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IN LIMBS.

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JEFFRIES WYMAN, M. D.

From the Proceedings of the Boston Society of Natural History, Vol. XI.,
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I.

SYMMETRY.

Anatomists who have compared the fore and hind limbs of man and animals, have mostly described them as if they were parallel repetitions of each other, just as are any two ribs on the same side of the body. By a few they have been studied as symmetrical parts, repeating each other in a reversed manner from before backwards, as right and left parts do from side to side.* We have adopted this last mode of viewing them, because, though open to grave objections, as will be seen further on, the difficulties met with are, on the whole, fewer than in the other, and because too, it is supported by the indications of fore and hind symmetry in other parts of the body.

*The following are among the more recent articles in which the homologies of the limbs and their symmetry are treated of at length.

S. R. Pittard. Article Symmetry—Cyclopædia of Anatomy and Physiology, Vol. IV, p. 845.

Observations on the Limbs of Vertebrate Animals. By George Humphrey, M. D., F. R. S., etc., Cambridge, 1860.

Charles Martins. Nouvelle Comparaison des Membres. Mémoires de l'Acad. des Sciences de Montpellier T. II, p. 461. 1857.

Also by the same author, Mémoire sur l'Ostéologie Comparée des Articulations du Coude et du Genou. Ann. des Sciences Naturelles. T. XVIII. 4me série. 1862.

Homologies des Membres Pelviens et Thoraciques de l'Homme, par le Docteur Foltz. Journal de Physiologie, T. VI, 1863, p. 49.

On Morphology and Teleology, especially in the limbs of Mammalia. By Burt G. Wilder, S. B., Cambridge, 1865. From the Memoirs of the Boston Society of Natural History.

Also by the same author, Morphological Value and Relations of the Human Hand. Am. Journal of Science, Vol. XLIV, July, 1867, p. 44.

Among animals, two organs or parts, generally speaking, are said to be symmetrical when they are situated on opposite sides of an axis, and are alike in form and size, but one is the reverse of the other, as is everywhere obvious in those which are right and left. It is not to be understood, however, that this likeness is absolute; for while it is very generally true that such right and left parts are alike in size and form, or very nearly so, it occasionally happens that they are very unlike in these respects, still retaining, however, a certain amount of symmetry. We have striking illustrations of this in the claws of many Crustaceans, as in *Astacus* and *Gelasimus*, and in the right and left halves of the body of *Bopyrus*. Among Acephalous Molluscs, this difference is in some cases very remarkable, as in *Radiolites*, *Monopleura*, etc., where one of the valves is conical and spirally twisted, while the other is quite flat, and in its relation to the other valve, resembles the operculum of certain Gasteropods.

Among Vertebrates such differences are much less frequently met with; they however exist, and symmetry of right and left parts, even in the human skeleton, is not constant; it may even be doubted whether absolute symmetry exists anywhere. Attention has recently been called to asymmetry in the base of the skull, and by a comparison of the bones of the fore arm in ten skeletons, we have found the right ulna longest in eight, the left in one, and in one the right and left bones were equal. Differences in length and weight were also found in the clavicles, the humerus, and other parts of the skeleton, but in different degrees. The close approach to absolute symmetry in some of the minuter details of structure is sometimes quite remarkable, as in the arrangement of the papillæ on the tips of the fingers and toes of most individuals; in some, however, the asymmetry of these parts is quite marked, and in others even the pattern of the figure on the two sides is changed. More marked instances of asymmetry exist in the unequal nostrils, and more or less bent vomer of some Cetaceans, in the rudimentary right, but immensely developed left tusk of the Narwal, in the lower jaw of the adult male Mastodon which has a tusk on the left side, but none on the right, in the unequal development of the ovaries and oviducts of most birds, as also in a similar condition of the carotid arteries. In the human brain the hinder lobe of one of the hemispheres, more commonly the left, is longer than the other, as may easily be seen in the cranium by the depth of the corresponding fossæ. In the illustrious Bichat, the inequality of the two sides of the head amounted to deformity. The most striking instances of all are to be found in the halibut (*Hippoglossus*), flounders (*Pleuronectes*), and other flat fishes, in which the bones of the face, the brain and organs of sense are all more or less distorted, and the eyes especially are unsymmetrically placed.

All organs which are thus unlike or unsymmetrical in the adult, have been shown by embryologists, as by Steenstrup in the case of the flat fishes, and also in the crabs, molluscs, etc., by other observers, to be alike in the embryo, the deviations from true symmetry taking place as development advances. We have seen a lobster nearly three inches in length, in which the right and left anterior claws were still symmetrical.

The organs of the great cavities in adult vertebrates are almost uniformly unsymmetrical; nevertheless in the embryo the symmetry of these parts, even of the liver, is complete. In some fishes this is true of the liver of the adult, and in a few instances this is divided into a right and left organ. The fundamental idea of the organs of organic life involves the condition of symmetry. The other kind of symmetry, viz., that which is believed to exist between the fore and hind parts of the body is much less obvious, and would in fact be generally overlooked, the deviations from true symmetry being so great. In many Articulates, however, this deviation is comparatively slight, especially in the genera *Jaera* (Fig. 1), *Oniscus*,

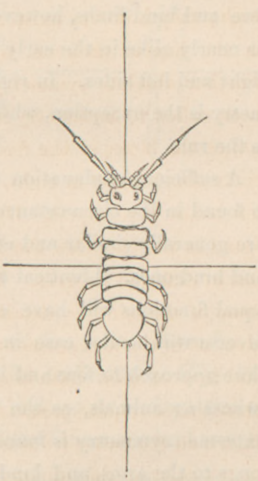
Fig. 1.

Porcellio, *Asellus*, *Cymothoa*, and other Isopods, also among Myriapods, as in the genera *Scutigera*, *Scolopendra*, etc., in which the limbs are repeated oppositely, though with different degrees of inequality, from the centre of the body backwards and forwards. If to the general symmetry of such fore and hind parts we add certain details of structure occasionally seen, especially the fact that some of the worms and Crustaceans have organs of special sense developed in the last as well as in the first segments, the evidence that the fore parts are repeated in the hinder becomes much stronger.* Among Vertebrates, as will be seen further on, the resemblance between the fore and hind limbs is quite obvious, and the symmetry of plan easily recognized; but in the majority of animals, whether vertebrate or invertebrate, fore and hind parts, though symmetrical in plan, actually differ largely from each other, both in size and form, and thus present a distorted symmetry like that which has already been noticed between right and left parts. The analogy holds still further, since the fore and hind limbs, however widely they may differ in the adult, are as nearly alike in the early embryo as are corresponding limbs on the right and left sides. In right and left parts, however, distorted symmetry is the exception, while in the fore and hind parts of *adults* it is the rule.

A sufficient explanation of this deviation from complete symmetry is found in the circumstance that in right and left parts the functions are generally similar and equal, while this is seldom the case in fore and hind ones. Identical and homologous parts having similar and equal functions will have equal growth and development, while the reverse will be the case in those having the opposite conditions. A close approach to fore and hind symmetry of limbs is found in certain swimming animals, as the *Ornithorhynchus* and *Ichthyosaurus*, while extreme asymmetry is found in birds, in which aerial locomotion belongs to the arms, and land or aquatic locomotion to the legs, or as

* Leuckart and Van Beneden have shown that *Mysis* has an ear in the last segment, and Schmidt has described an eye in the same part in *Amphicora*, a worm Nat. Hist. Rev., April, 1862, p. 133. See also Quatrefages, Mémoire sur la Famille des Polyophthalmiens, Ann. des. Sc. Nat. 3^{me} série, T. XIII, p. 5.

in the kangaroos and other jumping animals, where the hind limbs predominate so largely over the fore ones, and in the apes and three-toed sloths, where the reverse is the case. Similar extreme differences are still better indicated by the animals whose tracks are left in the Connecticut River sandstones, as for example, in *Anomoepus* and analogous forms.

The facts brought to light by the study of embryos, offer additional evidence in support of the view that the fore and hind portions of the body are in idea symmetrical. As already stated, this is the more noticeable the nearer the embryo is to the earliest stage of its development; and it is to this that attention should be carefully turned, for as the embryo becomes more specialized, and its organs take on those forms which adapt the individual to its future conditions of life, the differences rapidly increase.

In the general development of the vertebrate embryo, the *first* fact which strikes us, as it increases in size, is that this increase is not from a growth from before backward, but from a central, and, as it were, a neutral point, both backwards and forwards, so that the two ends are made to recede from the centre in opposite directions, just as do the radicle and plumule of a plant from the point where these are continuous. By this process the head and tail both become free, while the central part of the body remains attached to the yelk. *Secondly*, the primitive groove of the nervous axis in its earliest stage (Fig. 2) is nearly symmetrically enlarged at either end, so as to form two opposite dilatations:* one the precursor of the future cerebral vesicles,

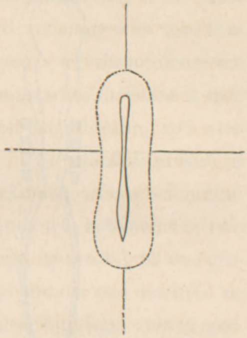

Fig. 2.

