

CHAPTER XIV.

DIGITS : RECAPITULATION.

IN the remarks preliminary to the evidence of digital Variation it was stated that this group of facts is interesting rather as bearing on morphological conceptions than from any more direct relation to the problem of Species. The indications to be gained from the evidence will be treated under the following heads :

- (1) Comparative frequency of digital Variation in different animals.
- (2) Particular forms of digital Variation proper to particular animals.
- (3) Symmetry in digital Variation.
- (4) The manus and pes as systems of Minor Symmetry.
- (5) Duplicity of limbs.
- (6) Homœotic Variation in terminal digits when a new member is added beyond them.
- (7) The absence of a strict distinction between duplicity of a given digit and other forms of addition to the Series.
- (8) Discontinuity in digital Variation.
- (9) Relation of the facts of digital Variation to the problem of Species.

(1) *Comparative frequency of digital Variation in different animals.*

In reviewing much of the evidence of Variation and especially in the evidence concerning the variations of teeth it has been seen that the frequency of these variations is immensely greater in some classes or species than in others. This is remarkably clear in the case of the variations of digits. Compare for instance the great frequency of polydactylism in the Horse with the complete absence of recorded cases in the Ass. It is true that the latter is the rarer animal, but it might still be expected that some record would have been found if the variation were as frequent in the Ass as in the Horse. Again polydactyle Cats are certainly not very rare and specimens are in several collections having been acquired at many

dates. On the other hand digital Variation in the Dog seems to be confined to the formation of a hallux in the hind foot, and to duplicity of hallux and pollex¹. Similarly though digital Variation is so common in the Pig it is very rare in the Sheep, only one or two clear cases being so far known to me. Note again that polydactylism is common in the Fowl and has been often seen in the Pheasant, while in other birds it is very rare.

Some one will of course remark that the Fowl is a domesticated bird and the Pheasant is partially so; but pigeons, ducks² and geese³ are as much domesticated and in them digital Variation does not seem to be known. The cases in Apes deserve mention in connexion with this matter. One case of syndactylism was quoted in *Pithecia* No. 525, a case of polydactylism in *Macacus* No. 504, in Orang No. 511, and in *Hylobates* No. 508, and a case of ectrodactylism in *Macacus* No. 526. These five cases surely suggest that Meristic Variation is something more than a mere result of high feeding or of "unnatural" conditions. It is not a little strange that among Apes Meristic Variation should be frequently met with in so many systems of organs.

(2) *Particular forms of digital Variation proper to particular animals.*

Of more significance than the frequency with which digital Variation recurs in certain animals is the frequency with which in particular animals it approaches to particular forms, or to particular conditions in a series or progression of forms. This has been seen in the Cat, Man, Horse, Pig, Ox, &c. In each of these the mode of occurrence of Variation has in it something distinctive, something that marks the phenomenon as in some way different from the similar phenomena in other forms. Taking for instance the curious series of cases found in the human manus, ranging

¹ Both these variations are of course very common and may be seen in any walk in the streets. The hallux is very frequently present in the Dachshund and is common in Collies, Mastiffs and other large breeds. In the Mastiff dew-claws (hallux) are not a disqualification (SHAW, *Book of the Dog*). In the St Bernard the hallux is very often *double*, perhaps more often than not. This is largely due to the fact that the monks of the Hospice considered the presence of the dew-claw of the utmost importance and preferred it double if possible (SHAW, *l.c.*). The same writer states that 'the more fully the dew-claws are developed the more the feet are out-turned.' This fact suggests that there may be a change of Symmetry like that in the Cat, but I have no observations on the point. I have several times seen simultaneous duplicity of hallux and of pollex in the same individual (Dachshund, &c.). Other digital variations must be rare in dogs as there are hardly any recorded cases. A problematical case of ectrodactylism is given by BAUM, *Deut. Ztschr. f. Thierm.*, xv. 1889, p. 709, *fig. [q. v.]*. I once saw a mongrel Fox-terrier with no pollex on either manus, but I was not satisfied that they had not been cut off, though there was no suggestion of this.

² For an interesting account of a Duck with the webs of the toes almost wholly absent see MÖBIUS, *Zool. Gart.*, xviii. 1877, p. 223. Another case of the same kind MORRIS, F. O., *Zool.*, iv. p. 1214.

