MORPHOLOGY OF THE FEET IN POLYDACTYL CATS

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EIGHT FIGURES

Phases of morphology which relate to the ultimate nature and meaning of homology have remained consistently baffling. For three quarters of a century it has been considered as axiomatic that each animal species has had a long phylogenetic history during which it has progressively deviated from earlier ancestral forms; and, for a somewhat lesser period, it has been considered as almost equally axiomatic that manifest evolutionary change is merely the outward expression of ultra-microscopic changes in the germplasm. But even if both these postulates are accepted in full, there still remains a formidable array of subsidiary questions which are as yet unanswered. Some of the latter have been discussed, from rather divergent points of view, by Bateson (1894), Boyden ('43), Hubbs ('44), Danforth ('25), and others. One of the most difficult of them is that of assessing the degree of phylogenetic and ontogenetic autonomy possessed by individual structural elements such, for example, as a metacarpal bone, or the tibialis anterior muscle.

Polydactyly in the cat provides excellent material for the study of some of these morphological problems. The condition is one of no great rarity and parallels, at least superficially, similar manifestations in man and several other species. Descriptions of feet from individual polydactyl cats have been published by several authors, notably Wilder (1868), Howe

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('02), and Regnault and Lépinay ('11), but it seems to the present writer that the trait itself deserves more attention as a genetic and morphological entity than it has thus far received. Feline polydactyly acquires an enhanced significance from the demonstration that, despite a wide range in its manifestations, all grades are conditioned by a single dominant gene. (Cf. Danforth, '47). This fact helps to fix the rôle of a genetic determiner more precisely than is usually possible in morphological studies, and greatly enhances the value of the material.

During the past few years some 150 polydactyl cats have been examined, and the feet of many of them have been dissected. Embryological material has also been prepared for the study of developmental stages. For the present report it seemed better to consider the trait as an entity rather than to describe in detail a selection of individual polydactyl specimens. In the following account, the term *normal* is used to indicate conditions found in the great majority of ordinary cats and described in such textbooks as that of Reighard and Jennings ('01). Structures that are not otherwise mentioned are believed to have been normal or to have shown only such minor variations as may occur in cats which are not polydactyl. However, only a few dissections of the entire body were made, and even the limbs usually were not examined in detail above levels of the knee and elbow. This leaves open the possibility that there may be other bodily anomalies to some degree correlated with polydactyly, but if there are they have not been recognized as such.

GROSS MORPHOLOGY OF POLYDACTYLY

In all polydactyl cats studied, the anomaly was limited to the pre-axial side of the limb (figs. 1 and 2). It is interesting that the gene is almost completely without effect on the 4 ulnar digits of the manus and the 3 fibular digits of the pes. Its degree of expression frequently differs on the 2 sides, and the anterior limbs are more consistently affected than the posterior (Danforth, loc. cit.). In addition to the extra digits,

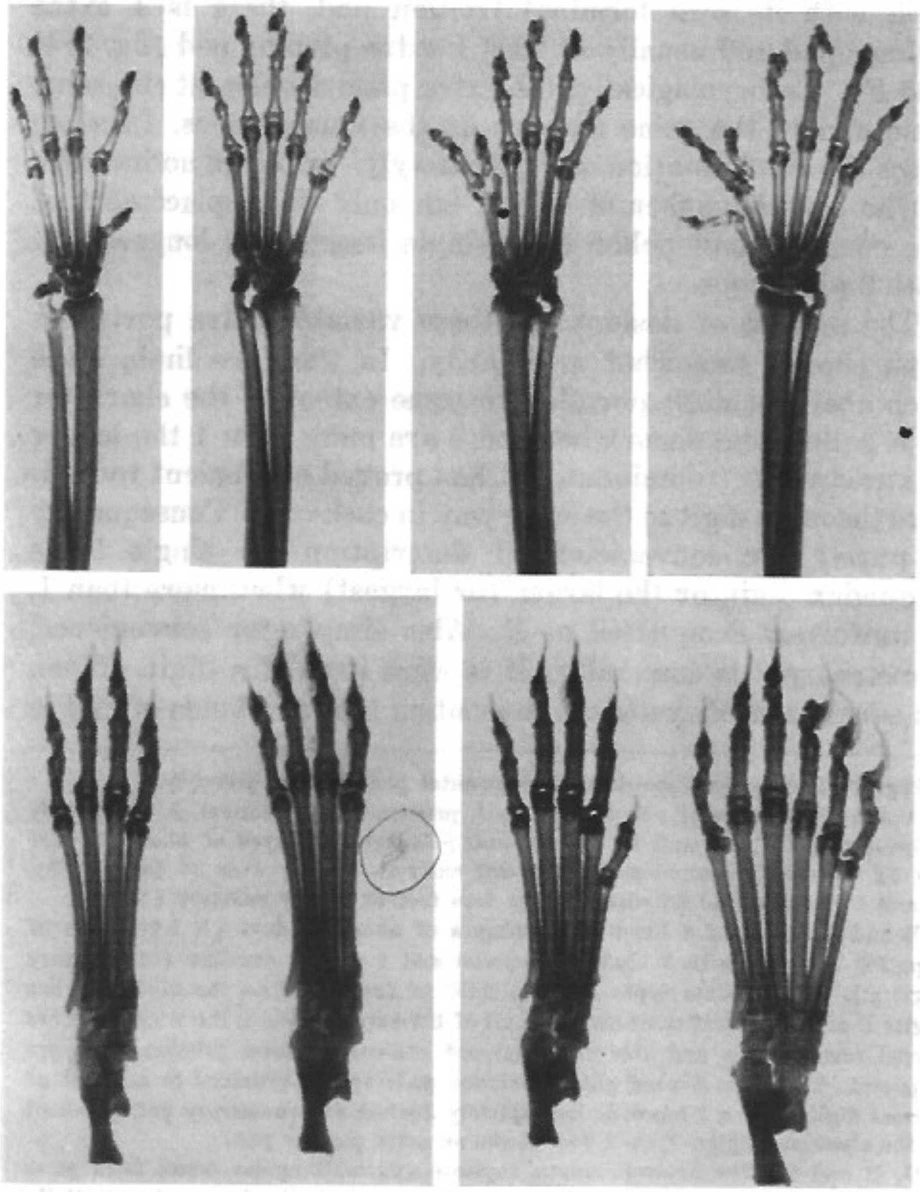

Fig. 1 X-ray pictures from normal and polydactyl fore and hind feet.

Upper row: fore feet *from left to right*, normal, type B, type BC and type ABC. The first 2 are lefts, the second 2 are rights; the 2 middle ones are from the same animal.

Lower row: left hind feet, *from left to right*, normal foot, foot with dewclaw (faint shadow to right of metatarsals), foot with 1 extra digit, foot with 2 extra digits.

each with its own terminal friction pad, there is 1 extra palmar pad and usually at least 1 extra plantar pad (fig. 2, E and F). Embryologically, the extra pads develop at the same time and in the same manner as the normal ones. In some cases the manifestation of "polydactyly" involves no increase in the actual number of digits, but only the replacement of the normal small pollex by a single larger and longer digit with 3 phalanges.

