *l*, lumbricales; *m*, median nerve; *p*, tendons of the flexor profundus digitorum; *s*, tendons of the flexor sublimis digitorum; *us*, superficial branch of the ulnar nerve; *x*, remnants of the flexor brevis superficialis.

and is in contact by its volar edge with the second portion just mentioned but distinguishable from it in transverse sections by the greater obliquity at which it is cut at its origin. This third portion does not concern us now, since there is reason to suppose that it is a portion of a deeper layer and therefore belongs to a different group of muscles than the other two which, it may be remarked, insert into the outer surface of the base of the proximal phalanx of the thumb. The first portion seems to be entitled to the name *abductor pollicis* applied to it by Young and Brooks, while the second may be termed the *flexor brevis pollicis,* although it corresponds only to the radial head of that muscle as recognized by the authors named. I shall consider the reasons for this difference in connection with the third portion of the thenar mass.

I would recognize, then, in the opossum the following representatives of the flexor brevis superficialis: (1) the abductor pollicis, (2) the flexor brevis pollicis, (3) the tendons of the flexor sublimis digitorum with their associated muscle slips, (4) the flexor brevis minimi digiti, (5) the abductor minimi digiti and (6) the palmaris brevis.

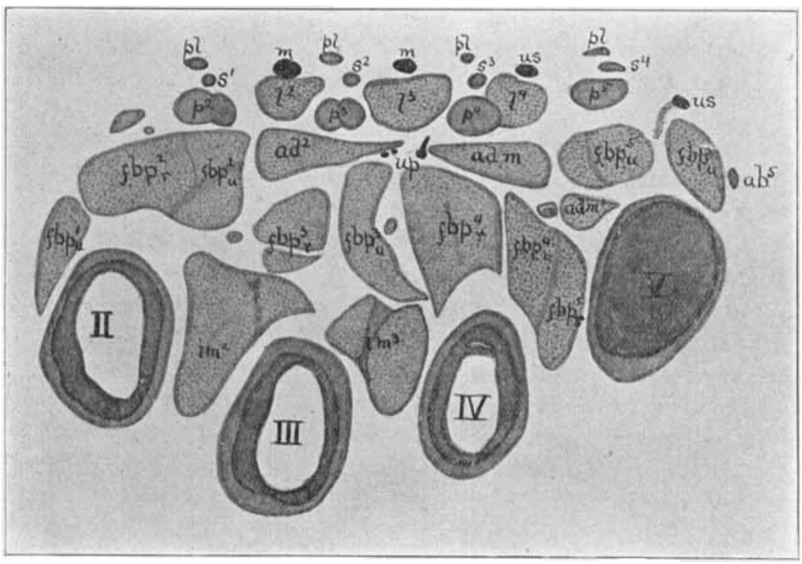

FIG. 8. Transverse section through the hand of a cat embryo of 7 cm. ad^2, adductor indicis; $ad.m$ and $ad.m^1$, adductores minimi; ab^5, abductor minimi digiti; fbp_r and fbp_u, radial and ulnar slips of the flexores breves profundi; *im*, intermetacarpales; *l*, lumbricales; *m*, median nerve; *p*, tendons of the flexor profundus digitorum; *pl*, tendons of the palmaris longus (i.e. prolongations of the palmar fascia) *s*, tendons of the flexor sublimis digitorum; *up* and *us*, deep and superficial branches of the ulnar nerve.

In the cat and the mouse there is a somewhat greater distinctness of the various muscles belonging to this layer, together with a certain amount of reduction, seen especially in the cat. Thus there appears to be no representative in that form of the flexor brevis minimi digiti and the abductor minimi digiti (Fig. 8, ab^5) is much reduced in size as is also the abductor pollicis. This last muscle is represented by two slips arising one in the dermal tissue over the tendon of the palmaris longus, the other from the radial side of the sheath enclosing the long tendons. The two slips converge to a delicate tendon which was lost in the dermal tissue over the metacarpal bone of the pollex, although in the adult it has been traced to the proximal phalanx, the muscle being that known as the abductor brevis pollicis.

It is probable that the muscle which has been termed the flexor brevis pollicis (*cf.* Reighard and Jennings, 1901, p. 184, Fig. 89*a*)[1] is also a derivative of the superficial flexor. It arises from the os magnum and the volar surface of the fascia covering the tendon of the flexor carpi radialis and is inserted into the radial side of the proximal phalanx of the thumb. In sections it seems to lie in a plane entirely dorsal to the long profundus tendons, but it must be remembered that it represents a marginal portion of the flexor superficialis which wraps around the margin of the hand to a certain extent. Its origin overlaps somewhat the origin of the adductor pollicis and this relation combined with the fact that it is supplied by a branch of the median nerve leads me to regard it as a portion of the flexor superficialis rather than to incline to the other possibility that it is a portion of the flexor brevis profundus.