³ Pygmelian geese often recorded; e. g. CLELAND, *Proc. Phil. Soc. Glasg.*, xviii. 1886, p. 193, *fig.*; WYMAN, *Proc. Bost. N. H. S.*, viii. 1861, p. 256.

from the addition of a phalanx to the pollex up to the condition of Nos. 488 or 490, and comparing them with the essentially similar series of cases in the hind foot of the Cat, there is this remarkable difference: that though both progressions lead up to a similar kind of Symmetry in the series of digits, in the human manus an approach is made to a system of Symmetry whose axis lies internal to the index, while in the Cat's feet the axis lies external to the index (see Section (4)). The series of forms in the manus of the Cat is still more peculiar and is not like any case of polydactylism in other animals.

(3) *Symmetry in digital Variation.*

From the evidence it will have been seen that digital Variation in most of its manifestations may be similar and simultaneous in the limbs of the two sides of the body, though not rarely it affects the limb of one side only; and still more frequently the form which it assumes on one side differs in *degree* from that found on the other side. Considerable difference in kind between Variation on the right side and on the left is much rarer.

Almost the same statement may be made respecting simultaneity of Variation between the manus and the pes, though in the pes the manifestation of Variation is rarely *identical* with that in the manus of the same individual. Some variations, as for instance duplicity of pollex and hallux, or extra digit external to minimus, are not rarely found simultaneously in both pes and manus, but there are many cases in which no such agreement is found. The frequency of this simultaneous variation in the case of syndactylism in the Pig may be specially noticed.

Certain variations in certain animals seem to be almost or quite restricted either to hind limb or to fore limb. The form taken on by the pes of the Cat upon increase in number of digits is distinct from that assumed by the manus. The development of the digit II in the Horse is much more common in the manus. The extra digit (or pair of digits) in the Pig is so far as I know seen only in the manus. On the contrary the *three-toed state* in the Ox is found in the manus and also in the pes. Generally speaking, Meristic Variation is much commoner in fore limbs than in hind limbs.

One fact here calls for special notice. Though general statements are hazardous, we are perhaps justified in affirming the principle that *large* Meristic Variation, involving great departure from the normal, very rarely affects exclusively one side of a bilaterally symmetrical body. In cases of variation in vertebræ, in spinal nerves, in teeth, in the oviducts of *Astacus*, and many more, it is seen that on the occurrence of *great* variation the change is seldom restricted wholly to one side of the body, though the condition reached by the two sides is frequently of differing degree. Now in

the extreme forms of double-hand as seen in Man there is a curious exception to this principle. For in nearly all the extreme cases the abnormality was on one side only, the other being normal. This was seen in Nos. 492—500 and 501—503, and also in *Macacus* No. 504. The case No. 500 is probably an exception to this general statement. As to the significance of this absence of correspondence between the right and left sides in extreme cases of digital Variation I can make no conjecture. It has seemed that perhaps in such cases the absence of symmetry between the two sides of the body may be connected with the fact that in these extreme forms of double-hand an approach is made to a bilateral symmetry completed within the series of digits. But against this suggestion must be noticed first the fact that a similar bilateral symmetry is established in the six-toed pes of the Cat (Condition IV of the pes, p. 316), but the variation is nevertheless found on both sides of the body; and secondly the case of double-foot in the lamb (No. 566), though for reasons stated this latter case may perhaps be open to question.

(4) *The manus and pes as systems of Minor Symmetry.*

This is a subject to which it is most difficult to give adequate treatment. Several of the phenomena have as yet been studied in far too small a range of cases to justify sound generalization, and with further knowledge the suggestions arising from the facts now before us may not improbably be found to have been misleading wholly or in part. Besides this there is a serious difficulty in finding modes of expressing with clearness even those principles of form which seem to underlie the phenomena. This difficulty proceeds first from the vague and contradictory character of the indications, and next from the total absence of a terminology by which diversities of symmetry and the form-relations of parts may be expressed. Nevertheless it has seemed best to abstain from the introduction of new terms until the ideas to be expressed shall have been more clearly apprehended. It need scarcely be said that the remarks which follow merely represent an attempt to state some of the lines of inquiry along which the facts point.

