from the author

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23.

INTERMEMBRAL HOMOLOGIES.

THE CORRESPONDENCE OF THE ANTERIOR AND POSTERIOR LIMBS OF VERTEBRATES.

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PROFESSOR OF COMPARATIVE ANATOMY AND ZOÖLOGY,
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INTERMEMBRAL HOMOLOGIES.

INTRODUCTION.

The general correspondence of the limbs with each other was recognized by the ancients. The first detailed comparison was made by Vicq d'Azyr, in 1774. Since then the subject has received attention from nearly all anatomists, and there have come to my notice about seventy-five works wherein it is discussed. Of these about one half have appeared since 1860, and the number and eminence of their authors give reason for expecting much work to be done in coming years upon intermembral homologies. Yet so radical is the present difference of opinion among the more earnest workers, and so many and profound are the problems involved, that there is little hope of its final settlement within the present century. For several years I have lost no opportunity of collecting material upon the subject, and have announced my intention to devote myself chiefly to its investigation, in the hope of deciding one great question in homologies; but I had also resolved to publish no more upon the subject until I could begin the publication of a series of monographs treating in full of the various subdivisions of the question. My intention has been altered by the following circumstances: —

1. Several recent English writers have regarded the question as already decided in their favor, Flower, 66,[1] 240; Rolleston, 61, 219;

[1] The numbers refer to the bibliographical list at the close of this paper, the rst number indicating the *work*, the last the *page*, and the middle one, when it occurs, the volume.

Humphrey, 72, 68; Mivart, 279, 163, in spite of the published opinions of Foltz, 39, Wyman, 55, and the writer. They hold that the relation of the membra is one of *syntropy* or *parallelism*, and that pollex (thumb) is the homologue of primus (great toe); we hold, on the contrary, that the relation of these parts is one of *analogy*, and that the true homologue of pollex is quintus (little toe), and that of minimus (little finger) primus, the membra being *antitropically* or *symmetrically* related.

2. During the past year a new and vigorous ally has entered the discussion. Dr. Coues' admirable papers, 70, have already been briefly noticed,[1] and will be reviewed at more length hereafter.[2] I now merely express my gratification and my hope that together, under the guidance of our eminent teacher, Professor Wyman, we may be able to show that a very small minority may yet be in the right.

3. I have recently been led to modify my previous views respecting the *normal position* of the membra in which they should be compared together, and I am anxious to admit this change since it involves a concession to those who hold the view of syntropy.

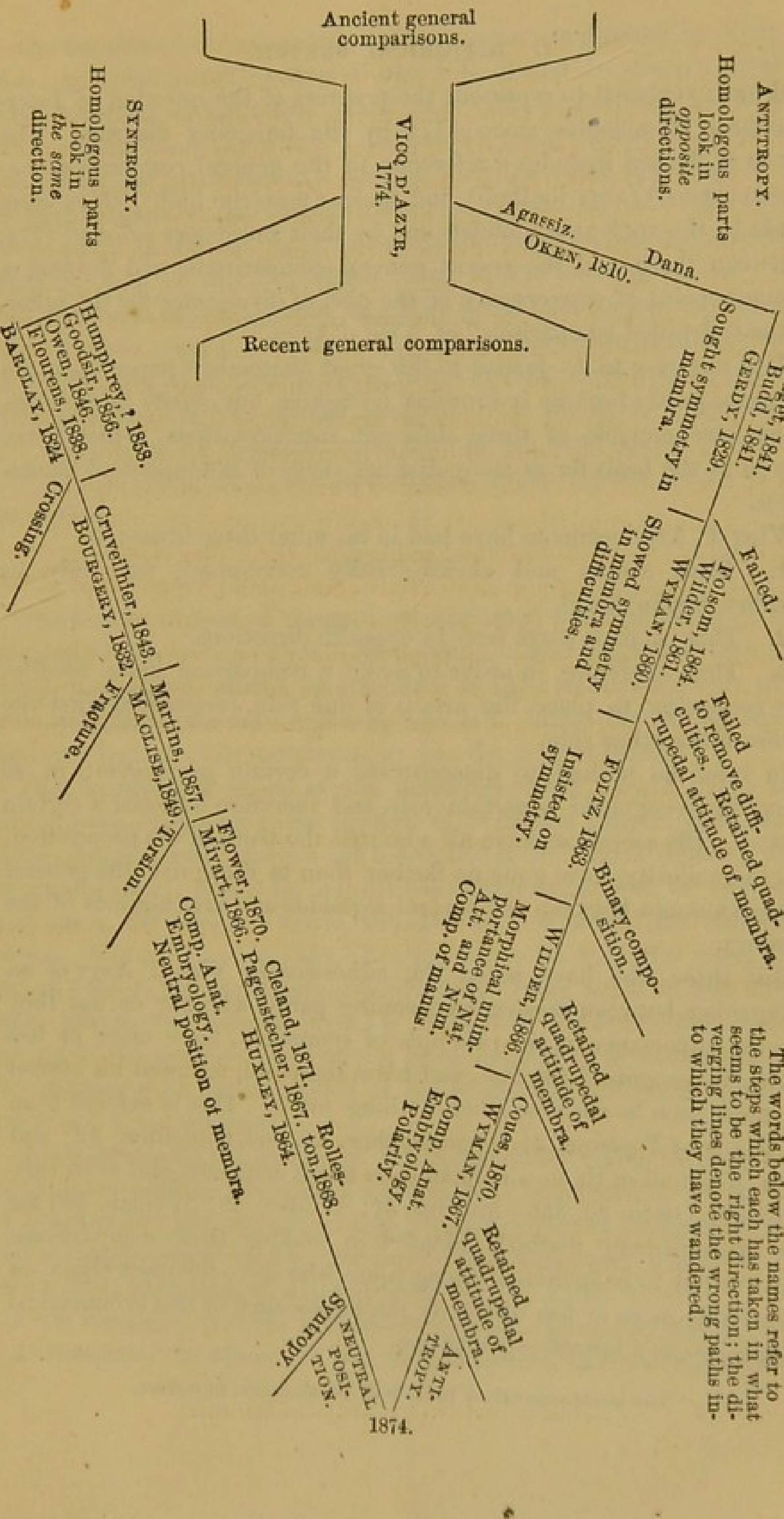
Still, the present paper is intended mainly as an index of what has been done, and of what remains to be done for intermembral homologies, and as a prodromus of the works which I hope to offer in coming years.