The method of designating these variable extra parts has been chosen somewhat arbitrarily. In the fore limb, since each aberrant digit partakes to some extent of the character of a pollex, and since when there are more than 1 the larger is structurally "dominant," it has proved convenient to indicate the main digit in the same way in each case. Consequently — purely for convenience of description — a single large pre-index digit, or the larger (or largest) when more than 1, is uniformly designated as B. Also simply for convenience, a metacarpal is counted as if it were part of a digit. When an equal or smaller digit is present on the radial side of B it is

Fig. 2 Photographs showing developmental phases of polydactyly.

A and A′, embryos of about 20 days, A presumed to be normal, A′ potentially polydactyl (× 4). B and B′, normal and polydactyl embryos of about 23 days (× 3). C and C′, normal and polydactyl embryos slightly over 24 days (× 3). D and D′, normal and polydactyl right fore feet of 33-day embryos (× 3).

E and F. Feet of 2 litter-mate embryos of about 45 days (× 1.4). E is of type BC in front, with 1 hind foot normal and 1 with a dewclaw (rudimentary digit B). F represents types AB and ABC in front, and on the hind foot has digits B of slightly different sizes. In all of the anterior limbs, the sites of future carpal tactile hairs and the well-developed conical pisiform friction pads are apparent. The usual 3-lobed palmar friction pads appear proximal to each set of normal digits, and a 2-lobed or incompletely 3-lobed supernumerary pad proximal to the abnormal digits. Only 1 foot shows an extra plantar pad.

G, H and I. The naviculo-lunate, capitate and multangular bones from paws of types B, AB and ABC, respectively. The capitate is free and essentially the same in all. The multangular bones are somewhat fused in H and I. The naviculo-lunate has an abnormal anterior projection on its radial side in G and H, but in I this is a free bone serving as an accessory multangulum (× 1.2).

J-O. The metatarsals, from the third medialward, the cuneiform and the navicular bones in normal and polydactyl feet. J, K, L, N and O from adults (× 0.5); M from a kitten (× 0.8). (Two epiphyses were lost from M in cleaning. K and O are from right feet, the negatives having been reversed in cleaning.)

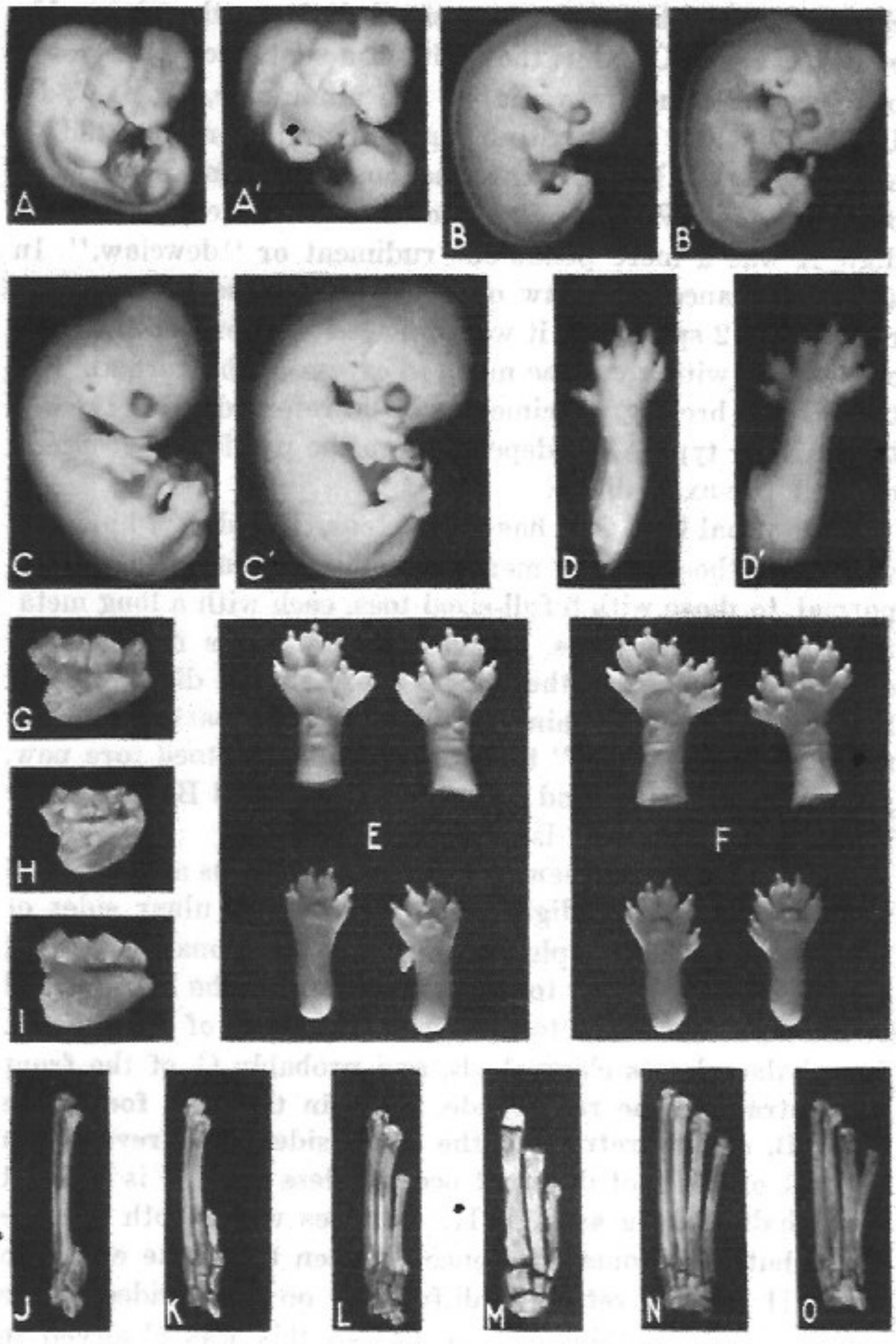

Figure 2

called A, and when there is a small digit on the ulnar side of B it is called C. Thus the digits of a septadactyl cat would be, counting from the radial to the ulnar side, A, B, C, II, III, IV, V. For a cat with 5 digits the numbering would be either B, II, III, IV, V, in case the most radial one is enlarged, or I, II, III, IV, V, if it is normal. In a very few cases digit A was a mere pendulous rudiment or "dewclaw." In several instances the claw of this digit was somewhat aberrant and in 2 specimens it was replaced by a broad, flattened, curved nail with a volume much in excess of the normal. For the sake of brevity, specimens will be referred to as type B, type AB, or type ABC, depending on the particular grouping of their pre-axial digits.

The normal hind foot has only 4 toes. Polydactyl hind feet vary from those having merely a small dewclaw in excess of normal, to those with 6 full-sized toes, each with a long metatarsal and 3 phalanges. In the present series no case was encountered in which there were more than 6 digits on any hind foot. The 6-toed hind foot generally appears more symmetrical and "normal" than does the 6- or 7-toed fore paw. Extra digits on the hind foot are called A and B when there are 2, or B when there is only 1.