On p. 88 mention was made of the fact that in a Bilateral Symmetry the organs which occur as a pair, one on the right and the other on the left, in so far as they are symmetrical are optical images of each other, this relation of images being what is implied by the statement that these organs are bilaterally symmetrical. The hands and feet of vertebrates are organs of this kind, the right hand and the right foot being approximately images of the left hand and foot respectively. But beyond their symmetrical relations to each other in the Major Symmetry of the whole body each manus and each pes may exhibit the condition of a Minor Symmetry within the limits of its own series of digits. Not only may each limb geometrically balance the limb of the other side

but its own external parts may more or less balance its own internal parts. This relation differs greatly in different animals, the Minor Symmetry being nearly complete in the Artiodactyles and in the Horse, but much less so in the human *manus* and *pes*, &c. The matter now for consideration is the influence or consequences of the existence of this symmetry in the Meristic Variation of digits; and conversely the light which the observed phenomena of Variation throw on the nature of that relation of symmetry. It will be seen that in some points the two halves of a bilaterally symmetrical limb behave just as do the two halves of the bilaterally symmetrical trunk, while in other points their manner of Variation is different.

Thus, the digit III of the Horse may divide into two halves related to each other as images, bearing hoofs *flattened on their adjacent edges*; that is to say, the two resulting parts are formed not as *copies* of the undivided digit, but as *halves* of it, a condition never seen in division occurring anywhere but in the middle line of a bilateral Symmetry.

In the syndactyle feet of the Pig or the Ox the converse phenomenon exists; for the digits III and IV, which normally stand as images of each other, are here wholly or in part compounded to form a digit to which the uncompounded digits are related as halves.

Thus far the connexion between the geometrical relations of the digits and the modes of their Variation is clear and simple, and does not differ from that maintained in the Major Symmetry. But in proceeding further there is difficulty.

If, for instance, the *manus* or *pes* of a Horse possesses within itself the properties of a bilateral Symmetry, then the splint-bone II may be supposed to be in symmetry with the similar bone IV. It would therefore be expected that on the occasion of the development of II to be a full digit, the splint-bone IV would at least not unfrequently develop, thus exhibiting that similarity and simultaneity of Variation which we have learnt to expect from parts in symmetry with each other. Nevertheless such an occurrence seems to be extremely rare. Then arises a further question: if the digit II develop simultaneously, say in the two fore feet, would the mechanical conditions of which Symmetry is the outward expression be satisfied without a corresponding change in the digit IV of the fore feet? Is the frequent absence of symmetry in the variation of the halves of the Minor Symmetry in any way connected with the possibility that the two Minor Symmetries together may be maintaining their relations to each other as parts of a Major Symmetry? Of course as to this we know nothing, but the existence of this double relation should be remembered.

In several other phenomena of digital Variation the influence of Symmetry is to be suspected. Reference may first be made to the series of changes seen in the Cat's hind foot in correlation with

numerical change. The bones of this pes do not normally exhibit any very clear bilateral symmetry¹. Yet on the appearance of new digits the foot is reconstituted and its parts are, to use a metaphor, 'deposited' in a system of bilateral symmetry² whose completeness is proportional to the degree of development of the new digits. What may be the meaning of this extraordinary fact one cannot yet guess. The fancy is constantly presented to the mind that there is in the normal foot a condition of strain, that the balance between the right foot and the left is a condition of imperfect stability, and that upon the introduction of some unknown disturbance this balance is upset and each foot settles down as a separate system. But I see no way of testing this fancy and no way of following it further.

Still more complex are the facts seen in the human hand. There is here first the fairly complete series of conditions ranging from the normal, through the three-phalanged thumb up to the several Conditions in which extra digits upon the internal side of the limb seem to have sprung up to balance the four normal digits; but on the contrary there is the exceptional case of the Macaque's foot (No. 504) where the extra parts are, as I believe, *external*. (Besides these there are the wholly distinct series of "double-hands," which will be spoken of below.) The former cases taken alone would certainly suggest that there is an imperfect balance or system of symmetry subsisting between the thumb and the four fingers of the normal manus, but to this suggestion there are numerous difficulties which need hardly be detailed in this preliminary glance at the phenomena.

With more confidence it can be maintained that the pollex and perhaps the hallux of Man is in itself a Minor bilateral Symmetry, apart from the four fingers, for it may divide into equal parts related as images. The same is true of the hallux of the Dorking (p. 390), and probably of the extra digit or digits sometimes arising from the tibio-tarsus of the Turkey for example (see No. 603).

Besides this the facts of the frequent syndactylism between the digits III and IV of the human manus, taken in connexion with the phenomena of the Pig and Ox, suggest that the four fingers may have among themselves again a relation of the nature of Symmetry.