* In some adult fishes the spinal marrow ends in a ganglionic enlargement, forming a kind of caudal brain. We have found such a ganglion quite conspicuous in the American *Lophius*, and Quatrefages describes one in *Amphioxus*, which is all the more striking, since it is only a diminutive repetition of the fore end of the axis. The distribution of the last pair of nerves, as seen in his admirable figures, is also symmetrical with that of the first.

and the other of the rhomboidal sinus, which last has only a temporary existence in the mammals, but is permanent in the birds. *Thirdly*, when the spinal groove closes up by the union of the dorsal laminæ, it does so, as Reichert has shown, by the union of its lips, first in the middle portion, and then gradually in a symmetrical manner towards either end. *Fourthly*, in the four classes of vertebrates the first traces

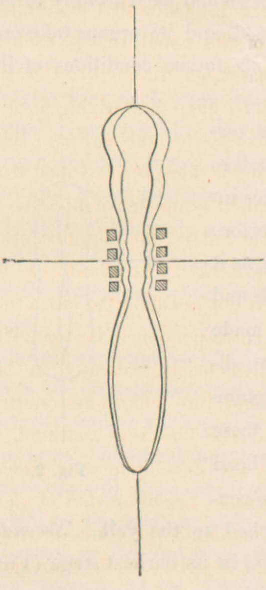

Fig. 3.

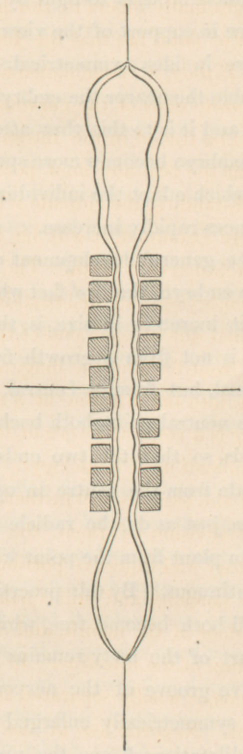

Fig. 4.

of the vertebral segments are to be found in three or four pairs of plates which appear on either side of the primitive axis midway between the two ends, from which region they are multiplied and extended forwards to the head, and backwards to the tail, by the development of new plates, thus lengthening the column in a symmetrical manner (Figs. 3, 4). The ossification of the bodies of the vertebræ takes place in the same order, beginning in the middle and extending in either direction. During the first half of fœtal life, and even beyond it, in the human body, the bodies of the vertebræ first ossified, viz., those in the middle, are the largest, and from these the column of bodies gradually tapers to the head and coccyx. It is only towards the end of fœtal life that the lumbar vertebræ assume larger proportions. *Fifthly*, a resemblance analogous to that which exists between the opposite ends of the nervous system and of the vertebral column, can also be traced in the intestinal canal. Oken first maintained the idea that the oral and anal portions of this canal repeat each other. Notwithstanding the ridicule which has been directed to this view of his, fairly examined, it will be found to have, underlying it, at least the semblance of a truth. The two opposite ends agree in this, that in the embryos of all air-breathing animals there is developed from the abdominal side of each end of the straight symmetrical intestine a sac; that in front forming the lung, and that behind the allantois, and each opening into the intestine by a narrow neck. The allantois as well as the lung is a respiratory organ, but it is not justifiable to cite a function as an indication of homology. The correspondence between the two ends of the canal is still further, but less clearly, indicated in the subsequent division of them, the fore end into mouth and nostrils, or respiratory and digestive portions, and the hind into anal and genito-urinary portions, and still further by the development of the tongue on the floor of the mouth, and of the male organ on that of the genital portion of the intestine. In most mammals the genito-urinary portion becomes wholly separated from the digestive, while the respiratory does not. Nevertheless in the embryo the first retains its connection for a certain time, as is permanently the case in the birds and reptiles.

The most striking facts bearing upon the idea of fore and hind symmetry are to be found in the development of the limbs. Von Baer has described the phases which the limbs assume, as also their attitudes as they advance towards their permanent condition. We have traced these successive positions in several embryos, and from them the following description is drawn. The limb-buds, when first formed, are simply tegumentary outgrowths, and project at right angles from the sides of the body in the form of half oval discs. As they increase in length they become divided into a somewhat flattened, disc-like end, which becomes the future hand or foot, and a pedicle which connects this with the trunk. This pedicle is transformed into the fore arm and leg, and partly into the arm and thigh; the remaining portions of these last, when developed, result from a still further outgrowth from the body which takes place at a later period. In the *second* stage the limbs are each bent to an angle at a point near the trunk, so that their ends are directed downwards, and what were previously the under sides of the disc-like hands and feet (the body being supposed to be horizontal), have now become vertical and face inwards; they are the soles and palms. The angle formed in the limbs corresponds with the elbows and the knees, and thus marks off fore arms and legs from arms and thighs, these last being very short. *Thirdly*, during the stage just mentioned, both upper arms and thighs projected at right angles from the sides of the body. They now begin to change their direction with reference to the trunk, but in a perfectly symmetrical manner. The elbow which has thus far projected outwards, now swings backwards to the side of the thorax, and the knee forwards towards the side of the abdomen. This condition of things is readily seen in a human embryo in the writer's collection, measuring 0.60 inch in length, and represented in Fig. 5. The effect of this change of position would be to make the palms face forwards, and it makes the soles face partly backwards. This tendency, however, as regards the hand, is counteracted by a remarkable change of position in the fore arm. This is slowly rotated inwards, so that the palm is made to face almost backwards. In those animals which walk on the palms of their hands, the hand is bent on the fore arm, so that its back is raised, the palm directed more or less downwards, and thus the limb is

Fig. 5.

adapted to walking or crawling. At the same time a similar change takes place in the feet, the backs of which are raised towards the fore part of the leg, and the toes directed forwards, and the sole downwards. The rotation of the fore arm just mentioned is the chief cause of the interference with the symmetry of the limbs; were it not for this the hands and feet would have assumed exactly symmetrical attitudes, the toes projecting forwards and the fingers backwards, the back of the foot looking towards the fore part of the leg, and the back of the hand towards the hind part of the fore arm.

If we admit the idea of symmetry in structure between arms and legs, and would compare the movements of the two in man and animals, we must change in some respects the terms flexion and extension, from those ordinarily used in the description of the human body. We will suppose the human skeleton suspended with the vertebral column horizontal, the limbs slightly flexed, the toes and fingers pointing downwards, the palms facing forwards and the soles backwards. Flexion of the humerus would be backwards, of the femur forwards; of the fore arm forwards, of the leg backwards; of the hand backwards, that is by carrying the back of it towards the back of the fore arm, and the foot forwards. Thus the movements would be symmetrical throughout in the two limbs. Supposing the limbs to be of equal strength, somewhat flexed, the soles and palms resting on the ground, they would antagonize each other in their action; the fore limbs, if extended, would, in consequence of their obliquity, tend to push the body upwards and backwards, and the hind limbs under the same conditions upwards and forwards. The two acting together would give rise to a resultant motion upwards. By the rotation of the fore arm in the embryo the action of the fore limb is reversed, and thus in the forward movement of the body coöperates with, instead of antagonizing, the hind limb.

When fully developed, therefore, the fore and hind limbs of animals have a general symmetry except in the following respects; the bones of the fore arm cross each other, while those of the legs do not, and the toes and fingers are both directed forwards. If, however, the fore arm be rotated outwards through half a circle, so as to make the bones parallel, as in the leg, thus counteracting the change which took place during development, the *general* symmetry would be restored, and be complete. There would, however, exist a certain amount of special asymmetry in the position of the thumb and great toe, for these would be on opposite sides of the two limbs. Of this difficulty we shall speak again further on.

The symmetry of disease to which attention has of late years been called,* also helps to sustain the idea of fore and hind symmetry. Certain maladies, as psoriasis, leprosy, syphilis, etc., not only attack corresponding or symmetrical portions of right and left parts, but also of fore and hind parts. Certain skin diseases attack the backs of the hands and feet, or the palms and soles, or the elbows and knees. The earthy deposits in the arteries show a similar tendency to symmetrical distribution. Such instances, however, are quite rare in comparison with the vast proportion of diseases in which no such tendency is apparent. They nevertheless tend to show that homologous parts, either on the right and left, or fore and hind parts of the body, have such a constitution that they are more amenable to the influence of a given disease than other parts.

We pass by only with a mention a third kind of symmetry, which has been much insisted on by some anatomists, viz., that between the dorsal and abdominal parts. Under certain circumstances this kind of symmetry becomes almost exact, as may be seen, for example, in a vertical section of the tail of a fish, where the arrangement of the bones, etc., below a horizontal line, passing through the vertebral column, is only a reversed copy of the parts above.