The mouse possesses both a palmaris brevis and a flexor brevis minimi digiti (Fig. 9, fb^5) as well as an abductor minimi digiti (ab^5), all having essentially the same relations as the corresponding muscles in the opossum. The abductor pollicis is represented by two slips which arise from the crescentic sesamoid cartilage of the wrist joint and are inserted into the radial side of the first pollical phalanx and a well developed flexor brevis pollicis (Fig. 9, fb^1) is also present, arising from the volar surface of the anterior annular ligament as far medially as the line of the long profundus tendon for the index and passing to the outer side of the proximal phalanx of the thumb. In addition to these two muscles a third occurs in close association with the flexor brevis, consisting of a thin band lying immediately beneath the pad on the radial side of the hand, and having the same relations to it as the palmaris brevis has to the ulnar pad. It seems to owe its existence to the separation of some fibres from the flexor brevis pollicis and might be termed the *palmaris brevis radialis.*

I have not been able to distinguish any structures in the mammalian hand which could with certainty be looked upon as representatives of a stratum profundum of the flexor brevis superficialis such as occurs

[1] I refer to this work alone of those that have been written on the anatomy of the cat, since it does not seem necessary to enter into an extended discussion of the myology of this form and this is the latest extended work on the subject.

in the reptilia. Certain possible elements of such a layer will be discussed later in connection with the lumbrical muscles.

The *flexor digitorum brevis medius.*—As I have already stated, the stratum superficiale of this layer is represented by the lumbricales, arising from the tendons of the flexor profundus digitorum and passing to the four inner digits.

In the reptilia it was noted that the portion of this stratum which passed to the minimus inserted only into the radial side of that digit, while the portions to the annulus and medius divided to pass to either side of the proximal phalanges. In the opossum (Fig. 7) one finds an

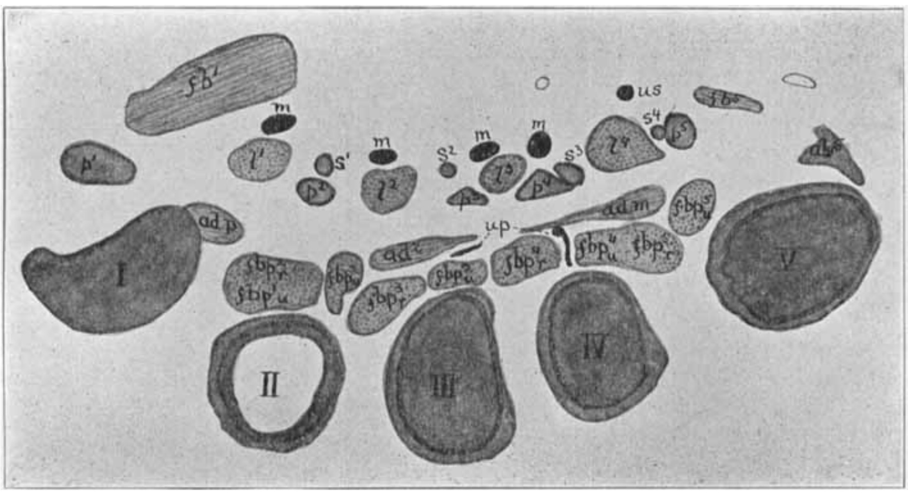

FIG. 9. Transverse section of the hand of a new-born mouse. ab^5, abductor minimi digiti; *ad.m*, adductor minimi digiti; *ad*, *p*, adductor pollicis; ad^2, adductor indicis; fb^1, flexor brevis pollicis; fb^5, flexor brevis minimi digiti; fbp_r, and fbp_u, radial and ulnar slips of the flexores breves profundi; *l*, lumbricales; *m*, median nerve; *p*, tendons of the flexor profundus digitorum; *s*, tendons of the flexor sublimis digitorum; *up* and *us*, deep and superficial branches of the ulnar nerve.

interesting suggestion of a similar arrangement, the lumbricals to the medius and annulus each consisting of two distinct portions, one large portion (l^2 and l^3) which inserts into the radial side of the proximal phalanx of its digit and a smaller one (li^2 and li^3). The smaller portion of the third lumbrical arises from the radial side of the fourth long profundus tendon and passes distally, retaining its independence throughout its entire course, to be inserted into the sheath enclosing the long tendon just where the sublimis tendon spreads out to allow its passage; the corresponding portion of the second lumbrical arises from the ulnar side of the profundus tendon to the index and is inserted into the ulnar side of the sheath of that tendon. The first lumbrical in Liolepisma has also two insertions, but in Iguana it passes only to the ulnar side of its digit; in the opossum it has only one portion which passes to the radial side of the index. It may be stated that von Bardeleben (1902) mentions incidentally the occurrence of two portions in the lumbricals of certain mammals.[2]

I was not able to detect any indications of a doubling of any of the lumbricals in either the cat (Fig. 8) or the mouse (Fig. 9), in both of which the muscles present the usual mammalian relations. The fact that we have a bilateral insertion for the second and third lumbricals in the lacertilia inclines one to the view that the doubled condition of the corresponding mammalian muscles may be a relic of the reptilian arrangement. There is, however, another possibility, namely, that the smaller slips of the mammalian muscles represent persistent portions of a stratum profundum of the flexor brevis superficialis. In Callisaurus slips from this stratum pass to the second, third and fourth digits, and these slips are associated at their insertions with the sheaths of the corresponding profundus tendons. It is not at all impossible that the smaller slips of the second and third lumbricals of the opossum may represent the corresponding portions of the stratum profundum of the reptilian flexor brevis superficialis, the portion to the third digit being indistinguishable.

Which of these two views may be the correct one the material I have had for study does not determine. The nerve supply of the various slips, so far as my observations go, throws no light on the question.