In the normal cat, when the claws of the manus are retracted those of the 4 ulnar digits slide back on the ulnar sides of the respective middle phalanges, that of the small first digit directly back or barely to the radial side. On the hind foot all of the claws are retracted to the fibular sides of their digits. In polydactyl cats claws A, B, and probably C, of the front foot retract to the radial side, while in the hind foot those of A, B, *and II* retract to the tibial side. This reversal in digit II of the foot does not occur unless digit B is at least about half as long as digit II. In cases where both B's are short, but with some difference between them, the claws on digits II may be retracted differently on the 2 sides of the same animal. Nothing comparable to this was observed in the anterior limb.

Skeletal elements representative of different grades of polydactyly are shown in figures 1 and 2.

EMBRYOLOGY OF POLYDACTYLY

In our animals estrus usually occurred between December and July, and the gestation period was quite consistently 63 days in length. When matings were made between normal individuals and those known to be heterozygous, very few litters failed to contain both normal and polydactyl young. It was thus possible to obtain pairs of litter-mate embryos showing desired stages in the development of normal and polydactyl limbs (fig. 2, A-D).

Evidence of prospective polydactyl may be detected by about the twentieth day of intrauterine life. At that time a small, but definite, excess development is apparent on the cephalic margins of anterior limb buds in those embryos which may be presumed to be genetically polydactyl. At this stage the limb bud shows very little internal organization. In both types the marginal vein has developed and follows the contour of the limb. There are other blood vessels and nerves proximally, but the remaining tissue is nearly homogeneous, showing many mitoses but very little differential condensation. So far as the techniques employed reveal, the only difference between potentially polydactyl and normal specimens is in the amount of undifferentiated tissue on the pre-axial border of the limb. It seems not impossible that induction of an early excess in the number of cells at this point may be the chief, perhaps only, direct effect of the mutant gene, and that all other associated morphological deviations are merely secondary to this initial volumetric increase. Whether or not there is any simultaneous spurt in growth and comparable increase in undifferentiated cells elsewhere in the body cannot be answered at this time.

In later stages the excess tissue on the anterior margin of the limb bud is apparently incorporated in, or as a whole becomes, that part of the hand or foot plate which ordinarily gives rise to digit I, but in polydactyly the developmental behavior is such as to suggest that the increased amount of tissue results in a certain confusion in some of the ontogenetic processes which usually show a smooth interplay. Before the end of the fifth week the definitive form of the limb has taken shape and skeletal, muscular, nervous and vascular components are easily comparable with those of the adult (fig. 3).

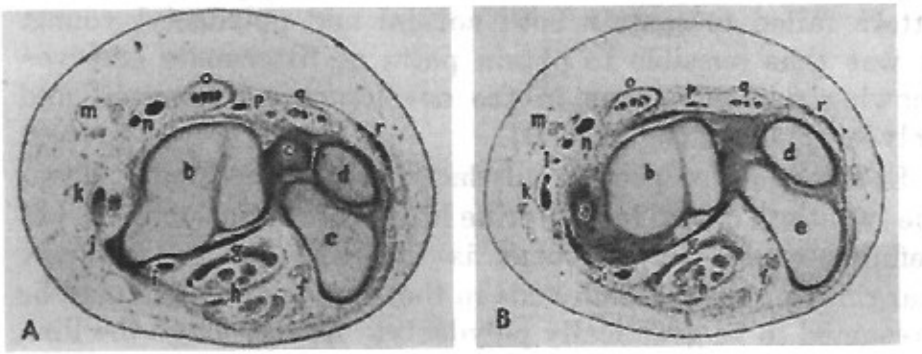

Fig. 3 Cross sections through the wrists of normal and polydactyl embryos of 33 days: A, normal; B, polydactyl. a, multangulum majus. b, naviculo-lunate. c, triquetral. d, styloid process of ulna. e, pisiform. f, ulnar nerve and artery. g, flexor digitorum profundus. h, palmaris longus muscle, transverse carpal ligament, median nerve, superficial flexors. i, flexor carpi radialis. j, periosteum of radial sesamoid (A only). k, tendon of extensor (abductor) pollicis brevis (in A about to join the radial sesamoid, in B dividing into 2 slips to metacarpals A and B). l, aberrant tendon from brachioradialis (functioning as an extensor carpi radialis). m, superficial radial nerve and cephalic vein. n, extensores carpi radiales longus and brevis (superficial to which in B there are 3 small accessory extensor tendons to digits A and B). o, extensor digitorum communis (with extra tendon in B). p, extensor indicis proprius (2 tendons). q, extensor digitorum lateralis. r, extensor carpi ulnaris.

Early development of the posterior limbs lags somewhat behind that of the anterior, but the processes are roughly similar. The normal posterior limb bud (which produces only 4 toes) gives the impression of having a certain deficiency on its anterior border, while a polydactyl limb bud has a well filled out contour more like that of a normal, or even polydactyl, fore limb.

THE SKELETAL SYSTEM

After the appearance of the initial unorganized bulge on the pre-axial side of the prospective polydactyl limb, the first clearly apparent indication of organization is a lobulation of the margin of the limb bud, followed (or accompanied) by condensations in the wrist or ankle and along the axes of future digits. The pattern for digits II-V is practically the same in both types of embryos, as is strikingly shown when outlines of comparable limbs are superimposed. But for regions anterior to digit II the outlines are not superimposable. In the polydactyl limb, perhaps because of the greater amount of tissue to be organized, the lobulation is aberrant and excess cartilages are laid down. While it might have been suspected that the impulse for differentiation is centrifugal, deviations from normal in the osseous and other systems appear as if they were contingent on the primary lobulation of the limb bud and the concomitant precartilage pattern. Cartilages in normal and polydactyl fore paws of 33-day embryos are shown in figure 4. In later stages it is often difficult to judge whether abnormal bones, especially incompletely bipartite ones, reflect imperfect differentiation of cartilages or fusion of cartilages which were originally distinct. Bones of the adult were studied in the course of ordinary dissections, and after having been cleaned. For cleaning bones of this size, solutions of sodium hypochlorite proved satisfactory.

Bones of the fore limb

No deviations from normal were noted in bones proximal to the wrist, and none of significance in bones of the ulnar side of the manus and carpus.

Phalanges. In polydactyl cats the phalanges are chiefly normal but, particularly in defective digits C, the basal one may be no more than a mere nodule, sometimes displaced to the side permitting partial articulation between the middle phalanx and the metacarpal. Where only 2 phalanges are found in digit C, it might be imagined that the basal one had been reduced to the vanishing point. The entire digit may be reduced to a nodule forming a transition between type B and BC (fig. 1, second specimen). In what is probably the majority of cases A and B each have 3 phalanges, but in some specimens, especially where there is also a C, digit A has only 2, being quite thumb-like, even though generally larger than a normal digit I.

Metacarpals. There is always a metacarpal for digit B, and almost invariably one for A when A is present. Both are long, and A is slender. B may also be slender, or it may be largest of the metacarpals. It occasionally has extra distal articular facets or is bifurcated, with 2 distal ends, to accomodate both digits B and C. In none of the specimens did A, B, and C each have complete and wholly distinct metacarpals of their own. In cats with 7 digits, metacarpals B and C were always united, at least at the base. The position of the epiphysis in metacarpal B throws no new light on homologies since it does not differ consistently from the position in metacarpal II.