The statements which have been made in the previous pages are intended to show that even in right and left parts, symmetry is of various degrees, and is rarely, if ever, absolute. Asymmetry, however, is in most cases slight, but may in certain others become as great as that between fore and hind limbs, in accordance with the degree of

* William Budd. Medico-Chirurgical Transactions, London. Vol. xxv, 1852.
James Paget. Surgical Pathology. Philadelphia. 1860. p. 27.
Burt G. Wilder. Pathological Polarities, or What has been called Symmetry of Disease. Boston Medical and Surgical Journal, April 5th, 1866.

difference in the function of the two sides. These differences do not, nevertheless, prevent our recognizing the idea of symmetry of plan underlying the structure of such parts. In comparing fore and hind limbs, it has been shown that they are sometimes nearly symmetrical, but generally the symmetry is largely distorted. But if we bear in mind the fact that the limbs which in the adult are the most unsymmetrical, are quite symmetrical in the embryo, the hypothesis that the idea of symmetry underlies their structure is rendered highly probable.

II.

ANALOGY BETWEEN SYMMETRY AND POLARITY.

From what has been stated it is obvious that in the early stages of development there is at work a force which regulates the distribution of the particles of matter out of which the embryo is formed in a symmetrical manner, and that up to a certain stage there is symmetry, not only of right and left, but of fore and hind parts. The essential characteristic of this force is that it gives rise to similar but reversed forms on the two sides as well as on the two ends of the axis of the body.

If we look for any thing among known forces analogous to this force, it is to be found, if anywhere, in those known as polar forces. The essential features of polarity, as of symmetry, are antagonism, oppositeness or inversion, either of qualities or forms. Studying the subject from the most general point of view, there are striking resemblances between the distribution of matter capable of assuming a polar condition, and free to move around a magnet, and the distribution of matter around the nervous axis of an embryo.

In every complete series of magnetic curves formed by particles in a polar condition, there are two neutral lines (Fig. 6, A), one extending lengthwise of the magnet, so that the curves formed may be divided into right and left; secondly a transverse one, the particles on each side of which form the north and south curves, or which for purposes of comparison might be called fore and hind curves. In the right and left series those which are on one side of the long axis are symmetrical with those on the other and not in themselves, and in the north and south series those on either side of the transverse neutral line are symmetrical with each other, and not in themselves.

If these curves are projected on paper, and this be folded on the line of the longitudinal, or north and south axis, the curves of opposite sides or opposite ends will correspond as right and left hands or other double organs do when applied to, or placed opposite each other. The same is true of the north and south curves when the paper is folded on its transverse axis.

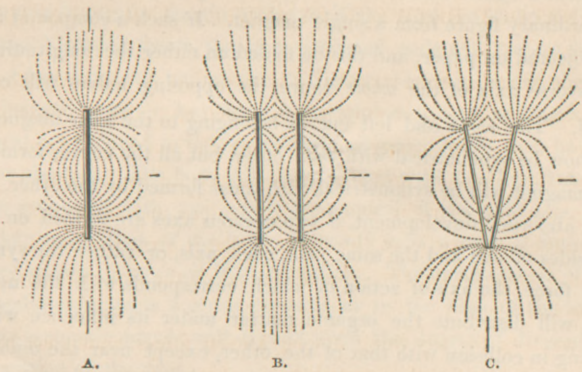

Fig. 6.

The distribution of particles just described, corresponds, first, to all that we designate as right and left in normal development; second, to all that we designate as fore and hind with reference to the long axis of the body, and which is characterized by symmetry in structure.

Not only is there this analogy between the distribution of matter around a magnet, and that around the nervous axis of the normal embryo, but the analogy is still more striking in the curves formed by the combined action of two adjoining magnets and the appearances found in more or less double monsters.

If two magnets are placed parallel to each other (Fig. 6, B), and at a distance, two sets of curves are formed as in the usual way; but if they are brought so as to be within each other's influence, the two magnetic figures are combined, and now form a single compound one, the middle portion of which consists of the curves from the two adjoining sides of the magnets; and the particles from either series of curves do not pass beyond the line where the forces of the two magnets are in equilibrium, but are deflected upwards or downwards, north or south. In this manner that portion of the figure formed by the particles arranged between the two magnets becomes symmetrical, one half consisting of particles belonging to the right magnet, and the other half of those belonging to the left. The symmetry of the whole compound figure thus formed is in all respects as perfect as that of the ordinary figure from a single magnet. If such a compound figure is projected on paper, and this be folded on either the longitudinal or transverse axis of the *whole* figure, the opposing halves will correspond. The right and left curves belonging to the *same* magnet will not now be symmetrical with each other, but all the curves formed by one magnet will be symmetrical with those formed by the other.

In abnormal development, if two nervous axes are formed on opposite sides of one and the same yelk, each axis, or rather the symmetrical force, the axis of action of which corresponds with the nervous axis, will distribute the organic matter under its influence without coming in collision with that of the other, except near the umbilicus, so that two nearly perfect embryos will be formed, as in the case of the Siamese twins.

If the two axes are formed side by side, and so near to each other that the particles under their respective influence come in contact, then at the line of contact a series of intermediate organs or limbs, will be formed in connection with the two axes, as is commonly seen in those double monsters which present what is called lateral doubling. Here, too, as in the case of the double magnetic curves, the right and left parts connected with one and the same nervous axis will no longer be symmetrical with each other, but those connected with the right half of one axis will be symmetrical with those connected with the left half of the other, or in other words, the two bodies thus united will be symmetrical with each other, but will not be bilaterally symmetrical in themselves.

If the magnets are now inclined towards each other (Fig. 6, C), so as to touch at one end, forming a V, then we shall have the particles arranged so as to produce a figure double at one end, but single at the other. The ends of the magnets which are separated will arrange their particles so as to form a double series of curves, which are completely independent of each other; but as the magnets come nearer together the intervening curves are gradually modified or suppressed, and at last a single symmetrical terminal figure is formed. One half of this terminal portion is however formed under the influence of the right, and the other of the left magnet.

Likewise in certain double embryos if the axes are inclined so as to form a V-shaped figure, the two separated ends will have a head more or less complete, but as the two axes converge below, the organs become more or less fused and suppressed, and at length the hindmost are reduced to the normal type, all intermediate ones having become obsolete. The body will be provided with two legs, but one will be connected with, and under the control of the right axis, and the other under that of the left. Precisely such a case is found in the well known instance of Ritta-Christina. The completeness of the intermediate organs in a given instance, as in the case of the intermediate magnetic curves, will depend upon the degree of divergence or separation of the axes.

In comparing the results of the symmetrically acting force in animals with a polar force like that of magnetism, it is not intended to imply that the two forces are the same, but only that they have like modes of acting, and that when left to themselves undisturbed by other influences, each tends to produce symmetrical figures. The type or general idea of any of the double monsters may be imitated by the combined action of two magnets.

In the preceding paragraphs we have spoken of the symmetrical distribution of the particles of matter around the nervous axis as if the distributing force emanated from this axis. It is not to be inferred that such is actually the case, since the force is already in action before the nervous axis itself is formed, and may be said to be manifested in the first stage of the segmentation of the yelk; for when the whole yelk, or as in some cases, a limited portion of it, divides into two distinct segments, such division shows that a symmetrically acting force is already present; in fact, we have now right and left parts. Such force is again manifest when a new division takes place at right angles to the first, separating each right and left portion into two others, which may be compared to the fore and hind divisions of the body; even the nervous axis itself is symmetrically developed under the influence of this same force. The nervous axis, however, when formed, coincides with the axis of the symmetrically-distributing force.

The use of the term polarity in connection with organic structures has long been familiar to physiologists, but apparently with very varied signification. Oken in his celebrated "Programm" uses the following words with regard to the skeleton: "This skeleton repeats itself at the two poles; each pole repeats itself in the other, and they are head and pelvis." It does not appear from this, nor from any other statement of his that we have seen, precisely what he understood by the word pole. At the present day few will agree with him that the head and pelvis repeat each other. Still, although these parts are not comparable, the idea underlying his statement, viz., that the two ends of the body do repeat each other, may be, and we believe is, correct.

In order, however, that they may be repeated as if under the influence of a polar force, or of a force acting in a manner analogous to one, there should be a more or less symmetrical repetition of homologous parts.

The term pole is often used in the description of eggs and of cells; in the former to distinguish the portion of the egg where the oily matters are collected from the opposite side where there is only albumen, and in the latter, simply to designate the two ends without intending thereby to imply any difference of quality or force. In the nervous system cells are described as "unipolar," "bipolar," or "multipolar," which only means that they are prolonged into one or more points, "caudate appendages," or processes which connect them with the nerve tubes.