We come now to the consideration of the *stratum profundum*[3] of the flexor brevis medius, being the first of the three layers described by Cunningham and that which is constituted by the adductor muscles of the mammalian hand. The arrangement of these muscles in the opossum has been well described by Young (1879) and Brooks (1886 *bis*), but on comparing their descriptions a slight difference in the limitations of one of the muscles is noticeable, a portion of the muscle recognized by Brooks as the adductor pollicis, namely, its ulnar head, being regarded by Young as a portion of his flexor brevis pollicis, *i. e.*, of the intermediate layer of the pollical muscles. My observations lead me to agree with Young on this point, the relatively thick muscle

[2] Von Bardeleben refers to certain observations of his own upon this point which I have not been able to consult.

[3] I use this term here in a strictly mammalian sense. The stratum is probably equivalent to the str. medium of the reptilian hand.

bundle which forms the radial border of Brooks' adductor having its origin from the fascia covering the first and second metacarpals decidedly proximal to the origin of the adductor and being overlapped, furthermore, on its ulnar border by the adductor. In accordance with Young's description of the adductors then, there is a large fan-shaped adductor pollicis (Fig. 7, *ad p*) and a similar adductor minimi digiti (*ad m*) which arise mainly from a median fibrous raphe in the line of the middle metacarpal and insert into the ulnar and radial sides respectively of their digits. In addition there are two other adductors ($ad^{2\text{-}4}$), much less extensively developed, arising from the dorsal surface of the adductor raphe and inserting into the ulnar and radial sides respectively of the second and fourth digits.

In the cat the correct interpretation of the deeper muscles of the hand is rendered difficult by the flexor brevis profundus elements being pushed volarly so that some of them come to lie in apparently the same plane as the adductors and are, furthermore, traversed near their volar surface by the deep branch of the ulnar nerve, thereby seeming to be partly epineural structures. If, however, these two peculiarities be taken into consideration, an arrangement of the various portions of the flexor brevis medius and profundus essentially similar to what occurs in the opossum and the mouse can be made out.

It is the profundus portion for the index (Fig. 8, fbp_r^2 and fbp_u^2) which is especially obtrusive in the way mentioned, occupying a position so far volar as to separate the adductor pollicis from the adductor indicis. The former of these muscles arises from the surface of the os magnum and is inserted into the ulnar side of the proximal pollical phalanx, while the latter (Fig. 8, ad^2) arises in continuity with the rest of the adductor layer from the fascia covering the volar surface of the carpal bones and the bases of the metacarpals and is inserted into the ulnar side of the base of the proximal phalanx of the index. In addition to these two muscles there are two others belonging to the adductor layer; they arise together and are closely associated throughout the greater part of their course, the more ulnar one ($ad\ m^1$), however, inserting into the radial side of the shaft of the fifth metacarpal, while the more radial one (*ad m*) passes to the base of the proximal minimal phalanx. I suspected at first that the more radial of these muscles belonged to a different layer than the other, but the evidence available makes it preferable to regard the two together as equivalent to the adductor minimi digiti of the opossum whose insertion has been partly extended proximally upon the metacarpal.

In the mouse three muscles may be recognized as belonging to the adductor layer: (1) an adductor pollicis which arises from the fascia covering the first metacarpal and is inserted into the ulnar side of the proximal phalanx of the pollex (Fig. 9, *ad p*), (2) an adductor indicis (ad^{2}) and (3) an adductor minimi digiti (*ad m*), both of which arise from the fascia covering the bases of the third and fourth metacarpals and are inserted into the proximal phalanges of their respective digits. No separation of the adductor minimi digiti into two portions, as is the case in the cat, occurred.

Of the stratum profundum of the middle flexor which occurs in the reptilia I have found no representative in the mammalian hand if the identification of the adductor minimi digiti of the opossum with a part of the stratum medium be correct. It is to be noted, however, that superficial to the adductor there is clearly to be seen in sections a very thin layer of muscle tissue, separated from the surface of the adductor by a narrow but quite distinct layer of areolar tissue. Its fibres are directed less obliquely than those of the adductor and, becoming tendinous, it fades out in the fascia beneath the profundus tendon of the fourth digit. It is possible that this muscle really represents a portion of the stratum medium and that the adductor represents the stratum profundum. I have been able, however, to find no corresponding muscle toward the radial side of the hand in the opossum and it seems hardly possible that the adductor minimi digiti represents a different layer for the adductor pollicis when their general similarity and their origin from a common median raphe are considered. In the higher mammals studied I have found nothing which corresponds to this muscle.

But instead of regarding it as part of the stratum medium another interpretation is possible for it, and that is that it represents in a diminished condition the more superficial radial slip of the portion of the median flexor which passes to the fifth digit in the Iguana (Fig. 4, fbm^{5}_{s}). Its relations to the remaining portions of the stratum medium are essentially the same as those of the reptilian muscle and there seems to be no obvious reasons for not regarding it as identical with the latter.

I conclude, therefore, that the deep stratum of the reptilian flexor brevis medius is unrepresented as a distinct stratum in the mammalian hand.

The *flexor digitorum brevis profundus* and the *intermetacarpales.*—We come now to the epineural muscles of the mammalian hand, those which correspond to the flexores breves profundi and intermetacarpales of the lower vertebrates and to the intermediate and deep layers of Cunningham's scheme. It must be pointed out that while the two layers taken together correspond with Cunningham's two layers, individually the layers of the two sets are quite different. I shall not discuss this point here, however, but reserve it for the concluding chapter, and, in the meantime, would merely point out that the flexores breves profundi and intermetacarpales are so intimately associated in the mammalia that it is not feasible to discuss them separately.