Carpals. The wrist bones of the cat normally consist of a large naviculo-lunate, a triquetral and a pisiform in the proximal row; a smaller multangulum majus, a larger multangulum minus, a capitate and a hamate in the distal row. In addition to these, there is also in the distal row a small "radial sesamoid" in the tendon of the abductor pollicis longus (or "extensor pollicis brevis"), and interposed somewhat above and between the most radial extension of the naviculo-lunate and the lateral part of the base of the first metacarpal.

In polydactyl cats the radial sesamoid is rarely, if ever, present. In some instances its approximate position is occupied by an anteriorly directed process of the naviculo-lunate (fig. 2, G and H) and it might be thought of as incorporated in this bone. Howe ('02) so interprets it, but the homology is perhaps open to some doubt.

The carpus of polydactyl cats with only 5 metacarpals, whether or not there are 2 digits borne on B, shows little deviation from the normal except that the radial sesamoid is absent, as such, and the most radial metacarpal (B) articulates extensively, rather than very slightly, with the naviculo-lunate as well as with the multangulum majus. The other wrist bones in polydactyl cats with a total of only 5 metacarpals are normal. But when there are 6 metacarpals, all the carpals except the pisiform may be affected to some extent, the effect being chiefly that of flattening the wrist and slightly displacing bones on the ulnar side with resulant minor changes in their articular surfaces. In such cases the triquetral and hamate may be rotated somewhat ulnaward, and the capitate may

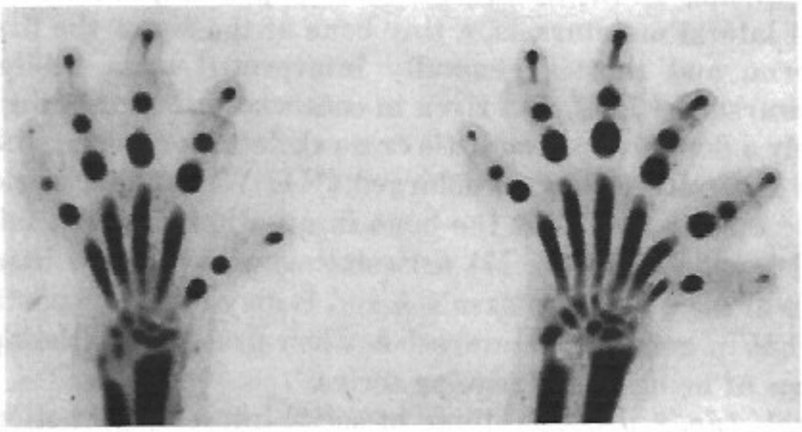

Fig. 4 Van Wijhe preparations of normal and type AB polydactyl fore limbs from 33-day embryos.

The polydactyl specimen is believed to be an exact counterpart of the adult specimen shown at H in figure 2. The 2 specimens are not exactly parallel in development, but the composite nature of the naviculo-lunate is apparent in both. The multangular bones are shown only faintly. Attention may be directed to the similarity between digit I in the normal left and a polydactyl right fore paw.

be much reduced in size. On the radial side, the region of the multangulum majus is occupied by 2 bones, metacarpal B articulating chiefly with the more ulnar one, while metacarpal A articulates primarily with the radial one and slightly, if at all, with the naviculo-lunate except in those cases where the latter has an anterior extension. The most radial multangulum might therefore be thought of as possibly representing that process or the radial sesamoid, or they both might be considered the same. In 1 case the equivalent of the 2 more ulnar ossa multangula was a single bone with the aspect of 2 fused elements and with articular surfaces for the respective metacarpals. Three variants in the arrangement of the more radial carpals and metacarpals are shown in figure 2 (G, H, I).

Bones of the hind limb

Phalanges. The phalanges seem to present no features of special interest, those of A and B tending to be 3 in number, although occasionally only 2 in the more tibial digit.

Metatarsals. In the normal cat there is present, in addition to the 4 lateral metatarsals, a tiny bone at the tip of the first cuneiform, and this is generally interpreted as a vestige of metatarsal I (fig. 2, J). Even in cats where the extra digit is merely a dewclaw having little or no skeletal component this bone is generally somewhat enlarged (K). When the new element becomes a full digit the bone in question develops into a regular metatarsal (L, M) articulating with the new basal phalanx of digit B. Metatarsals A and B may rarely be partly fused, but in general, metatarsal A when present has the appearance of being 1 of a regular series.

Tarsals (fig. 2, J-O). Nothing of secial interest was noticed in the calcanens, talus or cuboid in any of the polydactyl feet. In normal cats cuneiforms I and III meet beneath cuneiform II, which consequently does not reach the plantar surface, and the same is true of feet with a fully developed B but no A. When a digit A is present the pattern is less constant. For example, there may be a double first cuneiform with facets for both metatarsals A and B. Presumably this double bone is derived from 2 original elements (though embryological data on this point are not available), and a larger series might show cases in which the 2 parts of the bone are distinct even in the adult, giving a total of 4 cuneiforms. In another arrangement, metatarsal A has a basal prolongation which reaches to and articulates with the navicular. This basal process might well be interpreted as representing a cuneiform element. On its fibular side is an obviously double bone which articulates with cuneiform III and has articular facets for metatarsals B and II. In the most extreme variant observed (fig. 2, O), there was no distinct cuneiform I or II, the position of the forms being taken by a prolongation of metatarsal A, and that of the latter by an interpolated process from the navicular. In all cases cuneiform III is essentially normal, but in 6-toed feet it may have 3, albeit partly fused, elements medial to it. Six-toed cats are distinctly flat-footed as compared with the normal where cuneiform I is definitely on the side (scarcely on the dorsum) of the foot, and metatarsal I is pretty well rolled under metatarsal II.

Briefly, the occurrence of 5 toes is accompanied by very little change in the tarsal bones, but with 6 fully developed toes there appears at least 1 partially free new element in the cuneiform series, flattening of the transverse arch and minor concomitant changes in the articular facets of the navicular. The carpus and tarsus agree in that with extreme polydactyly an extra element may appear on the pre-axial side in the distal row of bones while the adjacent bones in the proximal row are modified to only a minor degree, if at all.

MUSCLES

Muscles of the forearm and hand

In those portions of the flexor muscles of the forearm which are proximal to the wrist, in the extensor carpi ulnaris, in the extensor digitorum lateralis and the intrinsic muscles of digits II-V, no deviations outside the usual range of variation were noticed. Other muscles show apparent effects of the polydactyly in all or many of the specimens. In general, the degree of deviation from normal is roughly proportional to the grade of polydactyly.

Extensor digitorum communis. In cats of type B there is frequently, but not always, a tendon to the radial digit (fig. 3 B, o, and fig. 6). When present it is related to digit B as the other 4 tendons are to digits II-V. In BC the presence or absence of a tendon to C is related to the size of the latter. Digit A may also have a more or less distinct communis tendon, while in some cases an ABC complex may lack it altogether, there being only 4 tendons in all. This situation, at first sight paradoxical, apparently depends on whether the radial complex of digits deviates little or much from the plane of the other digits; the more it approximates the position of a simple index the more likely it is to have at least 1 communis tendon. Hence in this situation the development of accessory tendons is inversely related to the grade of polydactyly.