Owen appears to make use of the term polarity in the sense in which it is made to stand as representing the quality of a force acting in animal bodies, and producing symmetrical results. After comparing the dorsal and abdominal portions of the vertebral arches, and showing that they repeat each other, he says "symmetry and polarity, or serial *homology* of the parts of the same vertebral segment is usually still more strictly observed in the transverse direction, and is so obvious as to have immediately led to the detection of the homologous parts, which are accordingly distinguished as *right* and *left*."* He does not, however, recognize the symmetry of fore and hind parts.

Prof. Dana uses the term in the same manner. "An animal is embodied or concentrated force, which force manifests polarity in the results of its action in development, that is in the oppositeness of the anterior and posterior extremities of the structures evolved, and also in the dorso-ventral relation of these structures." †

Polarity, according to Mr. Faraday, may be considered as "an axi of power, having contrary forces exactly equal in opposite directions." This power will produce perfectly symmetrical figures, however, only when wholly free from the influence of a superior force. In the presence of such it may be interfered with, or have the results of its action so changed as to give rise to forms whose symmetry is more or less distorted, as is so frequently the case in crystals; these, we are told, being exactly symmetrical only in idea.

In the vertebrate animal, the plan of construction appears to be in accordance with the idea of general symmetry, which in the early stages of development is maintained at the two ends as well as the two sides of the axis, but subsequently is more or less interfered with to adapt the animal to its special conditions of life. This force, producing symmetry, acts in a manner analogous to a polar force. To designate the disturbing, or rather adapting force, by which the force tending to act in a symmetrical manner is interfered with, we must still retain the term vital or life-force, although this may in the end prove only a physical force acting under special conditions.

* Archetype and Homologies of the Vertebrate Skeleton. London, 1848. p. 166.
† Am. Journal of Science. Vol. XXVII, p. 157, 1864. See also Vol. LXI, p. 154, 1866. See also Wilder *op. cit.* p. 9.

III.

HOMOLOGY.

Owen defines a homologue to be "the same organ in different animals under every variety of form and function." * When parts are repeated in the same animal, not from right to left, but from before backwards, either on the middle line of the body, as the vertebræ or sternal pieces, or on the same side, as the ribs, such parts are homologous, but not in the same sense as when they are repeated in different animals; in the first case he calls them *homotypes* and in the second *homologues*.

As a general rule, homologous parts resemble each other in form and uses, and by these are easily recognized. But there are instances in which form and use are insufficient for the determination of the homology of a given part. The "prickly pear" (*Opuntia*) which has the appearance of being all leaves, is in reality all stem, and this has not only the form but the function of leaves. Two homologous bones from different animals may be so unlike that an anatomist might be excused for taking them for different parts; and on the other hand, two different parts may be so nearly alike that were one not on his guard they would be considered homologous. Even Cuvier, in his earlier days, mistook the coracoid of a turtle for the scapula, on account of its shape.† Among teeth molars and premolars interchange forms. Even here Cuvier was misled by this circumstance and described the large back teeth of the feline carnivora as true molar. Owen has shown that these supposed molars were the successors of deciduous teeth and therefore premolars. Human anatomists have gen-

* Archetype and Homologies of Vertebrate Skeletons. p. 7.

† Leçons sur l'Anat. Comp. 1r edit. T. I, p. 252.

erally misunderstood the homology of the articulating surfaces of the atlas and the upper part of the axis; and from their use have described them as if they were "articulating processes," while in man and most mammals, these processes do not exist in the vertebræ mentioned. True, articulating processes are found in the Cetacea, and some birds and reptiles, co-existing with the articulating surfaces above mentioned, and occupying the true position of articulating processes which the "surfaces" do not. We might extend the list of such instances, but it is unnecessary.

As the form and use of a given part under certain circumstances may leave us in doubt as to its homology, we need some other guide. This may be found, as Geoffroy St. Hilaire long since pointed out, in the relative position. The tusks of the elephant and mastodon are only known to be incisors by their position in the intermaxillary bones, and the radius and ulna of *Icthyosaurus* and *Plesiosaurus* are identified by their relation to the humerus and carpus, and not by their forms or uses. Had these been the only parts of the above mentioned animals which had been discovered, naturalists would have hardly suspected them to be ulna and radius. So in the determination of homotypes we are not to expect precise similarity of forms, as these are liable to differences analogous to those of homologues, as is especially the case in the carpus and tarsus.

If we are justified in accepting the conclusions set forth in this paper, then by an application of them the homotypes in the two limbs may be readily determined, for *those parts will be homotypes which have the same relative position, and are symmetrically placed with regard to each other.*

IV.

SCAPULAR AND PELVIC ARCHES.

The *general* homology of these has attracted less attention than the determination of the corresponding parts of the two with each other. Oken, Spix and Carus, considered them as ribs, and in this respect have been followed by Owen, who has presented his views with much more precision than his predecessors. Admitting them to be specially modified ribs, to what vertebræ do they belong? The pelvic arch has been assigned with much unanimity to the sacral vertebræ in the immediate neighborhood of which it always is; but the scapular arch offers a much more difficult problem, since in the three higher classes of vertebrates, the vertebræ near which it is found are all provided with ribs, and in many animals all the cervical vertebræ are rib-bearing, independently of the arch in question. Spix, who has been followed by Owen, regards this as being made up of the ribs of the occipital vertebra, and Owen urges in confirmation of this view, that in fishes the scapular arch is an appendage to the occiput.

The objections to this view, though we are not sure but that they are more apparent than real, are, first, that in only one of the four classes of vertebrates, viz., fishes, would the arch be found, so to speak, in its normal place; second, each such rib in the larger portion of the vertebrate series higher than fishes, would be provided with two "cartilages" or "hæmapophyses," viz., the coracoid and clavicle. This same difficulty presents itself in connection with the pelvic ribs, since these would also have two cartilages, the ischium and pubes. Third, the objection urged by Agassiz appears to have much weight. He objects that this arch and the limbs supported by it, derive their nerves in all classes from the spinal, not from the cranial series, while the reverse should be the case if they were truly cranial ribs. A branch of the vagus, or of the lateral nerve formed by the union of the vagus and trigeminus is, it is true, distributed to the scapular arch in addition to its spinal pairs. This, however, would not make the scapular arch an appendage to the head, any more than it does the trunk or even the tail to which this same nerve sends branches in fishes and Urodel batrachian reptiles.

In view of these objections one cannot but feel that additional evidence is needed, especially that to be derived from embryology, before definite conclusions can be reached. Extensive observations on the development of the scapular and pelvic arches may be expected to throw much light upon this problem. We have studied the development of the pelvis in frogs, and find that this does not take place after the manner of ribs. In the tadpole of the Bull-frog (*Rana pipiens*, L.) the first trace of the pelvis consists of a plate of cartilage situated on the median line in front, and which corresponds in position with the future ischium and pubes. This cartilage subsequently becomes extended on either side, and at last forms a connection with the transverse processes of the sacral vertebræ. Its first stage, it will be seen, corresponds very nearly with the permanent condition of the pelvis in most fishes. In Cetaceans, the pelvis consists of ischia, or ischia and the bones of the pubes alone; the ilia do not exist. This would seem to be an indication that in mammals the development of this part followed the same course as in frogs and fishes; that is, it begins its development on the median line in front.

In most vertebrates the *special* homology of these arches is more obvious, though somewhat masked, since the physiological requirements of the two differ so widely; strength and solidity being essential conditions in the pelvis and mobility in the shoulder. If, however, they are compared in those animals whose habits are more strictly aquatic, and whose locomotion is effected more nearly equally by the fore and hind limbs, as, for example, in the *Ornithorhynchus* among mammals, and the marine saurians among reptiles, the scapular arch, in consequence of the greater development of the coracoids, and of the union of these as well as of clavicles with the sternum, or with each other, will be found to have almost the firmness of a pelvis. On the other hand the attachment of the pelvis to the vertebral column may become comparatively slight. In the chameleon the pelvis is nearly as moveable as the scapular arch, and in the *Icthyosaurus* it appears to have been entirely free, and to have embraced the ribs behind as the scapular arch does in front. (See Cuvier's Oss. Foss., Pl. 260.) Although the two arches never repeat each other exactly in one and the same animal, they do sufficiently to show that they are constructed upon one and the same plan. The scapular arch of one animal, however, often very nearly resembles the pelvic arch of another, as, for example, the first taken from a frog, Fig. 7, when compared with the second taken from a chameleon, Fig. 8, but in the *Enaliosaurians* the resemblance of these parts in the same individuals is still more striking.

Fig. 7.

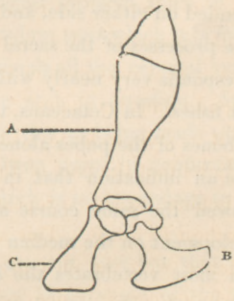

Fig. 8.

Fig. 7. Scapular arch of a frog. A, scapula; B, clavicle; C, coracoid.
Fig. 8. Pelvis of a chameleon. A, ilium; B, ischium; C, pubes.