In the opossum and other marsupials Young, Brooks and Cunningham have recognized in their intermediate layer a series of flexor muscles corresponding to the various digits, each muscle being composed of two slips which pass to the ulnar and radial sides of a proximal phalanx. Such a condition recalls, it is true, the amphibian arrangement of the profundus layer, but it must be remembered that the reptilian arrangement is quite different, one of the two slips of certain muscles transferring its insertion to an adjacent digit, and I believe that in the mammalian hand there has been a similar transference of some of the slips.

In the opossum I find on the ulnar side of the hand two muscles belonging to the flexor brevis profundus, one (Fig. 6, fbp_u^5) arising from the fascia enclosing the long tendon to the fifth digit and being perforated close to its origin by the deep branch of the ulnar nerve, and the other (Figs. 6 and 7, fbp^5) taking its origin from the base of the fifth metacarpal and lying to the radial side of the first. The ulnar muscle passes directly distally and inserts into the base of the proximal phalanx of the minimus, while the other passes obliquely across the interval between the fifth and fourth metacarpals and unites with the intermetacarpal of that interval and with the ulnar slip of the flexor brevis profundus of the fourth digit to be inserted into the proximal phalanx of that digit. The ulnar muscle I take to be the radial slip of the portion of the intermediate layer passing to the minimus as described by Young and Brooks, but they seem to have overlooked the radial muscle, although it is evidently identical with the slip which Cunningham has described in Thylacinus and Phalangista (1882) as a palmar slip entering into the formation of the fourth dorsal interosseous. The ulnar minimal slip which these authors recognize in the fifth digit belongs, I believe, to the abductor mass and therefore to an entirely different layer from the radial slip.

The muscles referred by the same authors to portions of the intermediate layer passing to the annulus medius and index are identical with those which I take to be the flexores breves profundi of the same digits (Fig. 7, fbp^4, fbp^3 and fbp^2); they arise in pairs from the bases of their metacarpals and are inserted one into either side of the base of the proximal phalanx of the same digit. In the case of the pollex, however, the arrangement of the slips is similar to that occurring in the minimus, one of them (Fig. 7, fbp_u^1) passing across the intermetacarpal interspace to be inserted into the radial side of the base of the proximal phalanx of the index, uniting with the radial slip of the flexor brevis profundus of the index and with the first intermetacarpal, while the other (fbp_r^1) passes directly distally to be inserted into the ulnar side of the phalanx of the thumb. In this digit, as in the minimus, the oblique muscle has been overlooked by Young and Brooks, or rather has been considered to be a part of their dorsal layer, while the other is identical with the ulnar slip which they ascribe to the thumb. Their radial slip is, I believe, a portion of the flexor brevis pollicis and, consequently, belongs to the flexor brevis superficialis.

The intermetacarpales are distinctly muscular, thus differing from those of the lacertilia which are throughout converted into ligaments. The second, third and fourth intermetacapals (Fig. 7, *im*) arise each by two heads from the sides of adjacent metacarpals near their dorsal surfaces and converge to a tendon (im^4) which passes distally in the intermetacarpal space and finally bifurcates to be inserted into the adjacent sides of the neighboring proximal phalanges, the radial branches of the third and fourth tendons uniting with the tendons of the flexor brevis profundis slips inserted into the corresponding phalanges, while the ulnar branch of the second tendon similarly unites with the radial slip of the flexor brevis profundis of the third digit. What I take to be the first intermetacarpal (im^4) differs from the others in that it arises by a single head from the first metacarpal and is situated more volarly than its fellows. It passes obliquely across the first intermetacarpal interval to unite with the ulnar slip of the flexor brevis profundus of the pollex and the radial slip of the same muscle of the index and inserts with them into the proximal phalanx of the index.

In the cat an arrangement of the flexor profundus muscles comparable to that occurring in the opossum is readily discerned, but the intermetacarpals are not in all cases so distinctly separated from the muscles with which they unite. In the fifth digit one finds the ulnar muscle dividing into two slips (Fig. 8, fbp_u^5) which are inserted into either side of the base of the proximal phalanx; the radial muscle (fbp_r^5), however, passes across to the proximal phalanx of the annulus. This digit, the medius and the index each possesses two slips, those of the annulus and medius having undergone a distal recession so that they arise from the shafts of their metacarpals instead of from their bases, and those of the index having assumed a volar position so as to lie, as has already been pointed out, in the same plane as the adductors. The thumb possesses two muscles of the flexor profundus set, an ulnar one which passes across the intermetacarpal space (*fbp*[1]) to be inserted into the index and a radial one which is inserted into the proximal phalanx of its own digit. The first and fourth intermetacarpals I was not able to distinguish, they being probably intimately united with the muscles with which they insert. Those of the second and third intermetacarpal spaces (im^2 and im^3) are fairly distinct, but less so than in the opossum, and are more volar in position.

In the mouse (Fig. 9) the general arrangement is practically the same as in the two forms already described and need not be discussed in detail. The intermetacarpals are even less distinguishable from the slips of the flexor brevis profundus with which they are associated than are those of the cat.

IV. The Muscles of the Human Hand.

In considering the musculature of the human hand it will probably conduce to clearness if, instead of discussing it from the standpoint of the fundamental layers, the various muscles be taken up in sequence.

1. The *palmaris brevis* occupies a characteristic position with reference to the superficial branch of the ulnar nerve, being the only muscle which lies volar to it. Throughout the series of forms studied this relation is constant and affords a simple clew for the identification of the muscle, which, be it noted, is in the opossum closely associated with the flexor brevis minimi digiti. It is evidently a portion of the flexor brevis superficialis.