Extensor indicis proprius. This muscle often sends a tendon to digit III and frequently a small slip to digit I. When B is present in place of I there is a strong tendon to B and a weaker one to II (and sometimes III). In polydactyly of a higher grade the large radial tendon tends to send slips to all the digits in the pre-axial complex but is likely to be blurred and aponeurotic. While in normal cats the 2 tendons usually begin to diverge at about the level of the wrist, in polydactyl specimens the division is often much higher up in the forearm so that in some instances 2 distinct muscles might be recognized with individual tendons passing through separate compartments in the dorsal carpal ligament (fig. 6). When this situation obtains, the larger, higher and more radial muscle is, at least in function, an extensor pollicis longus. Howe ('02) noticed this condition in the polydactyl cat which he dissected.

"*Extensor pollicis.*" In the normal cat, this muscle inserting through its sesamoid on the radial side of the first metacarpal is much more an abductor than an extensor. In B-type cats the normally clear-cut and sharply defined tendon is likely to be in at least 2 parts, the proximal being essentially like the normal, except for its lack of a sesamoid, while the distal extends up a little way on the metacarpal or on through an aponeurosis to the digit itself. In higher grades of polydactyly the proximal part sends tendons to the lower surface and medial aspects of metacarpals A and B, while the distal part sends dorsal slips to each of these digits or to the general dorsal aponeurosis. The latter in effect serve as true functonal extensors. In the more extreme cases the 2 sets of tendons each have their own muscle bellies, and it would then seem proper to speak of independent abductor longus and extensor pollicis brevis muscles. The latter, when distinct, arises from the lower third of the ulna and the adjacent interosseus membrane, scarcely at all from the radius. Thus in some cases the so-called extensor indicis proprius and extensor pollicis are replaced by 4 muscles (fig. 6) which could properly be designated as extensor indicis proprius, extensor pollicis longus, extensor pollicis brevis and abductor pollicis longus, all arranged in much the same manner as in man.

Brachioradialis and radial extensors. In most of the specimens studied the brachioradialis was normal, but it was found that it may, in whole or in part, pass over the usual site of its insertion to join into the tendon of the extensor carpi radialis brevis or insert independently as if it were itself an extensor carpi radialis. The radial extensors seem to show about the same amount and kind of variation in the polydactyl as in the normal, but when there are 6 metacarpals the brevis may supply an extra tendinous slip, and the longus may also be more or less double with some part of its insertion being confluent with that of the extensor pollicis brevis; but so far as observed it invariably has 1 normal insertion on the base of metacarpal II. In the region dorsal to metacarpals A and B there is a considerable network of inter-related tendinous extensions and aponeuroses.

Long flexors. The *palmaris longus* was found to send slips to the base of B and A when present. The *flexor digitorium sublimis* was mostly normal as to its origin, but in polydactyl cats there may be an accessory head from the transverse carpal ligament. It is a relatively insignificant muscle which sends tendons to A and B, B and C, or possibly at times to all 3 of these digits when present. The *flexor digitorum profundus,* which normally sends a tendon to digit I (and consequently one to B), has the same 5 heads in the polydactyl as the normal. On entering the palm of the former it gives off from its broad tendinous expansion strong tendons to digits A and B, a double tendon to B and C, or a tripartite tendon to A, B and C. These tendons diverge from the others at a more acute angle than does the normal tendon to digit I. In paws of the B type there may be only 4 *lumbricals*, arising between the tendons to digits B-V, or 5, 1 of them on the radial side of B. When there are 6 tendons a fifth lumbrical is apparently regularly present.

Intrinsic muscles. There seems to be complete correspondence between the intrinsic muscles of polydactyl and normal paws except for such muscles as are directly related to A, B and C. In the normal paw each metacarpal bone is covered by a muscle mass which divides distally to be inserted on the

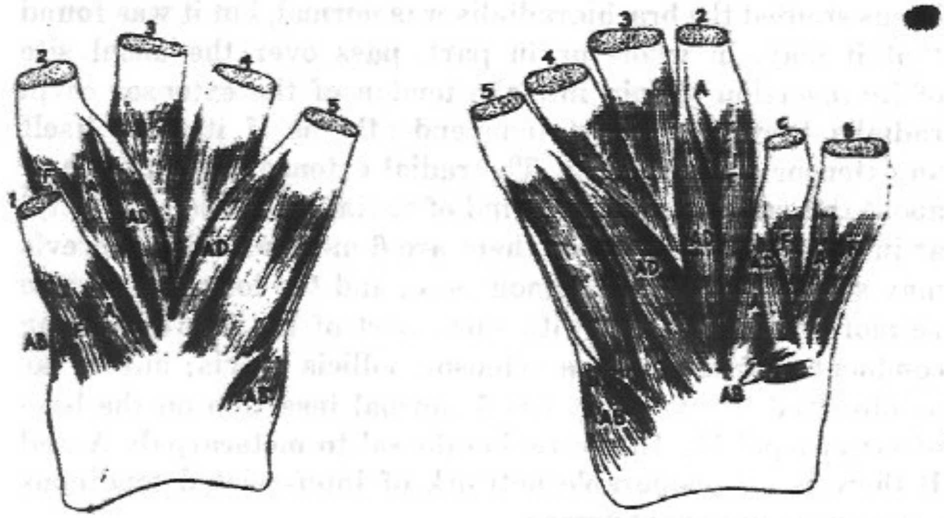

Fig. 5 Intrinsic muscles of a normal left and a polydactyl right fore paw. B, C, 1, 2, 3, 4, 5, digits, counting from the pre-axial border; AB, abductors; AD, long adductors; A and F, interossei broken down into short adductor and short flexor components.

2 sides of the basal phalanx of the corresponding digit. This makes 10 single, or 5 double, muscles which may be called *interossei*. Arising slightly superficial to these, and at about the level of the capitate, are 2 more muscles which diverge to be inserted, 1 on the ulnar side of the basal phalanx of digit II, the other on the radial side of the same phalanx of digit V. These 2 muscles (fig. 5, AD) are the (long) adductor of digit II and the adductor ("opponens") of digit V. Their insertions are slightly distal to those of the interossei. Finally

each marginal digit also has an abductor muscle (AB) and, as a frequent anomaly unrelated to polydactyly, there may be an abductor indicis (possibly representing a special slip of the dorsal interossus to digit II). At the risk of obscuring the relative simplicity of this arrangement, the radial parts of the first and second interossei may be designated as short flexors (F) and the ulnar components as short adductors (A) of the first 2 digits. Responses of the intrinsic musculature to polydactyly will be indicated by several examples.

In a cat of type B, the musculature of digit II was normal and that of digit B was similar to that of a normal digit I, except that all the muscles were of greater size and there was in addition a long adductor similar to that of digit II. In other words, this B digit had an abductor typical of the pollex, an adductor longus typical of an index, and a short adductor and a flexor typical of both. A similar arrangement occurred in a manus with a small digit C. In one with a larger digit C (fig. 5) there were 2 very small basal transverse muscles which it seemed could best be interpreted as slightly displaced abductores pollicium, 4 muscles which could be fairly well identified as flexors and short adductors for B and C, and an aberrant long adductor for C. The latter was not entirely distinct from the short adductors.