It will contain:—

1. An historical sketch of the question.
2. A revision of the nomenclature of parts.
3. A revision of the nomenclature of ideas.
4. Evidence as to the morphical unimportance of numerical composition.
5. Indication of general problems.
6. Indication of special problems.
7. Chronological list of special works upon intermembral homologies.
8. A glossary of morphological terms.
9. Alphabetical list of collateral works.

[1] American Naturalist, April, 1871.

[2] American Journal of Science, July, 1871.


Ancient general comparisons.
Recent general comparisons.
VICQ D'AZYR, 1774.
ANTITROPY. Homologous parts look in opposite directions.
SYNTROPY. Homologous parts look in the same direction.
Agassiz.
OKEN, 1810.
Dana.
Paget, 1841.
Budd, 1841.
GERDY, 1829.
Sought symmetry in membra.
Failed.
Folsom, 1864.
Wilder, 1861.
WYMAN, 1860.
Showed symmetry in membra and difficulties.
Failed to remove difficulties. Retained quadrupedal attitude of membra.
FOLTZ, 1863.
Insisted on symmetry.
Binary composition.
WILDER, 1866.
Morphical unimportance of Nat. Att. and Num. Comp. of manus.
Retained quadrupedal attitude of membra.
Coues, 1870.
WYMAN, 1867.
Comp. Anat. Embryology. Polarity.
Retained quadrupedal attitude of membra.
ANTITROPY.
The words below the names refer to the steps which each has taken in what seems to be the right direction; the diverging lines denote the wrong paths into which they have wandered.
Humphrey, ? 1858.
Goodsir, 1856.
Owen, 1846.
Flourens, 1838.
BARCLAY, 1824
Crossing.
Cruveilhier, 1843.
BOURGERY, 1832.
Fracture.
Martins, 1857.
MACLISE, 1849.
Torsion.
Flower, 1870. Cleland, 1871. Rolleston, 1868.
Mivart, 1866. Pagenstecher, 1867.
HUXLEY, 1864.
Comp. Anat. Embryology. Neutral position of membra.
NEUTRAL POSITION.
Syntropy.
1874.

I. HISTORICAL SKETCH.

I have ventured to represent the progress of the question of Intermembral Homologies since 1774, by the foregoing diagram. The brace at the left includes a reference to the general comparisons between armus,[1] (anterior limb), and skelos (posterior limb), which were made by the ancient anatomists and by their successors prior to 1774. Between these and the recent general comparisons, and forming a common point of convergence of the one, of divergence for the other, is the "detailed comparison" of Vicq d'Azyr.