As each arch consists of three pieces, the first step is to determine which are the corresponding ones. Vicq d'Azyr comparing bones from opposite sides, Gerdy, Bourgery, Blandin, Flourens, Cruveilhier, and Owen* comparing those of the same side, agree in considering the ilium as the serial homologue or homotype of the scapula, the pubes of the clavicle and the ischium of the coracoid.

Charles Martins compares the bones of the two arches in the following manner: "The reader may place the shoulder of one side reversed over the ilium of the opposite; or what amounts to the same thing, he may place on his left an ilium of the right side, and on his right the reversed scapula of the same side. The outer surfaces of the two bones will then be opposite to him, and may be studied in this position, the spectator being between the two."† Any one who will follow his directions with the bones in his hands, will find that the two ways above mentioned do not amount to the same thing. In the first method, the glenoid and cotyloid cavities will face in the same direction, and in the second in opposite directions. In the last these positions will be symmetrical, but not in the first. After comparing the axillary border of the scapula with the inguinal border of the ilium, the coracoid with the ischium, and the clavicle with the pubes, he concludes as follows: "En resumé l'homologie de l'epaule et du bassin me parait complète. Un ceinture massive, soudée a la colonne vertebrale, se'st renversée et transformée en un appareil leger et mobile suspendu dans les chairs."‡

If it be true, as he says, that the shoulder is the pelvis reversed, then it follows that the part of the latter which is farthest backwards, viz. the ischium, would be repeated in the shoulder by the clavicle, which is farthest forwards. This arrangement of the parts would be in accordance with the idea of symmetry, and with which M. Martins' description certainly does not agree.

* "I commence with ilium as being the homotype or correlative of the scapula in the fore limb. The ischium, which is the homotype of the coracoid, is confluent with the ilium, as the coracoid is with the scapula; the pubes, which is the homotype of the clavicle, is confluent with both ilium and ischium." Philos. Trans., 1859, p. 809.

† Nouvelle Comparaison des Membres Pelviens et Thoracique chez l'homme et chez les Mammifères. Par Charles Martins. Extrait des Mém. de l'Acad. des Sciences de Montpeilier. T. III. p. 515.

‡ Ibid. p. 518.

Mr. Humphrey's determination of the parts, though based upon use and not upon the idea of symmetry, is strictly in accordance with it; the hinder edge of the scapula, according to him, being repeated in the fore edge of the ilium, the coracoid in the pubes, and the clavicle in the ischium.

Foltz adopts a method of viewing these parts quite different to that of either of the authorities alluded to above, but not unlike that made use of by Cruveilhier, and also by Martins, as will be seen further on, who compare a portion of one and the same bone in one limb, to two different bones in the other. The body of the pubes, according to Foltz, corresponds with the coracoid process of the scapula, while the descending branch corresponds with the clavicle.* He seems to overlook the fact that the body and descending branch are all of one piece, are ossified from a single centre, and never show themselves in any other way. Under these circumstances they cannot be considered other than as parts of one and the same bone, unless all ideas of the individuality of bones are abandoned. Following the principles of symmetrical development already laid down, the homologous parts will stand as follows:—

Scapula, Fig. 6, A.	. . . . . .	Ilium, Fig. 7, A.
Clavicle, " B.	. . . . . .	Ischium, " B.
Coracoid, " C.	. . . . . .	Pubes, " C.

* Homologie des Membres Pelviens et Thoracique. Par le Docteur Foltz. Journal de Physiologie. Paris, 1863. T. VI, p. 53.

V.

LIMBS.

The *general* homology of limbs, as has also been the case with the scapular and pelvic arches, has attracted much less attention than the special. Oken regarded them as "liberated ribs." In this view he has had but few followers, though Maclise in the article "Skeleton" in the Cyclopædia of Anatomy and Physiology, advocates somewhat at length a similar interpretation of these parts. Limbs are more commonly spoken of as "appendages" to their respective arches, and as "diverging appendages" by Owen, who at the same time considers them as serially homologous with the "oblique processes" on the ribs of birds, crocodiles and most fishes. With regard to the oblique processes just referred to, he suggests that while such rudimentary limbs in these animals never come to be more than spines attached to the edges of the ribs in the actual vertebrates, they might possibly under other circumstances, or in other worlds, rise to the dignity of perfect limbs. The possibilities of the vertebrate archetype may not as yet have been exhausted.* It does not appear, however, that the processes in question ever take on in the actual vertebrates an approach to a form which might be considered a limb, and it might be urged as an objection to Prof. Owen's view, that in fishes they seem to be an integral part of the muscular system, and that in neither fishes, reptiles or birds, do they occupy a position homologous with that of limbs, viz., at the junction of the rib with its cartilage, or of the pleurapophysis with its hæmapophysis.

* On the Archetype and Homologies of the Vertebrate Skeleton. London, 1848. p. 102.

It is unfortunate that in the attempts to determine the *general* homology of limbs so little attention has been given to their development, which is indispensable to the complete solution of the question. On studying their transitional phases in the embryo, we are, first of all, struck with the fact that in their primary conditions limbs have so strong a resemblance to the median fins of fishes and the flukes of cetaceans. The fins on the median line in fishes all agree in this, that they appear as an outgrowth from the integuments, in the form of a ridge extending continuously along the back, around and under the tail. This ridge is a mass of embryonic cells, all alike, but which subsequently become differentiated into fin-rays and other structures. The fin-rays are secondary structures, and cannot therefore be said, as has sometimes been asserted, to push out from beneath and carry the integuments with them. The adipose fin of the Salmonidæ permanently retains an early embryonic condition, and no fin-rays are formed at any period. The fore and hind limbs, in like manner, are outgrowths of the tegumentary cells, and for a time the cells undergo no differentiation into bones or other tissues. These are, at length, developed *in* the limbs, and subsequently grow *pari passu* with them. The bones do not, therefore, force the integuments out by their protrusion, but the integuments themselves have already grown out, and the limb is formed before the bones are developed. Limbs in their primary condition do not appear to be dependencies of the scapular and pelvic arches, any more than the median fins of fishes, or the flukes of cetaceans, which last have sometimes been compared to limbs, are dependencies of the vertebral column, or teeth are dependencies of the jaws, with which, notwithstanding their totally different origin, they become so intimately united at last In view of the above considerations, and in view of the fact, also, that in fishes the ventral fins never pass beyond the condition of appendages to the integuments, we believe there is ground for the hypothesis that limbs belong to the category of tegumentary organs, and that their connection with the vertebral column through the scapular and pelvic arches is only secondary, as is that of the teeth with the jaws.

All agree that these two are homotypes, the only question is whether they are to be compared as parallel or as symmetrical bones; this an-

HUMERUS AND FEMUR.

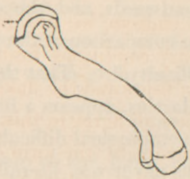

Fig. 9.

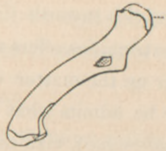

Fig. 10.

Fig. 9. Femur of an alligator. Fig. 10. Humerus of an alligator.

swered, the parts which correspond are easily determined. As has already been stated, the majority of anatomists describe them as parallel repetitions. One of the difficulties which is encountered in this mode, is the fact that the knees and elbows in all animals are bent so as to form angles pointing in opposite directions. To meet this, Vicq d'Azyr, in comparing the limbs, turned the elbow forwards, but in doing so the head of the humerus was found to face in one direction, and that of the femur in the opposite one. He then compared the limbs of opposite sides; in this case, not only was the limb placed in an unnatural position, but although the heads of the bones faced in the same direction, the thumb was on one side of the hand, and the great toe on the other side of the foot. He simply exchanged asymmetry of the heads of the humerus and femur for asymmetry of hands and feet, and so the difficulty was not obviated. Maclise, in his article "Skeleton," in the Cyclopædia of Anatomy and Physiology, and Martins in his Memoir, meet this difficulty by supposing the humerus twisted through 180°. "In primitive construction both members are identical, but this secondary modification, viz., the torsion of the humerus, is that circumstance which distinguishes them one from the other. While in idea I untwist the humerus, by bringing its back to the front, I at the same time unravel the gordian knot of that problem which has so long existed as a mystery for the homologist."* According to

* Cyclop. Anat. and Physiol. Article Skeleton, p. 666.