2. The *flexor brevis quinti digiti*.—The significance of this muscle has been discussed by Brooks (1886), with the conclusion that it really belongs to the adductor set, *i. e.* to the flexor brevis medius. Brooks has evidently been deeply influenced by Cunningham's views as to the layers of the palmar musculature, and his assignment of the muscle under discussion to the adductor layer may be taken as meaning that it is an element of a hyponeural layer, *i. e.* of a layer volar to the deep branch of the ulnar nerve. I have shown that in addition to the palmar (adductor) layer, which was the only hyponeural layer recognized by Cunningham, there are really two others to which that term may be applied, namely the lumbrical layer and the flexor brevis superficialis layer, and it seems highly probable that the flexor brevis quinti digiti

belongs to this last layer. Its exclusion from the adductor layer seems certain from its relations in lower forms, in which it is evidently a muscle arising volar to the profundus tendons instead of dorsal to them, and there seems to be no reason for supposing that this superficial origin has been secondarily acquired. I regard the muscle, therefore, as a second member of the flexor brevis superficialis.

It is unfortunate that by the application of the terms flexor brevis to their intermediate layer the English authors have introduced a certain amount of confusion into the nomenclature of the hand muscles, a confusion which becomes very evident in the perusal of Brooks' paper (1886). For finding that the flexor brevis quinti digiti is not a member of the intermediate layer he prints its name throughout in inverted commas and reserves the title of "the true flexor brevis minimi digiti" for what he regards as the ulnar slip of the intermediate layer. It seems far preferable to reserve the designation flexor brevis for muscles which belong to the superficial layer, since, in the first place, this layer has long been spoken of in the lower vertebrates as the flexor brevis digitorum, and, in the second place, we have for the members of the intermediate layer the long-established term interossei.

3. The *abductor quinti digiti.*—This muscle has been referred by Cunningham to his dorsal layer and regarded as the most ulnar dorsal interosseus. It seems to me that the relations of the muscle in the lower vertebrates strongly negative such a supposition and show it to be a derivative of the most superficial sheet of the hand musculature. For I take it that the mammalian muscle is the equivalent of the abductor minimi digiti of the lacertilia, the continuity of whose origin with that of the flexor brevis digitorum is so striking.

It is interesting to note that in the forearm the deeper layers of muscles, represented by the flexor profundus and the pronator quadratus, do not extend laterally beyond the lines of the radius and ulna, and that the deepest layer is more limited laterally than is the middle one. It is from the superficial layer, that farthest from the bones, that the marginal muscles, the flexores carpi radialis and ulnaris, are derived. Such an arrangement is just what might be expected, for it would seem natural that the layer farthest away from the bony axis should wrap itself to a certain extent around the axis at the sides, while the closer the relations of the layers to the bones the more their lateral extension would be limited. We may expect to find this same condition obtaining in the hand as well as in the forearm, and when in addition to this *a priori* argument we have that derived from the continuity of origin of the abductor with the flexor brevis digitorum, strong evidence is afforded for the reference of the former muscle to the same layer as the latter one.

Furthermore, it is worthy of remark that the occasional fusion of the abductor with flexor brevis quinti digiti in man, noted by Macalister and Le Double (1897) speaks in favor of a close phylogenetic relationship between the two muscles.

4. The *opponens quinti digiti.*—This muscle also stands in intimate relationship with the flexor brevis, with which, as Le Double states, it is in general more or less related, and it may also unite with the abductor. I regard it as part of the flexor brevis superficialis and probably a derivative of the abductor quinti digiti of the lower mammals. Brooks (1886) refers it, in part at least, to the adductor layer, but this may probably be interpreted to mean merely that it is not to be considered part of the epineural musculature, the reason for such an interpretation being that which has already been adduced in speaking of the flexor brevis quinti digiti.

5. The *flexor brevis pollicis*—This muscle has been the subject of a good deal of discussion, which has resulted in the establishment of the fact that, as usually understood, the muscle is really a compound structure, including elements from different layers; the exact significance of the different elements is yet open to discussion, however.

The description of the muscle given by Albinus has served as the basis for the accounts given in many and especially the English text-books, even the most recent of these, with the exception of that edited by Cunningham (1902), adhering to the original limitations of the muscle. According to this there is recognized in the muscle a *cauda prior vel exterior,* the outer head of the English texts, and a *cauda posterior vel inferior,* the inner head, which is again composed of three divisions. A very different view was that of Cruveilhier, who limited the term flexor brevis pollicis to that portion of the muscle which inserts into the outer side of the thumb and referred the rest to the adductor. Henle (1871), again, following Sömmering, regarded the outer head as part of the abductor and the greater part of the inner head as belonging to the adductor, confining the term flexor brevis to a small slip which divides to be inserted into both the ulnar and the radial side of the proximal phalanx and corresponds to the second and third divisions of the inner head of the English texts. Furthermore, Henle called attention to the existence of a deeper head arising mainly from the first metacarpal and inserting into the ulnar side of the proximal phalanx of the thumb, regarding it as the true first palmar interosseus, thus recognizing four of these muscles instead of the usual three.