It is not easy to do justice to this great anatomist's paper upon the membra, partly because it contains no figures, but chiefly because his words are capable of three different interpretations, which have served as the basis for as many distinct views of intermembral homologies.

Vicq d' Azyr seems to have had in his mind three ideas: —

1. That armus and skelos really correspond, not only as membra, but in detail.

2. That similar parts face in opposite directions.

3. That, therefore, in order to make a comparison more readily, it is *convenient* to place the armus of one side, *reversed*, against the skelos of the other side.

In brief, he wished to demonstrate a certain *proposition*; in so doing he recognized a certain *fact*, and therefore followed a certain *method*. His successors have all admitted the truth of the proposition, and the majority have gone no farther than to recognize the general correspondence between the several segments and articulations of the membra.

But those who have noted the admission by Vicq d' Azyr of an antagonism between these corresponding parts, whether or not they saw the importance of the principle of symmetry, have more or less distinctly recognized the fact, and have, therefore, followed his *method* of comparison as a *method*, and nothing more. This is evident from the words of Turenne, 21, Pagenstecher, 54, and Haughton, 62; and some, if not all of those who have been much criticized and even ridiculed (by Owen, 20, 335; Martins, 37; Wilder, 52; Wyman, 55) for the extraordinary methods adopted in making their comparisons, ought rather to be included among those who have followed Oken, in recognizing more or less distinctly the importance of this symmetrical antagonism as a law of organization.

[1] The nomenclature of parts will be discussed hereafter.

On the other hand, the *method* of comparison suggested by Vicq d' Azyr required that the armus of one side should be placed *parallel* with the skelos of the other. And this, with his frequent use of the term "parallèle," (by which I believe he really meant only *correspondence*,) has given rise to a class of views in which this method i in part adopted as an *end*, instead of a *means*; and the effort has been made in various ways to show that corresponding parts of the membra do, or at any rate should, face in the *same* direction. To this end, some have suggested ingenious serial homologies, leaving the parts in their natural attitudes, while others have altered the position of the membra or of their parts, in ways equally ingenious and plausible, yet, as I believe, equally unsound. But all these comparison are based upon the generally received opinion that pollex (thumb) and primus (great toe), are homologous, which opinion I hold to be incorrect.

SYNTROPY.

The former method of comparison originated with Dr. Barclay, the anatomical preceptor of Prof. Owen, who in 1824 suggested that the armus and skelos should be compared in their natural attitude with most mammalia, the manus pronated so as to bring the pollex upon the inner border of its membrum, as was the primus behind.

This involved a denial of the homology which Vicq d' Azyr admitted between the extensor surfaces of brachium (upper arm), and meros (thigh), and between the convexity of the ancon (elbow), and the genu (knee); and it further involved the compar*is*on of two *parallel* bones, the tibia and fibula, with two *crossed* bones, the ulna and radius. Nevertheless, in 1838 Flourens proposed a similar view, 14 and in 1846 it was vigorously supported by Owen, 20, 335, and 63 in many places, who carried it so far as to find the homologue of the patella in the sesamoid bone of the *biceps brachii* in certain bats, and the homologue of the olecranon in the projecting post-genual process (fabella), of the wombat.

From this and other details of Owen's peculiar views, Goodsir dissents; but in 1856 he enunciated what seems to be essentially the theory of Barclay and Flourens, associating with it, however, a belief in the quinary composition of the membra, which had been suggested by Oken, 285, 2380, Duges, 11, 44, and Gervais, 27, 32.

I was formerly, 52, 486, inclined to include Humphrey among the "Antitropists," by reason of his recognition of the antagonism between the proximal parts of the membra, 34, 600, and 36, 16, which had been previously pointed out by Agassiz, 26, 89, and others; but a more careful study of his works, especially of his later papers upon the subject, 64, and 72, has led me to regard his views as essentially syntropical; since, in his opinion, the above-mentioned antagonism is purely telical, and involves no idea of a general principle of symmetry; so that his comparison of the membra must either be included among the recent general comparisons, or associated with those of Owen and Cleland, in spite of their disagreements in respect to some special homologies. To Humphrey, however, is to be given the credit of indicating the value of comparative anatomy in this discussion, as to Goodsir belongs the honor of urging the importance of embryological studies, in order to determine the "morphology of limbs."