Martins, "the femur is straight and has no torsion. The humerus being a twisted femur, if we wish to compare the two, it is first of all necessary to untwist it (*detordre l'humerus*) the effect of which is to place the epitrochlea (inner condyle) outwards, and the epicondyle (outer condyle) inwards. This done, the comparison of the pelvic and thoracic extremities offers no further difficulty." * That this does not quite clear up the matter even to M. Martins, appears a little further on, where he admits what he calls a "metaphysical difficulty" (*difficulté metaphysique*), viz., that the humerus never was literally twisted; "it is a virtual torsion, which was never mechanically effected"; "but this virtual torsion has produced all the consequences of a real one." † In another place he informs us that "L'humerus n'est point un os d'abord droit, qui se torde ensuite. Il y a mieux l'humerus est tordu avant d'exister."! In order to put the bone in the untwisted condition he supposes it plastic, as when the lime has been removed by acid, or, to make a mechanical illustration practicable, he cuts the bone in two, puts a peg in the medullary cavity and rotates the lower half 180°. Any one, however, who will take an arm from an articulated skeleton, place the palm on the table, and then following his directions in imagination, or by the mechanical process, and rotates the humerus 180° from within outwards, (the direction necessary to untwist it) he wil find a real, and not a metaphysical difficulty. In the ordinary prone position of the hand, the radius is already partly wound around the ulna, and will completely encircle it when the humerus is "untwisted," thus producing a much greater distortion than the one attempted to be obviated. Mr. Humphrey has already pointed out other difficulties in the way of this view of Martins, and we will only add that the lines supposed to indicate torsion simply grow out of the mode of attachment of the muscles to the bone, and in no way indicate a twisting of it. The bone primarily was smooth, and the ridges were built up on it as the muscles themselves were developed, without the ends of the bones having in any way changed their relative position.

If the two bones are supposed to be symmetrical repetitions, no difficulties arise. They will have the position which is natural to them in

* Memoir, p. 482. † Idem, p. 490.

the animal series; the axis of the humerus will incline backwards, and that of the femur forwards. The articulating convex surfaces of the lower end of the humerus will face forwards, while those of the femur will face backwards. The back of the humerus, which is on the side of the extensor muscles of the fore arm, will be opposed to that part of the thigh which is on the side of the extensor muscles of the leg.

FORE-ARM AND LEG.

No portions of the limbs have given rise to more widely differing opinions than these, and it is in connection with them that nearly all the discussion of the homologies of the parts of the limbs have been made. Vicq d'Azyr, comparing opposite sides, considers the tibia as the homotype of the ulna, the fibula of the radius, and the patella of the olecranon. Meckel and others homologize the same parts, but compare limbs of the same side. Gerdy, on the other hand, compares the radius and tibia, the ulna and fibula, but asserts at the same time that the olecranon and patella are homotypes, in which case it is obvious that the patella should be attached to the fibula. He gets over this difficulty by assuming that its union with the tibia is an "anomaly."

Fig. 11.

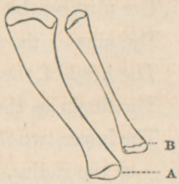

Fig. 12.

Fig. 11. Bones of the leg of an alligator. A, tibia; B, fibula.
Fig. 12. Bones of the fore arm of an alligator. A, ulna; B, radius.

Bourgery, and more recently Cruveilhier, seeking for a solution of the question by studying only the resemblances in the form and uses of parts, adopted the singular "*hypothése de croisement,*" which Cruveilhier states as follows :—

"1st. No bone of the leg singly represents one of the bones of the fore arms.

"2d. In each of the bones of the leg we find characters, some of which belong to the ulna, and some to the radius.

"3d. We admit that the upper end of the tibia is represented by the upper end of the ulna, and the lower half of the tibia by the lower half of the radius; while the fibula is represented by the upper half of the radius, and the lower half of the ulna."*

Martins homologizes the parts in question as follows: "The femoral end of the tibia in Monadelph mammals is formed by the humeral heads of the radius and ulna." "The upper third of the fibula is represented by the anterior or coronoidal part of the ulna." "In all mammals the two lower thirds of the tibia represent the corresponding part of the radius, and the two lower-thirds of the fibula that of the ulna." †

The view of Prof. Owen is as follows: "The skeleton of the Phalangista or Phascolomys plainly demonstrates that the tibia is the homotype of the radius, and that the fibula is the homotype of the ulna."‡ The same conclusions are adopted by Humphrey.

Thus putting together the views of the anatomists above cited, we have:

1st. The ulna = the tibia of the opposite side.

2d. The ulna = the tibia of the same side.

3d. The ulna the fibula.

4th. The head of the tibia = the heads of the radius and ulna.
The fibula = the coronoidal and lower two-thirds of the ulna.
The lower two-thirds of the tibia = the corresponding part of the radius.

5th. The tibia = the upper half of the ulna and the lower half of the radius.
The fibula = the upper half of the radius and the lower half of the ulna.

There seems to be no sufficient reason for entering into a discussion of the views of those who consider a bone of one limb homologous with

*Traite d'Anatomie Descriptive. Paris, 1843. T. I., p. 342.
† Op. cit., p. 534.
‡ Archetype, p. 167.

parts of two different bones in another. We do not know of any unquestioned analogy in the whole range of comparative anatomy which can be brought forward in support of it.

Prof. Owen sustains his opinion, already cited, by the following statement, and in this he is followed by Humphrey and others: "In the Wombat the part of the fibula representing the olecranon is a detached sesamoid, as the olecranon itself is in the penguin and the bat. In the *Ornithorhynchus* the fibula (Fig. 14, B) assumes the proportions and developes the process from its proximal end, the want of which in man and most mammals, deceived Vicq d'Azyr as it misled, more recently, M. Cruveilhier."

We are somewhat at a loss to know what is to be understood by the expression "detached sesamoid," inasmuch as a sesamoid, as commonly understood by anatomists, is always detached. The only interpretation which suggests itself to us is, that it is used synonomously with an epiphysis, and that the bone connected with the upper end of the fibula in the Wombat is the detached epiphysis of that bone, and this he considers homologous with the large process on the upper end of the fibula of the Monotremes. No evidence is brought forward to prove that the sesamoid referred to is in any way different from the bones found in tendons in other parts of the body, as *e.g.*, in the heads of the gastrocnemius of the opossums, and also of many rodents, and in the flexor tendons of the fingers and toes of many mammals, in the peroneus longus in man, and as an anomaly in the tendon of the human biceps cruris near its insertion into the fibula. Furthermore the part in question can hardly be considered as a detached epiphysis, since in those animals where a sesamoid is developed in the tendon over the head of the fibula, the normal epiphysis exists in the bone itself.

In the Penguin it does not appear that the part corresponding to the olecranon is of any less size than in other birds, although the sesamoid bones, which Prof. Owen supposes replace this process, are present. In the arm of a large Pteropus we have found the patella-like bone attached to the ulna by a ligament, as the patella is attached to the tibia. The ulna, however, has a projection at its upper end of about the same size as the olecranon in birds. But before this patella-like bone can be claimed to be a detached epiphysis, it must be ascertained whether the ulna has, or has not, an epiphysis in the immature bone. In many of the anatomical descriptions of the ulna, the olecranon process and the epiphysis have been described as if they were the same thing, which most certainly they are not. In mammals the olecranon is often much longer than in man, the epiphysis forming but a very small part of it, and in man is only a very thin scale covering its end. Properly speaking, the olecranon is a continuation of the shaft of the ulna. The cartilage of ossification interposed between the shaft and the epiphysis is remarkably thick, and has given rise to the belief that this was itself the epiphysis. The last only forms at a late period.

As to the argument drawn from the great development of the process on the top of the fibula in the *Ornithorhynchus*, it seems to us that this is an instance in which we are liable to be misled by form, and that the resemblance between the process in question and the olecranon is no proof of homology. It should be remembered that processes, and even bones, in different animals, are liable to every degree of variation according to the physiological requirements in individual cases. Compare the extraordinary processes of the humerus of the Mole, the Mylodon, or of the Ant-eaters, with the diminutive ones of the same bone in the Three-toed Sloth, the Cetaceans, or of the marine Saurian reptiles. The olecranon itself is a very variable process; it does not exist in Cetaceans, is hardly apparent in birds and most reptiles, but in mammals may become, as in the great Armadillo, almost half as long as the whole ulna. This development is in relation to the extensor muscles of the fore arm. The remarkable development of the fibula in the *Ornithorhynchus* may justly be compared with the great development of the olecranon in the Armadillo or the Mole, as a means of increasing the power of the particular muscles attached to it, but this resemblance is physiological only, and has no bearing whatever on its homology. The head of the fibula in the *Ornithorhynchus* is, however, not developed in relation to the extensor muscles of the leg, but of some of the unusually large muscles of the foot, which take their origin from it; viz., the large head of the gastrocnemius, the soleus, the two peroneal muscles, the common flexor of the toes, the long extensor of the great toe, the common extensors of the toes and posterior tibial muscle, but has not that relation to the muscles of the leg which the olecranon has to those of the fore arm. The mere form of the process of the fibula is no proof that the fibula and ulna are homotypes, although in many respects it resembles an olecranon. (Fig. 14, B.) The prolonged upper end of the tibia in

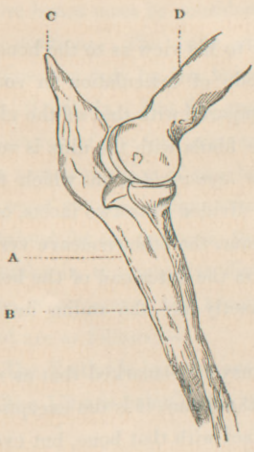

Fig. 13.