In 1887 Flemming reconsidered the question as to the proper significance of the various parts of Albinus' muscle and arrived at a conclusion somewhat similar to that of Cruveilhier, namely, that the term flexor brevis should be applied to the outer head only, the entire inner head being regarded as a portion of the adductor. To this view Cunningham (1887), on the basis of his earlier work (1878 and 1882), took exception. As already pointed out, he applied the term flexor brevis to the muscles constituting his intermediate layer and regarded each of these muscles as being typically two-headed. Accordingly, while admitting the correctness of the reference of the entire inner head of the flexor brevis pollicis of Albinus to the adductor, he maintained that the true flexor brevis was represented not only by the so-called outer head but also by the interosseus primus volaris of Henle, these two slips constituting the radial and ulnar heads, respectively, of the pollical portion of the intermediate layer. This same view he had already advanced in an earlier paper (1882^{bis}), and it is that presented by Patterson in the recently published text-book edited by Cunningham (1902).

Gegenbaur in his Lehrbuch der Anatomie (5th Ed., 1892) adopts essentially the view of Flemming and Cruveilhier, but in a paper published in 1889 he takes the position that the variation in the nerve supply of the muscle described by Brooks (1886) indicates that the muscle is a variable one and is not equivalent in all cases, portions of it present in one individual as indicated by the nerve supply being absent or replaced by portions of other muscles in other individuals.

There is thus a very considerable amount of difference in the limitations set to the muscle by different authorities. I believe, for reasons that have already been set forth in speaking of the flexor brevis quinti digiti, that the term flexor brevis pollicis should be reserved for that portion of the muscle as described by Albinus which is derived from the flexor brevis superficialis, and the portion which has that origin is the so-called outer head. Cunningham is, I believe, in error in referring this head to his intermediate layer; it seems to me clearly equivalent to the flexor brevis pollicis of the mouse, for instance, and this is undoubtedly a derivative of the flexor brevis superficialis, as is shown as well by its origin as from its supply by the median nerve.

On this point, then, my results are in accord with those of Flemming, and I am in agreement both with that author and with Cunningham in regarding the inner head as a portion of the adductor. What, then, is the interosseus primus volaris of Henle? Why, it is evidently just what Henle named it; it is the equivalent in man of the slip of the flexor brevis profundus which arises from the first metacarpal and inserts into the proximal phalanx of the thumb, and is the radial counterpart of the palmar interosseus of the fifth digit, as I hope to show later on.

The interosseus primus volaris is frequently indistinguishable from the deeper portions of the flexor brevis pollicis (*sens. lat.*), being possibly incorporated with it, although from the fact that in a human embryo of 6 cm. which I examined the slip (Fig. 10, fbp^1_r) was exceedingly small and showed evident indications of degeneration I am inclined to believe that the failure to distinguish it may frequently be due quite as much to its great reduction as to its fusion with the adjacent adductor. But if we suppose that it does frequently become incorporated in that muscle or at all events is included in the flexor brevis pollicis as limited

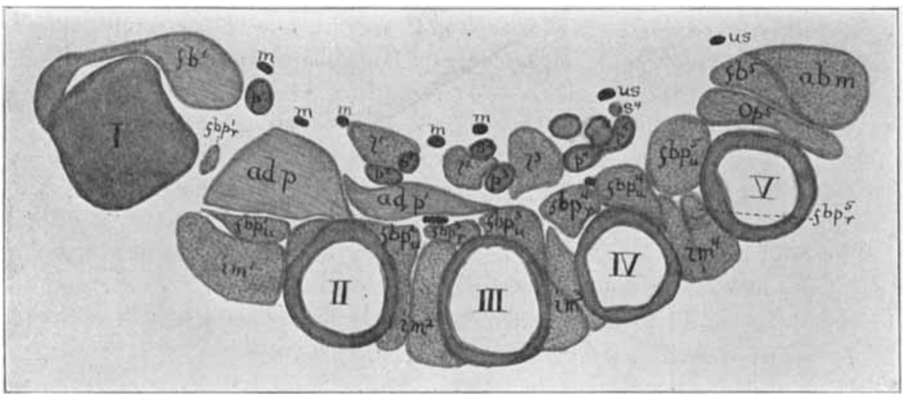

Fig. 10. Transverse section through the hand of a human embryo of 6 cm. *abm*, abductor minimi digiti; *ad.p*, caput obliquum and *ad.p*[1], caput transversum of the adductor pollicis; fb^1, flexor brevis pollicis; fb^5, flexor brevis quinti digiti; fbp_r and fbp_u, radial and ulnar slips of the flexores breves profundi; *im*, intermetacarpales; *l*, lumbricales; *m*, median nerve; op^5, opponens quinti digiti; *p*, tendons of the flexor profundus digitorum; *s*, tendons of the flexor sublimis digitorum; *us*, superficial branches of the ulnar nerve.

by those who adhere to Albinus' conception of the muscle, then the flexor in this sense is really composed of elements from three different layers, namely, the superficialis, the deeper stratum of the medius and the profundus.

6. The *abductor pollicis.*—The abductor pollicis does not seem to exist as a distinct muscle in the lower vertebrates I have studied; the mammalian muscle has appeared within the limits of that phylum and I believe, contrary to the opinion of Cunningham, that it is derived from the flexor superficialis. The *a priori* reasons which indicated an origin of the abductor quinti digiti from this layer holds also in the case of the

abductor pollicis and is strengthened by the origin of the muscle from the volar surface of the annular ligament, by its not unfrequent confusion with the flexor brevis pollicis (*sens. str.*) and by its nerve supply from the median.

7. The *opponens pollicis* is clearly allied very closely to the abductor and in all probability has the same derivation. Its occasional intimate union with the flexor brevis pollicis (*sens. str.*) is important in this connection as is also its supply from the median.