The evident objection to a comparison of two parallel with two crossed bones, led Bourgery, 10, and afterward Cruveilhier, 18, to suggest that the tibia was represented by the upper half of the ulna and the lower half of the radius, and the fibula, in like manner, by the upper half of the radius and the lower half of the ulna; but their view has not been adopted by any later writers.

Equally unnatural and unsupported was the "Torsion" theory of Maclise, 23, and Martins, 33, who at different times, but as it appears, independently, endeavored to preserve the syntropy or serial homology of the membra, the natural attitude of the manus, and at the same time remove the objections to the views of Barclay and Bourgery by admitting the homology of the convexities of ancon and genu, and the parallel relation of ulna and radius; they assumed that 'the humerus was a bone twisted upon its axis for 180°," and that it required to be *untwisted* in order to make the armus comparable with the skelos. A certain amount of "torsion" has lately been admitted by Gegenbaur, 59, but the conclusions of Maclise and Martins have been adopted by no other anatomists, and have been objected to by Humphrey, 36, Wilder, 45, and Wyman, 55.

A reaction from these speculative views took place in 1864, when Prof. Huxley proposed a comparison of the membra, 42, which differs in many respects from all others, even in the manner of its presentation; since its author appears to have attached so little importance to it that he has never written it out for publication or referred to it in his later works; and so far from believing, like the author of 23, that his method of comparison was to "unravel the gordian knot of that problem which had so long existed as a mystery for the morphologist," Professor Huxley admits that "it cannot be considered as thoroughly satisfactory since it has not been checked by the aid of the complete study of the development of the parts in question, the only method by which any morphological problem can be determined." The precise value of development in the determination of homologies will be discussed hereafter, but there can be no question that too little importance had been given to it in previous comparisons of the membra.

" Professor Huxley instituted a new comparison of the limbs, placed not in the position which they assume in adult life, but in the only one in which they really correspond with each other, viz., that which they first exhibit in the embryo. In this condition they stand out at right angles from the body, the extensor surfaces being placed dorsally, and the flexor surfaces ventrally, with both pairs of limbs. They then gradually become bent and afterward acquire the modified position which suits them for their function in life, and to which their various articulations become adapted. The embryonic position continues throughout life in many amphibia and reptiles and without much change in galeopithecus."

Huxley then proceeds to compare the premembral (anterior) borders of the membra together, making the radius and pollex homologous with the tibia and primus, upon the generally accepted principle of syntropy or serial homology; not realizing that the very same regard for the facts of development which led him to ignore the subsequent flexure and attitudes of the membra, should also require him to give no heed to those secondary modifications of the primordial buds which differentiate pollex and primus from their fellows, and cause them to resemble each other in many higher animals; but aside from his special interpretation of homologies, I am now ready to accept his method of placing the membra for comparison as the true one, of which more hereafter.

This general view of the method to be pursued in determining intermembral homologies has been adopted by Mivart in 1866, by Pagenstecher in 1867, by Rolleston in 1868, and by Flower in 1870; who, however, have each proposed modifications in detail, which I will not discuss here, since the special interpretations of muscular homologies depend upon the general view of membral homology, and stand or fall therewith.

Parker has not expressed a decided opinion upon the subject; let us hope that his late magnificent contribution to rational homology, 292, may be followed by a like work upon the membra, as a sound basis for all subsequent investigation.

Cleland has published two short papers upon intermembral homologies, 47 and 65; in the first he inclines to the general views of Goodsir, and in the latter makes the lower jaw serially homologous with the membra; but he kindly permits me to state that he is by no means satisfied with the present aspect of the question, and is even willing to admit the existence of "symmetry" in certain corporal organs; so that I venture to hope that he may yet recognize the antitropic relation of the membra, especially since I am now ready to agree with him that the antagonism of the membral flexures in many mammals, is the result of telical modifications of their primary and normal condition; therefore, in spite of his previous views, and his disagreement in detail with the muscular homologies of the others, he may not object to being enumerated among those who follow Huxley in basing their further investigation of intermembral homologies upon the facts of comparative anatomy and embryology rather than upon anthropotomy.

ANTITROPY.