¹ In the normal pes, though all the claws are retracted to the outside of the second phalanges, yet the claws of digits III and IV rest close together, that of III being external to its pad, while that of IV is *internal to its pad*, forming, so far, a relation of images between these two digits. In the polydactyle foot it is a remarkable feature that, though the bones are in symmetry about an axis passing between II and III, the relation of the claws of III and IV to their pads remains almost normal, still giving a superficial appearance of symmetry between these two digits. (In the polydactyle pes the pads are mostly rather narrower.)

² It will be remembered that this symmetry appears not merely in the lengths of the several digits but in the manner of retraction of the claws and in the corresponding form of the second phalanges, three digits being fashioned (in the case of six perfect digits) as right digits and three as lefts.

It has been mentioned that there is some evidence to shew that in the human pes it is the digits II and III which are most frequently syndactyle, even up to the point of being (in No. 529) apparently represented by a single digit, and in this connexion it will be remembered that in the polydactyle pes of the Cat it is also between these digits that the new axis of Symmetry falls.

These scanty allusions to the possible influences which Symmetry may exercise over Meristic Variation of digits will suffice to indicate the nature of the problem to those who may care to examine it. It is with hesitation that so indefinite a matter is spoken of at all. Nevertheless it is likely that if any one can find a way of interpreting these indications the result will be considerable.

(5) *Duplicity of limbs.*

In the evidence as to the digits of Man facts were given respecting the state known as Double-hand, and some similar cases were referred to in Artiodactyles. In these instances the digital series, and to some extent the limb, is in its new shape made up of the *external* parts of a pair of limbs compounded together in such a way that there is a partial *duplicity of the limb*, the two halves being more or less exactly complementary to each other and related as images¹.

This phenomenon in its perfect form must be essentially distinct from the other cases of increase in number of digits; for in the double-hands the limb develops an altogether new bilateral symmetry (see especially No. 492). Between cases of duplicity in limbs and the other forms of polydactylism confusion can only arise when the nature of the parts is ambiguous.

As has been stated, in all certain cases of double-limbs the two are compounded by their internal or præaxial borders, but the case of Macaque No. 504 was peculiar in the fact that there was in it a presumption that the two limbs were not a pair but in Succession.

In Arthropoda there are a very few cases of true duplicity in appendages comparable with the double-hands. These cases will be dealt with hereafter.

¹ The fact that a structure naturally hemi-symmetrical, needing the limb of the other side to balance it, may on occasion develop as a complete symmetry is most paradoxical, but no other interpretation of the facts seems possible. The phenomenon is of course comparable with that observed by DRIESCH in the eggs of *Echinus*, where each half-ovum developed into a whole larva on being separated from the other half-ovum (see p. 35, *Note*). It will be shewn that in almost every case in which such an appearance is found in the extra appendages of Insects this appearance is misleading, and that the extra parts have a Secondary Symmetry of their own; but no such way through the difficulty is here open.

(6) *Homœotic Variation in terminal digits when a new member is added beyond them.*

This is a principle that has been several times seen in Meristic Variation, and in Chapter x. Section 7, it was treated of at length in the case of teeth. Some few illustrations of the same principle occur among the evidence as to digits. It has been seen for instance how that, upon the appearance of an extra digit on the radial side, the digit which stands in the position of pollex may have three phalanges and resemble an index (No. 485, &c.). Similarly it was found that upon the formation of a large digit externally to the minimus the digit standing in the ordinal position of the minimus may have an increased proportional length (No. 509). Still more important is MORAND'S case (No. 510), in which the most external digit had muscles proper to a minimus, while the digit standing in the ordinal position of the minimus was without them.

The cases of extra digit in the Horse (No. 536, &c.) still more clearly illustrate the principle, if the view of the nature of those cases taken in the text be received.

It should be expressly stated that in digits, as in teeth, it is not always that the terminal member is promoted on becoming penultimate. Such promotion is indeed rather exceptional in digits, but the fact that it may occur is none the less a phenomenon of great significance.

(7) *The absence of a strict distinction between duplicity of a given digit and other forms of addition to the Series.*

This subject has been so often spoken of in connexion with special cases that it is unnecessary here to make more than brief allusion to it. The same principle was shewn to be true of teeth (p. 270) and of mammæ (p. 193), and there is little doubt that it is true of Meristic Series generally. Facts illustrating the matter in relation to digits will be found in the evidence as to duplication of pollex and hallux in Man (p. 351), as to duplication of the hallux in the Fowl (p. 391), in the evidence of cases in the Horse of variation intermediate between division of III and development of II (p. 371), and in the cases of three-toed Cows (p. 377).