8. *The lumbricales.*--The equivalency of these muscles to the superficial stratum of the flexor brevis medius of the reptilia has already been noted. In the two hands from different human embryos which I studied I found the lumbricales possessing their usual origins, *i. e.* the first and second from the radial sides of the profundus tendons of the second and third digits, and the third and fourth from the adjacent sides of the third and fourth and fourth and fifth tendons, the muscles making their appearance in sections just at the point of separation of those tendons from the common tendon. In none of the muscles could any certain existence of doubling be distinguished. In the embryo of 6 cm. the four muscles were inserted into the radial side of the proximal phalanges of the four inner digits, but in one of 4.5 cm. the third lumbrical divided just before its termination into two equal slips which were inserted respectively into the ulnar side of the proximal phalanx of the third digit and the radial side of the corresponding phalanx of the fourth digit.

The recent observations of Kopsch (1898) and Reinhardt (1902) have shown that the insertion of the third lumbrical into the adjacent sides of the third and fourth digits is of frequent occurrence, Kopsch finding it in 47 out of 110 cases examined (42.7 per cent) and Reinhardt in 43 cases out of 100. A satisfactory explanation of this variability has not yet been advanced. Von Bardeleben (1900) has suggested an association of the double insertion with a nerve supply of the muscle from both the median and the ulnar nerves, and in another place (1901) he has also suggested its possible reference to the doubling of the muscle seen in some of the lower mammals. As regards the first suggestion it may be noticed in the first place that it is rendered very plausible by the fact that Brooks (1887) found in twenty cases a double supply of the muscle in nine; Brooks' paper, however, contains no statements as to the mode of insertion of the muscle in the various cases, and, furthermore, I have been able to determine with certainty that in the embryo with a double insertion mentioned above, the muscle is supplied by a twig from the deep branch of the ulnar and by that alone.

The second suggestion would therefore seem to be the more satisfactory one; but, again, there are difficulties in the way of its being regarded as altogether sufficient: It is true that we find double lumbricales or a double insertion for them in the marsupials and monotremes, and it might be supposed that there is fundamentally a similar condition in man, sometimes persisting to the adult condition, but more usually giving place to a single insertion. The finding of a double insertion of the third lumbrical in an embryo of 4.5 cm. and but a single insertion in an embryo of 6 cm. is suggestive, but it completely loses weight when it is noted that in the younger embryos studied by Lewis (1902) this lumbrical had but one insertion. Furthermore, it is noticeable that while in the lower mammals it is the second and third lumbricals which are doubled, the second muscle in man is remarkably constant in possessing but one part, and, furthermore, a double insertion occasionally occurs in the fourth muscle in man, Kopsch and Reinhardt each recording ten cases of this nature, while Kopsch records four cases and Reinhardt one of a single insertion of the muscle into the ulnar side of the fifth digit.

It would seem, then, that neither of von Bardeleben's suggestions satisfy the requirements of the case, nor does there seem to be any morphological explanation of the variation at present available. May it not be, after all, that there is no such explanation required, what is required being rather a physiological explanation?

For, as has been seen in comparing the muscles of the amphibia, reptilia and mammalia, the shifting of an insertion from one digit to the adjacent side of another is by no means an uncommon phenomenon. In other words, there is not that morphological isolation of the digits from one another which we are apt to imagine; the hand develops as a whole rather than as a series of independent radiating units and the transference of a muscle from one digit to another is consequently a simple matter.

9. The *adductor pollicis*.—This seems to be the only representative of the deeper stratum of the flexor brevis medius which exists in the human hand. Its limitations have already been discussed in considering the flexor brevis pollicis and as a result of the conclusions then reached it is necessary to regard the muscle as consisting of two portions which have been termed the adductor obliquus and the adductor transversus. This nomenclature implies, however, the existence of two distinct muscles,

[4] This last argument is based upon the arrangement of the muscles which I have found in the Virginian opossum. If in other forms a doubling of the fourth lumbrical should occur, then the argument would lose its value.

and it would seem more satisfactory and more in harmony with the results of comparative anatomy to speak of only one adductor pollicis, regarding it, however, as consisting of a caput obliquum and a caput transversum.

10. The *interossei.*—From what has been said in connection with the flexor brevis pollicis it will be seen that I am in accord with Henle in his contention that there are really four palmar interossei present in the human hand, that to the thumb, however, being frequently unrecognizable either from its small size or on account of its incorporation with the oblique head of the adductor.

Recognizing the identity in number of the dorsal and palmar interossei, it remains to consider their mutual relationship and their equivalents in the lower vertebrates. Ruge (1880) in his paper on the development of the deep muscles of the human foot, considered briefly the interossei of the hand and, by showing that these muscles resembled in their development their homologues in the foot, established the important point that the dorsal interossei were in reality portions of the palmar musculature, their final dorsal position being secondary. He went, however, even farther than this and regarded the dorsal interossei of the foot as in all respects equivalent to the palmar interossei; in other words, he regarded them both as derivatives of the same foundamental layer, considering Cunningham's assignment of them to different layers as erroneous. It seems to me, so far as the interossei of the hand are concerned, that the correct position is an intermediate one between those held by these two authors. I believe that the interossei really represent two fundamental layers but that there has been a considerable amount of union between the two layers to form the dorsal interossei, these muscles consisting of elements from the flexor brevis profundus combined with the intermetacarpales.

For the sake of avoiding repetition of details I would refer back to what has been said in the previous chapter regarding the representatives of these layers in the mammalia I have studied and merely state that the intermetacarpals, though less evident than in the opossum, are yet much more distinct in the human hands I studied than in either the cat or the mouse, as may be seen from the inspection of the adjacent figure (Fig. 10, *im*).