In the commonest type, AB with B slightly larger than A, each has its own distinct long and short adductors and a flexor. Likewise in a manus with 7 digits, II, C and B had almost identical musculatures except that II had a somewhat unusual abductor indicis (whose presence in this case probably bore no relation to the polydactyly), while digit A had a normal flexor muscle but no long adductor and, for the short adductor, only a slip from the flexor of B. Digit A did have the usual small abductor, thus being more similar to a true pollex in this respect than were either B or C. Whether the absence of an adductor longus and presence of an abductor brevis were due to the marginal position of the digit or to its relative remoteness from the center for digit II is not apparent.

Muscles of the leg and foot

When digit B of the foot takes the form of a dewclaw, the *extensores digitorum longus and brevis* may appear normal and unaffected by presence of the rudimentary extra digit, but in some cases there are ill-defined tendinous or ligamentous reinforcements of the fascia which simulate tendons to the digit, even though it is difficult to establish their connection to any muscle mass. Such slips may run not only to the extra digit but along the tibial side of digit II. Even in some extra digits with more or less complete skeletal equipment, there may still be some vagueness about the extensor tendons and muscles. In specimens where digit B is of nearly full size a definite pattern begins to become apparent. The tendon of the *tibialis anterior* divides into several subdivisions, the most proximal retaining the character of a tibialis anterior, the other(s) in part entering the fascia on the side of the foot but especially serving in the capacity of extensor longus tendons for digit B. One slip from this tendon regularly joins with the normal tendon from the extensor digitorum longus to digit II. This union of tendons from the true extensor longus and from the tibialis anterior to form the extensor tendon of digit II is apparently characteristic of all feet in which the tibialis supplies a tendon to digit B (or to B and A).

With subdivision of the tendon of the tibialis anterior, the fleshy part of the muscle also becomes subdivided, either very slightly, or completely and throughout its full extent (fig. 7). The latter condition is apparently constant in hexadactyl limbs. In such cases the anterior compartment of the leg has 3, insead of the usual 2 muscles. The new muscle takes origin from the upper fourth of the interosseus membrane and from the upper end of the tibia, chiefly superficially, above the tendon of the extensor digitorum longus and across from the insertion of the patellar ligament to the origin of the peroneus longus muscle. It is wedged between the tibialis anterior and the extensor digitorum longus but is not appreciably overlapped by either of them, having a subcutaneous surface throughout its whole extent. Its nerve supply is a branch from the deep peroneal. Its tendon passes under the transverse crural ligament in a position distal to, but close by, the tendon of the tibialis anterior in a way that recalls the relation of the tibialis anterior and extensor hallucis longus

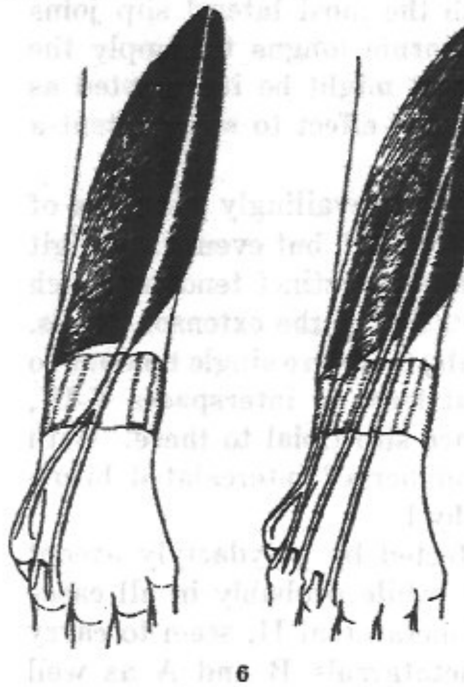

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Fig. 6 Sketches of normal and polydactyl left forearms and hands in dorsal view to show manner of separation of "extensor pollicis longus" and "extensor pollicis brevis" from the extensor indicis proprius and abductor pollicis muscles. The cut tendons are slips from the extensor digitorum communis.

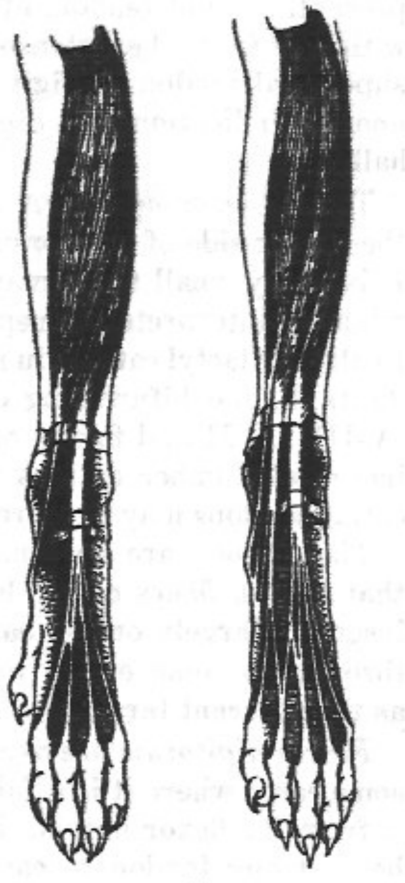

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Fig. 7 Sketches to show method of separation of "extensor hallucis longus" (right) from the tibialis anterior muscle.

in man. Indeed, if the first cats to be dissected had been 6-toed specimens this muscle, of which there is no trace in the normal, would no doubt have been unhesitatingly designated *extensor hallucis longus*. When this extensor hallucis longus is fully differentiated, the tibialis anterior has a single tendon of its own and nothing to distinguish it from normal except its somewhat smaller size and reduced area of origin. The only "aberrant" feature of the new extensor hallucis is that it consistently supplies a component to the extensor tendon of digit II, so that in contrast to the condition in man, the muscle always has at least a bifid or, in case digits A and B are both present. a trifid tendon, of which the most lateral slip joins with one from the extensor digitorum longus to supply the superficial tendon to digit II. This might be interpreted as another indication that digit II is in effect to some extent a hallux.

The *extensor digitorum brevis* is prevailingly a muscle of the fibular side of the dorsum of the foot, but even when digit B is fairly small there may be tiny indistinct tendons which might be interpreted as representative of the extensor brevis. In all polydactyl cats, as in normals, there are single tendons to digits V, and bifurcating ones at least to interspaces V-IV, IV-III, III-II and finally one more slip tibial to these. With increased number of toes the number of intercalated bifurcating tendons may be increased by 1.

The *peronei* are not much affected by polydactyly except that tendon fibers of the longus, while probably in all cases inserting largely on the base of metatarsal II, seem to carry through to some extent onto metatarsals B and A as well as the adjacent tarsals.

Flexor digitorum brevis. Where B is only a dewclaw, and in some cases where it is a fair sized digit, there is no tendon to it from the flexor brevis. But in other 5-toed feet there may be a strong tendon to each digit, and this is also true for 6-toed feet. In the latter the muscle shows an interesting tendency toward becoming subdivided, a large lateral part supplying the tendons to digits III, IV, and V, a smaller median part those to digits II, B and A. The 2 bellies begin to diverge well back toward the origin of the muscle. Here again digit II is aligned to some extent with the hallux-complex.