In almost all the animals in which any considerable range of digital Variation is to be seen it is possible to find a series of cases making an insensible transition from true duplicity, or division into two equivalent parts whose positions and forms are such that they may be reasonably looked upon as both representing a normally single member, up to the condition in which while the series contains a greater number of members, each member nevertheless stands in a regular Succession to its neighbour.

Upon the proper understanding of this proposition and upon the recognition of its truth hang those corollaries before enuntiated

touching the false attribution of the character of individuality to members of Meristic Series.

(8) *Discontinuity in digital Variation.*

The evidence that the Meristic Variation of digits may be discontinuous is often rather circumstantial than direct. If for example in the case of the Horse any one chooses to suppose that every polydactyle horse had in its pedigree an indefinitely long series of ancestors in which the size of the extra digit progressively increased, it would not be easy to produce direct evidence that this was not the fact. But as regards the human examples such evidence is abundant, many of the most marked cases being the offspring of normal parents and there can be no reasonable doubt that the same would be found true of other animals.

But it may fairly be replied that until it shall have been shewn that formations like those described as variations may be established in a natural race or species the contention that the Variation of digits may be discontinuous is so far weakened. To this I would reply by referring to the case of *Cistudo*, *Chalcides*, and the other similar examples; for though in respect of these forms the evidence is sadly imperfect yet it plainly indicates that very distinct and palpable variation may be found between different individuals. And since it is actually known that there may in these points be considerable differences between the two sides of the body it may safely be assumed that at least the same differences may occur between parent and offspring.

We may therefore take it that there is in these cases some Discontinuity of Variation, though until some one shall have examined statistically such cases as that of the Box-turtles or of the Kittiwakes, as to the magnitude of the Discontinuity it is not possible to speak. If hereafter Discontinuity shall be shewn to occur in many such cases it will be difficult to resist the suggestion that similar numerical diversity elsewhere characterizing the digital series of various forms may have come about by similarly discontinuous Variation.

(9) *Relation of the facts of digital Variation to the problem of Species.*

This relation is both direct and indirect: direct, inasmuch as some of the conditions seen to occur as variations are not far removed from those known as normals in other forms; and indirect, since those strange and paradoxically regular dispositions of digits which are found among the variations bear witness to the influence of the principles of Symmetry, and prove that there are modes in which Variation may be controlled and may produce a result which has the quality of regularity and order of form independently of the guidance of Natural Selection.

Of actual variations from the arrangement of digits characteristic of one form to that characteristic of another there are as yet scarcely any examples. The cases given on pp. 395 to 398 being the most evident.

For the rest, that is to say examples of arrangements happening as variations matching no normal, some may say in haste that with their like Zoology has no concern. It would be convenient if those who make this careless answer (as many do) would mark the point at which it is proposed to begin this rejection of the evidence of Variation. Few perhaps realize how impossible it is to give a real meaning to these distinctions. As regards digits, for instance, I suppose that no one who holds the doctrine of Common Descent would refuse to admit the evidence of Variation as to the hallux of Hedgehogs (No. 612) as exemplifying the way in which species *may* be built up—if indeed species are built up of variations at all. And if this case is admitted, by what criterion shall we exclude cases of the formation of a hallux in the Dog? But if these are not excluded it is difficult to shew good reason for not admitting the case of the three-phalanged digit placed as a hallux in the Cat (No. 472) with all the curious series of which that is only the first term. Are we quite sure that because there is no Carnivore with a three-phalanged hallux therefore such a creature could not exist in nature? Still more difficult is it to shew cause why duplicity of the hallux should be set apart as a variation not capable of being perpetuated or of becoming part of the specific characters of an animal, seeing that there is actual evidence both in the case of the Dorking fowl and in the St Bernard dog that it may become at least an imperfectly constant character.

In connexion with the subject of this section many suggestions with special bearing on particular cases, both positive and negative, will strike every reader. In the present imperfect state of the evidence it would be premature to pursue these. It may however be well to mention that several writers, especially JOLY and LAVOCAT (No. 554), have seen in the cases of divided digit III in the Horse an indication that the digit III of the Horse corresponds with the digits III and IV of the Artiodactyles. The evidence as to syndactylism between these two digits in Ox and Pig would probably be considered to give support to the same view. But while we may note that the relations of the digits with the carpus and tarsus of these forms, were comparative evidence absent, should absolutely prevent any one from seriously maintaining such an opinion, nevertheless the fact that such closely similar systems of Symmetry may thus arise independently of each other is of interest.