I believe the significance of the mammalian interossei to be as follows: The flexor brevis profundus is represented by a series of paired slips for each digit inserted into the opposite sides of the proximal phalanges, except in the cases of the first and fifth digits in which one of the slips is inserted into the adjacent side of the second and fourth digit, respectively, along with the radial (or ulnar, as the case may be) slip of that digit. Furthermore, the first and fourth intermetacarpals become associated with the combined muscles so formed, the three portions thus associated constituting the first and fourth dorsal interossei. The second and third intermetacarpals unite with the flexor brevis profundus slips of the third digit to form the second and third dorsal interossei, and the flexor brevis profundus slips of the first, second, fourth and fifth digits which do not unite with intermetacarpals form the palmar interossei. A diagram (Fig. 11) will, I trust, make this description clear and at the same time demonstrate the significance of the mutually complementing arrangement of the two sets of interossei.

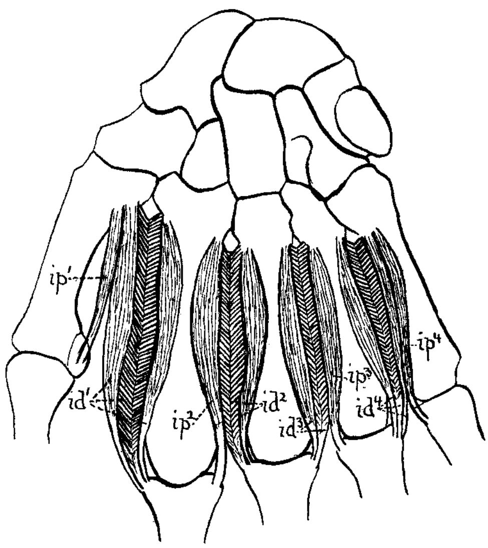

Fig. 11. Diagram showing the composition of the interossei of the human hand. *id*, dorsal interossei; *ip*, palmar interossei.

V. Summary.

It is difficult and tedious to follow a lengthy description involving reference to a number of separate structures even when an abundance of illustrations accompanies it. Owing to my results having been based very largely on the study of the serial sections it would require an undue number of figures to demonstrate all the points to which reference has been made in the preceding pages, and hence, I fear, only those who are especially interested in the subject will have the patience necessary for the thorough perusal of what I have written. And yet it seems that the importance of obtaining a correct idea as to the fundamental significance of the mammalian hand musculature is sufficiently great to interest all students of vertebrate morphology in the questions discussed. I have, therefore, endeavored to state in a series of propositions the main conclusions which I have expressed both in this paper and in a preceding one (1903) so far as it concerns the hand musculature.

1. In the urodele amphibia the volar hand muscles are arranged in *four* distinct layers which may be named the flexor brevis superficialis, flexor brevis medius, flexor brevis profundus and intermetacarpales.

2. In the lacertilia the number of these layers is increased to *seven* by the subdivision of the flexor brevis superficialis into a stratum superficiale and a stratum profundum, and of the flexor brevis medius into a stratum superficiale, a stratum medium and a stratum profundum.

3. In the mammalia the number of clearly recognizable layers is *five,* the str. profundum fl. brevis superficialis and the str. profundum fl. brevis medii of the lacertilia being apparently wanting.

4. In the mammalia the greater portion of the flexor brėvis superficialis has degenerated to form the palmar portions of the tendons of the flexor sublimis digitorum, marginal portions of it persisting, however, to form the abductor and opponens pollicis, the abductor and opponens quinti digiti, the flexor brevis pollicis, the flexor brevis quinti digiti, the palmaris brevis and, in some cases, a palmaris brevis radialis.

5. The palmar portions of the flexor profundus digitorum are derived from a layer of fascia which, in the lower forms, intervenes between the flexor brevis superficialis and the flexor brevis medius, the str. superficiale of the fl. brevis medius arising in these lower forms from this fascia.

6. The str. superficiale of the fl. brevis medius gives rise to the mammalian lumbricales.

7. The str. profundum of the fl. brevis medius gives rise to the mammalian adductors.

8. The flexor brevis profundus in the mammalia consists of paired slips for each digit. Certain of these slips remain distinct and form the palmar interossei; the remainder unite with the intermetacarpales to form the dorsal interossei.

9. The term flexor brevis as applied to muscles of individual digits (pollex and minimus) is appropriately limited to muscles derived from the flexor brevis superficialis.

10. The flexor brevis pollicis as defined by Albinus is composed of elements derived from both the flexor brevis superficialis and the str. profundum of the flexor brevis medius. Only the outer head which is de-

rived from the flexor brevis superficialis is entitled to be known as the flexor brevis pollicis.

11. The interosseus primus volaris of Henle is correctly so named, and there are typically four palmar interossei in the human hand.

12. The derivation of the palmar muscles of the human hand from the various layers may be tabulated as follows:

Flexor brevis superficialis.—Palmaris brevis, abductor quinti digiti, opponens quinti digiti, flexor brevis quinti digiti, abductor pollicis, opponens pollicis, flexor brevis pollicis.

Flex. brevis med. str. superficiale.—The lumbricals.

Flex. brevis med. str. profundum.—The adductor pollicis.

Flex. brevis profundus.—The interossei volares, the interossei dorsales (in part).

Intermetacarpales.—The interossei dorsales (in part).

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