Flexor digitorum longus. In normal cats the flexor digitorum longus and "flexor hallucis longus" are both present in the leg, but as their tendons enter the plantar region they fuse into a common mass. The same is true of all polydactyl cats studied, no case in which the tendons remained distinct having been observed. But even when a single extra digit is little more than a dewclaw it receives a distinct slip from the common fused tendinous plate, and when there are 6 digits each gets its own tendon. The *lumbricals* are not very constant, even in non-polydactyl cats. They are in 2 sets; the long ones arising from the plantar surface of the main tendon, the short ones from points of division and sides of the digital extensions. It would require more data than are now available to assess properly the variations in these muscles. The long ones may be increased in polydactyl feet; there may be an extra short one between tendons to digits II and B, but even on the other side of the same cat this latter may be entirely lacking and, moreover, in some polydactyl feet lumbricals normally present are not found.

Intrinsic muscles. As in the manus, no significant deviations were found in the intrinsic muscles of the post-axial side of the limb. Musculature of the new digits tends to duplicate that of the normal digit II. In a foot with a fair sized digit B, this digit had a complete normal set of 3 abductor muscles, but no adductor or flexor at all, while digit II had a full complement of muscles, abductors, adductor and flexor such as would be found in digit II of a normal cat. A 6-toed cat showed interesting asymmetries in these muscles. On the left there were well-developed abductors for A and B, II had only small flexors, and neither II nor B had an adductor. On the right side of the same animal digits A, B and II each had all the muscles found in a normal digit II. It is of interest that digit II which is marginal in the normal cat, usually retains all its intrinsic muscles, even in extreme polydactyly, although occasionally it fails to do so.

BLOOD VESSELS AND NERVES

It does not seem profitable for present purposes to attempt any extended account of the vascular system of polydactyl cats, but the following points are of interest. In the normal manus the dorsal branch of the radial artery passes down between the heads of metacarpals II and III and, so far as has been observed, it has exactly the same relations in polydactyl cats of all grades. However, while in the normal paw a volar branch given off at this level turns radially to supply digit II and to some extent digit I, in polydactyl cats this branch may be very small or absent, with its normal area and the extra digits supplied by a much enlarged volar branch of the main radial. Similarly, the dorsal artery of the foot sends its main branch down along the interspace between metatarsals II and III, both in the normal and in most polydactyl feet. The venous branches were found to conform in distribution to variations either in the arteries or such nerves as the superficial radial and deep peroneal.

Nerves of the fore limb. The superficial radial nerve, accompanied by the cephalic vein, normally divides at about the level of the wrist into a smaller branch which runs along the side of digit I and then across it supplying both sides of that digit and the adjacent side of digit II. The larger division gives off other common digital branches and anastomoses with the dorsal branch of the ulnar. The pattern of distribution for these latter branches is surprisingly constant in both polydactyl and normal limbs, but the smaller radial branch becomes larger and separates higher up as the grade of polydactyly increases, and its ultimate branches are multiplied in proportion to the increase in digits. There is some tendency for it to bifurcate giving off an intermediate portion which in some respects suggests the normal branch of the ulnar.

On the volar side, the superficial nerves in the polydactyl limb are distributed as in the normal except that in the B type the median, passing under the volar carpal ligament, divides palmately into 4 common digital branches instead of 3. The most radial of them supplies digit B. In the AB type the nerves divide similarly into 5 common digitals. In an ABC paw the branching is less regular but the median still sends proper digitals to all digits radial to the annulus.

Both median and ulnar send branches to the normal volar friction pad, the median (only?) to the accessory. The deep branch of the ulnar, whenever dissected in full, was found to supply all the deep intrinsic muscles of the palm including those of digit A. This means that in this one respect even the ulnar nerve is affected by polydactyly.

Nerves of the hind limb. In the normal cat, while the saphenous nerve may extend well down along the tibial margin of the foot, the superficial peroneal also reaches that region and sends a branch to the tibial side of digit II. The peroneal also has 3 additional branches which divide in the interspaces between digits II-III, III-IV, IV-V, and one to the fibular side of V. In a cat with a tiny pendulous dewclaw a branch of the peroneal to the tibial side of the foot entered that appendage. In a cat in which the extra digit was larger the superficial peroneal sent branches to both sides of B and to the tibial side of II, with other branches as usual. Finally, in a cat with a full sized B the arrangement was the same except that the saphenous nerve took over the tibial side of the extra digit and sent an anastomotic branch to that part of the superficial peroneal supplying adjacent sides of B and II. In one 6-toed cat the relations of the saphenous were the same with reference to digit A as they were for digit B in the preceding. This cat had an extra branch of the superficial peroneal to the interspace between A and B. In another cat the saphenous supplied both sides of A and B. Several of these variants are shown in figure 8. There is a certain amount of fine anastomosis between the saphenous and superficial peroneal nerves, but there is little doubt that the innervation of 1 or more toes may actually be from the saphenous trunk as indicated, since in 1 case at least this was demonstrated by shredding the nerve under a lens back to a point too high for it to have received contributory branches from the superficial peroneal.

The deep peroneal nerve and the dorsalis pedis artery are apparently little changed in polydactyly, or not influenced in a constant manner. Their largest branches are generally between metatarsals II and III in polydactyl as well as normal cats, but in 1 hexadactyl specimen the largest branch went between III and IV, while in another the nerve sent conspicuous trunks between II-B and A-B.

The plantar nerves are especially interesting in cases where the polydactyl reaches maximal development. It has already been stated that in the 6-toed cat the flexor digitorum brevis

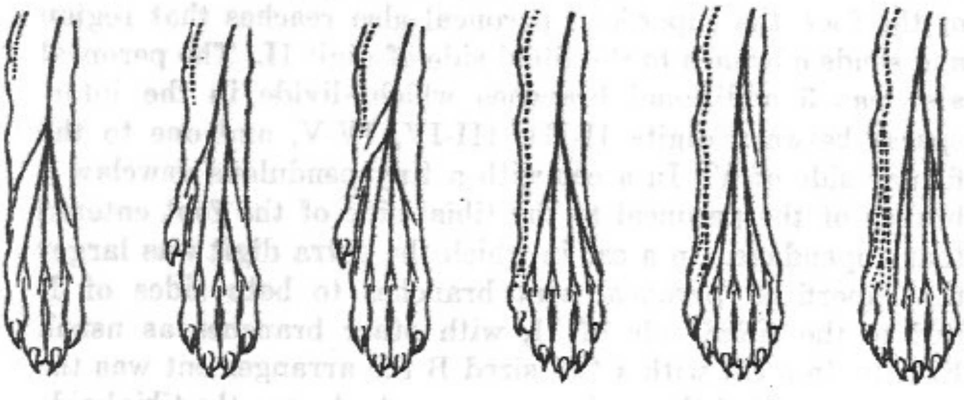

Fig. 8 Sketches to show extension of saphenous nerve in increasing grades of polydactyly. The saphenous nerve and its branches are indicated by broken lines, the superficial peroneal by continuous lines.

may be divided into 2 almost distinct muscles. Associated with this deviation there are 3 long plantar nerves all derived from the posterior tibial. The lateral plantar is normal, ultimately supplying both sides of digit V and 1 side of digit IV. A second nerve which runs along the medial side of the lateral flexor digitorum brevis (as if it were a median plantar) supplies contiguous sides of IV, III and II. Still a third nerve passes along under the more medial short flexor and gives off common digital branches to supply contiguous sides of digits II, B and A. Which of the latter 2 nerves should be called the median plantar might be open to question.