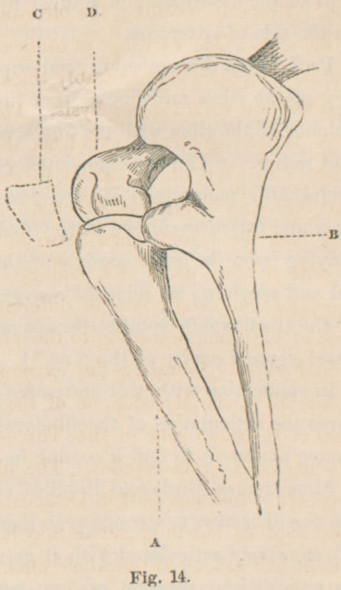

Fig. 14.

Fig. 13. From a grebe. A, tibia; B. fibula; C, upper end of tibia prolonged so as to form a process analogous to the olecranon; D, femur.

Fig. 14. From an Ornithorhynchus. A, tibia; B, fibula, with a process analogous to an olecranon; C, patella; D, femur.

the Grebes (Fig. 13, C), Loons, Penguins, Gannets, etc., can be brought forward with far more force to show that the tibia is the homotype of the ulna, for, in addition to its resemblance to an olecranon in form, "it affords extensive attachments by way of insertion to the extensors of the tibia,"* which the fibula does not.

If the fibula is the homotype of the ulna, then it follows that the flexor muscles of the leg, which are inserted into the upper end of it, are the homotypes of the extensor muscles of the fore arm, which are inserted into the olecranon; with this comes another difficulty growing out of the fact that the internal angle formed by the leg and thigh, and which is on the side of flexion, corresponds with, or is the homotype of, the external angle formed by the arms and fore arm, which is on the side of extension.

Prof. Owen derives additional support to his view as to the homology of the ulna and fibula, from the mode of articulation in some animals of the tibia with the fibula, as compared with that of the ulna and radius. "The correspondence of the fibula with the ulna is very remarkably maintained in the *Petaurus taguanoides*, in which the proximal articular surface of the fibula is divided into two facets, one playing upon the outer condyle of the femur, the other concave vertical and receiving an adapted convexity on the outer end of the head of the tibia, which rotates thereupon exactly like the radius in the lesser sigmoid cavity of the ulna."†

In connection with this statement it may be remarked that as regards the articulation of the fibula with the femur, it is the exception among mammals to find it coming in contact with that bone, but even in Monotremes, Birds and Reptiles, the extent of its articulation with the femur is always secondary to that of the tibia, and never becomes as extensively articulated with it as the ulna does with the humerus. As regards the rotation of one bone on the other, we have found, after a careful examination of the parts in an *Ornithorhynchus* which, through the kindness of Prof. Agassiz, we have recently had an opportunity to dissect, that it is the fibula which rotates, while the tibia is fixed, and in this respect the latter more nearly resembles the ulna. The fibula in the *Petaurista* resembles the ulna in having a sigmoid notch. This cannot be considered as a decisive character,

* Owen Cyclop. Anat. and Physiol. Vol. I, p. 287.

† Cyclop. Anat. and Physical. Art. Marsupialia. p. 285.

when it is remembered that the articulating surface of the lower jaw is convex in mammals, but concave in other vertebrates; the lower jaw does not in consequence change its homology in these last.

Admitting all the arguments which have been adduced to prove the fibula to be the homotype of the ulna, we have still another and greater difficulty than any thus far mentioned, growing out of its relative position. For of all the means of determining homologies, this is the most trustworthy. If the two bones of the fore arm and of the leg are placed in planes at right angles to the axis of the body, those bones must be considered homotypes, which occupy corresponding positions. The bone on the outside of the fore arm, viz., the radius, can only be the homotype of that on the outside of the leg, viz., the fibula. But few anatomists have made any allowance for the pronation of the fore arm, and most of them overlook the fact that the proper position of the bones of this segment for comparison with those of the leg, is supination. If the position of pronation is to be retained for the fore arm, the leg should go through a corresponding rotation in the opposite direction. Viewed in connection with the idea of symmetry, the homotypes are determined without difficulty, and are as follows:—

The Radius is homologous with the Fibula.

The Ulna is homologous with the Tibia.

THE PATELLA.

By Vicq d'Azyr, who has been followed by Meckel, Blainville, Martins, Humphrey and others, this bone has been regarded as the homotype of the olecranon, differing from it, however, in being attached to bone by a ligament. Soemmering, who has been followed by Bertin Bichat, Flourens, Owen and Cruveilhier, maintains that the patella belongs to the class of sesamoid bones, and therefore, properly speaking, does not belong to the skeleton at all.

We believe the latter view to be the correct one, for the same reason that the separate bone in the leg of the Wombat, already referred to, is a true sesamoid, and not a detached epiphysis of the fibula. Mr.

Humphrey, like the others, who regard the radius as the homotype of the tibia, and the olecranon as the homotype of the patella, is obliged to meet the difficulty which arises from the connection of the patella with the tibia, when, if it were the homotype of the olecranon, it should be connected with the fibula. Mr. Humphrey admits the possibility of a part of a bone, an epiphysis, being detached, and of becoming connected with another, and sustains his statement by the analogy of the ribs, which, he says, may be transferred from the upper to the lower transverse process, or *vice versa.** This does not seem to be an analogous case; for, in point of fact, the typical rib is attached to both, as, for example, in the foremost ribs of the alligator, and either the upper or lower attachment may become obsolete, without really shifting the relation of the ribs to the vertebra. There is not a single unequivocal instance in the whole range of comparative anatomy, of an epiphysis undergoing such a displacement as is claimed for the patella.

There are some facts, however, which seem to support the view under discussion. The researches of Robin have set at rest the question as to the nature of the odontoid process of the axis, and have proved that it is the body of the atlas coössified with that of the axis. This, however, would not be similar to the transfer of the epiphysis of one bone to the shaft of another *parallel* to it. The bodies of the vertebræ are in a *linear series*, and may be united without changing their relative position, as happens, for example, with the occiput and sphenoid, or with the epiphyses of the sacral vertebræ which may become united with each other before either of them becomes united with their respective bodies. The epiphyses of the ulna and radius in some ruminants, as the ox, may become coössified with each other before they are coössified with their shafts. But in all such cases the relative position of parts is strictly preserved, and there is consequently no transfer of an epiphysis from one bone to another, as is required by the hypothesis which is referred to above. We therefore conclude that the view of Soemmering and others, which regards the patella as a sesamoid, is the more reasonable.

* Memoir, p. 20.

HANDS AND FEET.

Admitting the existence of fore and hind symmetry, no difficulty is met with in comparing either the pelvic or scapular arches, the humerus and femur, or the bones of the fore arm and leg; provided the bones of the fore arm are rotated outwards enough to counteract the rotation inwards which took place in fœtal life. If we would compare hands and feet as symmetrical parts, the first step should be to put them in symmetrical positions. For this purpose suspend a human skeleton with the vertebral column horizontal, allow the legs and arms to hang vertically from it, and rotate the fore arm completely outward. The palms will now face forwards, and the soles backwards, the bones of the fore arm and leg will be in parallel planes, and these at right angles to the axis of the body. If now the foot is raised forwards, so that the sole shall be horizontal and at right angles with the leg, the hands should be raised backwards to the same position with regard to the fore arm; the fingers will now point backwards, and the toes forwards, and thus the general symmetry of all the segments of the limbs is secured. It is in this that the limbs of man and animals would have ended in the process of development, had not the tendency to symmetry been interfered with, for the purpose of adapting the skeleton to the different kinds of locomotion.

While the homology of tarsal and carpal bones, as groups, is obvious, that of individual bones is quite difficult to determine. The fact that in mammals the bones of these two groups are not conformably placed in the two limbs, and in addition to this the constant variations in the vertebrate series of the form and number of the pieces, sometimes reduced to two, as in the tarsus of a frog, and sometimes increased to eleven, as in the carpus of the armadillo, renders the probability of a satisfactory result being reached in the direction of special homology well-nigh hopeless. The homologies, in man and mammals, of the individual bones in the tarsus and carpus hitherto determined, rest largely on their physiological correspondence. The pisiform and the calcaneum, for example, are regarded as homotypes, because each, in certain animals, as the *Carnivora*, has a large tuberosity, and each is a lever for increasing the muscular power applied to the motions of the foot. But in these animals they are highly specialized parts, and are the farthest removed from the typical conditions which are most generally the best represented in the lowest animals of a given group. If anatomists had begun their studies with reptiles, such as Plesiosaurus and Icthyosaurus, or with lizards and turtles, the homologies now generally recognized would not have been so persistently brought forward.