DISCUSSION

The total number of excess structures among bones and muscles alone varied in the material under discussion from 1 (an extra phalanx) to more than 50. But this variation was far from random. For any given grade of polydactyly there was a degree of constancy that made it possible to predict with considerable accuracy what would be found in a second specimen of a type already dissected. A fairly dependable guide could be written for the dissection of cats with front feet of type AB and hind feet of type B (the most frequent combination). Nevertheless, this stability is not that of the normal, and the type itself obviously represents only one of several levels in a rather wide range, in which the differences are presumed to be fundamentally quantitative rather than qualitative. The fact that all of the grades are ultimately dependent on the same gene strengthens this assumption. The lesser frequency of the trait in the hind limb possibly may be due to the early relative retardation in that limb.

In the chick, in which polydactyly has been much studied, 2 theories as to the early morphogenesis of the trait have been advanced. One, recently emphasized by Gabriel ('46), assumes that the phenomenon involves a twinning tendency which leads what would have been a single digit to divide, often with resultant mirror imaging. The other view (Danforth, '19) holds that the cause of polydactyly may be an initial excess of digit-forming tissue. According to either view, the first step in aberrant organogenesis might be induced by an unusual balance between a mass of tissue and the organizing influences which affect it, as postulated by Stockard ('21). It would not be out of line with genetic experience to find a gene influencing either the structural or the functional components in such a case. That the development of polydactyly in the chick can also be influenced to some extent by external factors has been shown by Sturkie ('43), Warren ('44) and Gabriel ('46).

In the polydactyl cat, the increased size not only of the aberrant digits as a whole but of individual digits, points to something other than a mere tendency of parts to subdivide. Moreover, the morphology does not suggest simple division of units, but gradations between them. The extra digit is not clearly a I or a II but generally something intermediate between a I and a II. Howe (l.c.) concludes his paper with: "The only definite statement which can be made in regard to this case is that where normally two digits occur, three have here appeared, and that each of these three partakes more of the nature of the others than one of the two normal digits does of the other." In view of these relations, the embryological data, and the structural details presented in the body of the paper, it would seem that the best interpretation of polydactyly in the cat that can be formulated at present is somewhat as follows: The occurrence of an excess of digit-forming tissue on the pre-axial side of the limb bud, and directly dependent on the presence of a single dominant gene, so disturbs the normal balance of developmental processes that there results a change in the size or number of digital lobes produced; the abnormal lobation is associated with, or possibly induces, development of extra cartilages; multiple cartilages in some way attract to themselves tendon terminals which might normally go to only a single cartilage; this leads to division of tendons; divided tendons in turn lead to division of muscle bellies; and finally nerves, blood vessels and cutaneous structures adjust to the new relations. The particular grade of polydactyly attained may be presumed to reflect the degree of initial discrepancy in the amount of digitogenic tissue present at a critical moment in the organization of the limb bud.

This centripetal control, or induction, of differentiation is a matter of considerable interest embryologically. Of course the work of Lewis ('01) and others leaves no doubt as to the main features in development of the normal limb, but since polydactyly can call forth such new muscles as the extensors of the pollex and hallux, the question arises as to how far comparable normal structures are likewise determined by peripheral influences. Such influences must be relatively limited in range since the polydactyl limb rapidly becomes normal from the periphery inward.

In view of its known simple genetic background, polydactyly in the cat serves to emphasize the importance of a frequent lack of one-to-one homologies in anatomical structures of different individuals. Where there is a single metacarpal bone in 1 specimen, there may be 2 in another, or a single tibialis anterior muscle may seem to correspond to 2 discrete muscles with quite different insertions. This fact suggests caution in attempting to homologize structures occurring even in related species, and should also be taken into account in supposed cases of reversion. In the polydactyl guinea pig, both Stockard ('30) and Wright ('35) assume either that a suppressed gene has been unmasked or that a reverse mutation has occurred, resulting in the reappearance of a previously lost ancestral condition. While from the cat material selected specimens could be so chosen as to seem to support that hypothesis, the data considered as a whole do not sustain such an assumption.

It is generally assumed that in primitive mammals the pes as well as the manus had 5 somewhat similar digits. Among polydactyl cats specimens can be found in which the foot does have 5 such digits, B being characterized by a strong metatarsal and normal phalanges, well-defined extensor and flexor musculature, and appropriate vessels and nerves. In some cases this first toe is surprisingly similar to what the ancestral form may be presumed to have been (fig. 1, bottom row, third from left). Starting with such a foot, one could arrange a closely graded series showing progressive reduction, and final disappearance, of the entire first digit with loss of the flexor tendon, the whole long extensor muscle and all the bones except a minute vestige of the first metatarsal. But even if one were to go so far as to assume that each specimen in such a series represents some stage in cat phylogeny, there would still remain the problem of explaining those specimens which have still another full-sized toe. Since an ancestor which normally had 6 digits on the hind foot must have antedated anything remotely resembling a cat, it would seem that the sixth digit (A) must have undergone extensive specialization "in absentia" or that evolution of the foot has been not so much intrinsically in the digits themselves as in the *factors* which regulate their development. Whatever conclusion is drawn in regard to the digits as a whole can probably be extended to each of their constituent parts.

The marked parallelism between the polydactyly of the cat and that of many other forms is noteworthy. For example, the osteology of the poydactyl human foot described by Cummins and Sicomo ('22) and the polydactyl hands shown by Pryor ('36) can be paralleled with considerable fidelity by specimens from the cat material; and even the extra digits in chickens have many points in common with those of mammals. If polydactyly were the rule, there would probably be little hesitancy in homologizing digits "A" in many different forms, but since it is rare, any such homology (in the usual sense of the word) is naturally regarded as spurious. The point, however, is one deserving of consideration.

SUMMARY

Polydactyly in the cat, a trait induced by a single dominant gene, reveals a considerable range of expression with respect to the number and size of extra digits, and the structures related to them. The variations, some of which appear as if they were qualitative, are believed to be the discontinuous structural expressions of quantitative differences in the effect of organizing factors acting on an excess amount of digitogenic tissue on the pre-axial side of the limb bud. It is suspected that inducing this excess tissue may be the only direct function of the causative gene.

Regulation of differentiation in the limb bud is to some extent from the periphery inward, and by no means entirely centrifugal. The peripheral alterations which occur in polydactyly affect the organogenesis of most types of tissue in the distal part of the limb. Muscle tendons, for example, divide to reach new cartilages, and in turn split the muscles from which they arise. In this way "new" muscles, analogous to those in other species may be brought into existence.

The manifestation of polydactyly at times gives a spurious appearance of reversion, but some of the classical concepts of homology seem to be misleading, or of little value, for purposes of interpreting polydactyly and probably normal conditions as well.

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