The mammalian foot, which connects with the leg solely by the astragalus, gives one quite a different idea of the tarsus and its relations, from that derived from the same segment in reptiles, where, for the most part, the astragalus articulates chiefly with the tibia, the os calcis with the fibula, and a third bone is interposed between them. Furthermore, the os calcis, which is so highly specialized in mammals as to be distinguished at sight, has in reptiles the appearance of the other tarsal pieces, and resembles a cuneiform bone. Even in mammals the pisiform, as in man, is so reduced that it becomes relatively insignificant, which circumstance, and its relation to the tendon of the ulnar flexor, led Cruveilhier to class it among the sesamoid bones.

In the ideal vertebrate skeleton the tarsal and carpal bones having no special development, would be represented by two rows of polygonal or circular discs, all alike, as is actually the case in the marine saurians. Reducing all the bones in question to one and the same form, as in the lowest groups, form would cease to be a guide to the determination of the homology of any particular bone of the tarsal or carpal series. Those parts will be homologous which occupy similar and symmetrical positions; the inner bone of the wrist articulating with the ulna, will be homologous, or the homotype of the inner bone of the tarsus articulating with the tibia; or in other words, homologous bones are determined by the principle of symmetry and relative position, and not by their teleological relations.

Making use of this principle, we shall have the following bones homologous in the two limbs; beginning on the inside:—

HAND.	FOOT.
Pisiform	
Pyramidale	Scaphoid.
Lunare	Os calcis.
Scaphoid	Astragalus.
Unciform	1st cuneiform.
Magnum	2d cuneiform.
Trapezoid	3d cuneiform.
Trapezium.	Cuboid.

When applied to the human hand and foot with their high degree of specialization, this mode of comparison seems at first sight inadmissible, but bearing in mind the fact that the type is much more distinctly indicated in the lower, than the higher members of a series, and beginning our comparisons in the lowest, the difficulties growing out of the special developments are obviated. It will be found that in reptiles the tarsus, for the most part, articulates with the leg by two, and even three, bones instead of by one, as in ordinary mammalia; that the astragalus and os calcis neither of them have the peculiar characters which are exhibited in the higher vertebrates, while in the seals among mammals the astragalus develops a tuberosity backwards equal to that of the os calcis of the same animal.

We have placed no bone opposite the pisiform as its homologue. Some homologists, and among them Owen, regard the os calcis as, in itself, repeating the pisiform and pyramidale, and as consisting really of two bones combined in one, as the scaphoid and lunare are in the carpus of the cat and some other mammals. This view does not seem to be well supported; for while the coalescence of the scaphoid and lunare in various animals is a matter of observation, the existence of an os calcis in two parts has not been observed in any. In its mode of ossification, except in the development of a thin scale on the end of its tuberosity, it follows that of the other tarsal bones, viz., from a single centre. And in having an epiphysis it agrees with the astragalus in some lower animals, as the seal. The relation of the pisiform to the tendon of the "ulnar flexor" (extensor) of the wrist seems to justify Cruveilhier's view that it belongs to the category of sesamoids.

The metacarpal and metatarsal bones offer no difficulty in either of the two methods of studying the skeleton, since they agree in their relative position, and the only differences are purely teleological ones. Excepting in the thumb and great toe the same may be said of the phalanges. We have already alluded to the great difficulty which the exceptions just mentioned offer when the limbs are studied as symmetrical parts, and we know of no way in which it can be fairly and satisfactorily met.

The thumb and great toe are assumed by most anatomists to be homotypes. First, on account of their relative size. Secondly, because they have similar relative positions in the ordinary attitude of the fore arm. Thirdly, and chiefly, because they have only two phalanges each, while each of the other digits has three or more.

If the human hand and foot are alone examined, the relative size of the parts in question favors the view that they are homotypes. But this characteristic of size loses its value when they are studied in the lower animals. In the seal the thumb might, as regards its size, be considered the homotype of either the first or the fifth toe, which are the two largest and of equal size. In the walrus the first digit of the hand and the fifth of the foot, or the thumb and little toe, are the largest in their respective limbs. In the great ant-eater the third digit of the hand is longest, while the fourth is in the foot. If size were the criterion of homology, either of the fingers might in turn become the homotype of either of the toes, for the size of these parts being determined by their physiological adaptations, either may in turn become the largest or the smallest in the series.

The second reason, that based on the fact that they are both on the inside of their respective limbs, loses its force when it is remembered that the parts compared are, as it were, in a false position. That but for the rotation of the fore arm in the embryo, the thumb would have been on the outside of the hand, and would consequently have conformed to the position of the little finger.

The third argument, derived from the existence of two phalanges in each of the parts, is not so easily disposed of, and forms the greatest difficulty in our way. Notwithstanding the wide difference in the physiological value of these parts in different species of animals, and the consequent range of variation in the size of them, the number of phalanges may be said to be almost constant. It is true that in *Icthyosaurus*, *Plesiosaurus*, and other marine saurians, the thumb and great toe, like all the other digits, have their phalanges multiplied, and if our comparisons were confined to such animals as these the question of homologies would be easily answered, as it would also in some of the land turtles, where the number of the phalanges in all fingers and toes is reduced to two. If, too, we might apply the saying of Goethe, which holds true in so many instances, viz., "that it is in her monstrosities that nature reveals to us her secrets," we might call to mind an occasional monstrosity in which the thumb and great toe are each provided with three joints, and thus made to conform with the other digits. Lastly, we might call to mind the fact that in their mode of ossification, the metatarsal and metacarpal bones of the two parts in question agree with the phalanges, that is, in having the proximal epiphysis the last to unite with the shaft instead of the distal. Still the preponderance of facts is the other way, and, if we adopt the idea of symmetry, we must rest content with the assumption that the thumb with its two phalanges is the homotype of the outer toe with its three phalanges.

In the preceding pages the object has been to set forth some reasons for studying the fore and hind parts of vertebrated animals, but more especially their limbs, as if these parts and limbs were constructed not only after one and the same type, but in a symmetrical manner. They would repeat each other exactly in an ideal animal, just as the right and left parts do in the actual. In the actual animal the fore and hind parts are so modified as to adapt them to special conditions of existence, and as the conditions fulfilled by the two kinds of limbs are generally different, the limbs take on different degrees and phases of development. Right and left parts repeat each other almost exactly, because their conditions are the same, though even these, as we have already seen, may sometimes vary, and then we have a diversity in their development. In fore and hind limbs diversity is the rule, while in right and left it is the exception. Nevertheless, as we go back to the early stages of embryonic life, the symmetry and equality of fore and hind parts becomes nearly exact, however much they may vary in the adult.

We have not forgotten that in attempts like the present, comparisons should be made, not only between the bones of the limbs, but also between the muscles, nerves and vessels. We have confined our remarks chiefly to the bones, because their homologies are the most accurately determined. The attempts hitherto made for the determination of the homologies of the other parts, have been far less satisfactory. If a serious objection can be brought against the mode we have adopted of viewing the bones, far more serious objections can be brought against such a method of viewing the other structures. If the method fails in the skeleton, it will certainly fail elsewhere. On the other hand, if antero-posterior symmetry can be shown to exist in the bones, then we can feel some confidence, that whatever the difficulties at present may be with regard to the muscles, nerves and vessels, they will sooner or later be overcome. We may go still further, and assert that if the idea of fore and hind symmetry enters into the composition of animal structures at all, it will be traced not only in the limbs, but in all the great systems of organs. Unity of plan in the structure and composition of animals is much more likely to prove true than diversity.

Attempts have been made to construct an ideal skeleton, an "archetype" which is presumed to contain all the essential elementary parts of a vertebrated skeleton; these parts nowhere so developed as to be adapted to the wants of any individual, but capable, by a variation in the quantity and proportions of each, of being adapted to the conditions of life of every member of the series. Carus in his "Urtheilen des Knochen und Schalen gerüstes" attempted such an archetype. Owen in his "Homologies and Archetype of the Vertebrated Skeleton," has constructed another on essentially the same basis, but far more complete. Neither Carus nor Owen have, however, admitted the idea of fore and hind symmetry. If we admit this, then the archetype must be so modified as to conform to it. The typical structure which represents or occupies the place of the head at one end, if we will carry out the idea, must be represented by a similar reversed structure at the other. If, for example, we would adopt Owen's modification of Carus's archetype, we must divide it in the middle and replace the hinder half with a reversed repetition of the fore half. The skeleton would not in this way be provided with two heads, but only with the rudiments of these capable of being developed or arrested in development, in such a manner as the conditions of individual existence may require.

Whether we adopt the doctrine of fore and hind symmetry or not, such a conception as an archetype involves is necessary in our attempts to study the creative idea which underlies all animal structures apart from their adaptation to the modes of existence in each species; and just in proportion as such conception is based upon a more and more complete knowledge of the plan of structure and of development, anatomy will, in the same degree, become philosophical.