The suggestion that a symmetrical relation or antagonism exists between the cephalic and caudal regions of the vertebrate body, is contained in many paragraphs of Oken's Physio-philosophy, 285, Par. 2114, 2242, 2951, etc., and has been since alluded to by Agassiz,[1] and Dana[2]; but these eminent naturalists have never published any direct application of the idea to the membra, although it cannot be doubted that Oken would now be among the first to adopt the antitropical comparison, as Agassiz and Dana have privately done.[3]

The first published comparison of the membra upon the basis of antitropy was that of Gerdy in 1829, 9; he appears to have been an artist as well as an anatomist, and to have been thus led to look upon the whole body as a symmetrical structure, whose upper and lower ends repeat each other in opposite directions as do the right and left sides; he began to apply this principle to the membra, but unfor-

[1] Contrib. to the Nat. Hist. of the United States, Vol. I, pp. 308, 311, 312.

[2] Am. Jour. Science and Arts, Nov. 1863, p. 351.

[3] Prof. Agassiz also informs me that in Europe he noted the symmetrical relations between the manus and pes of the walrus, and afterward discussed the subject in a course of unpublished lectures at the Smithsonian Institution.

tunately employed those of man in the erect attitude, and was, moreover so impressed with the prevailing belief that pollex and primus must correspond, that he failed to discover the existence of the idea of symmetry in the distal portions of the membra.

A few years later, Budd, 79, and Paget, 80, observed some pathological evidences of a relation between symmetry and disease, to which I have made some additions in 50.

A more successful attempt to ascertain how far the membra are truly symmetrical structures, not in a telical sense, as Humphrey regarded them, but upon the basis of the ideas suggested by Oken and Gerdy, was made by Professor Wyman in 1860, 35. In a verbal communication which it was my good fortune to hear, this eminent anatomist clearly and impartially stated the views of previous authors, and pointed out the objections thereto ; no report is given of this remarkable communication, but as I recollect it, being then a student, and hearing of the subject for the first time, Professor Wyman expressed himself substantially as follows : —

"In order to compare the upper and lower limbs of man, the skeleton should be placed in a horizontal attitude ; the limbs then hang downward ; in their natural attitude, with most mammalia, the elbow looks backward and the knee forward; the shafts of the humerus and femur are inclined in opposite directions ; if now the hand be *supinated*, and the fingers pointed backward, there results a complete symmetrical homology between all parts, until we come to the thumb and great toe ; for the former is now upon the outer border of its limb, and thus opposed to the little toe ; this difficulty is a very serious one, and there seems to be no satisfactory method of removing it."

This view of the limbs was afterward freely discussed by Professor Wyman in his laboratory, and was made the basis of later and decided expressions of opinion by Folsom, 40, and myself, 45, who were not then able to perceive the full force of the objections which our preceptor had indicated to his own view.

Three years later, but apparently unaware that Prof. Wyman had treated the subject, Dr. Foltz published his very valuable papers, 39, in which the general subject of symmetry is ably discussed and shown to exist between the membra, even to the digits and dactyls; but, excepting the supination of the manus so as to face the palm forward as the sole faces backward, Foltz retains the quadrupedal attitude of the membra, and further encumbers his theory with the hypothesis of the "binary composition" of the pollex and primus, in order to get rid of the difficulty caused by their size in man; this makes us all normally sexdigitists; and as no sufficient reasons are given for this part of the view, and as man is the only species in which this special difficulty would arise, and as *size* is now admitted to be of very slight morphical importance, no one has adopted the view of binary composition of the pollex and primus.

My own contributions to the solution of this problem originated in the effort to remove the difficulties pointed out by Wyman, by suggesting that the morphical value of the manus and pollex was inversely to their telical importance, and that any difficulty with them should not be allowed to outweigh the teachings of the proximal portions of the membra; this suggestion was contained in my graduation thesis in 1862; and more fully presented in 1865; the same view was advocated in subsequent papers, 51, 52, 57 and 58, together with another respecting the morphical unimportance of the character "numerical composition"; both these points, with the distinction between natural attitude and normal position, I regard as demanding careful study in this connection, and they will be discussed hereafter; but in the above papers, I followed Wyman and the rest in comparing the membra in the condition they present in the quadrupeds, which I now believe to be *not* their normal condition.

In compliance with the oft-repeated request of former students and others interested in the subject, Prof. Wyman at length completed and published his paper on Symmetry and Homology in Limbs; 55. In the words of a reviewer, "certainly no modern inquirer has searched the secrets of Nature more closely, or clothed his discoveries in more concise and modest language." After showing that "in right and left parts distorted symmetry is the exception, while in the fore and hind (cephalic and caudal) parts of adults it is the rule," Wyman points out the remarkable analogy which exists between symmetry as brought about by vital forces and the effects of physical polarity; then discusses the signification of *homology*, and concludes, "those parts of the limbs will be homotypes which have the same relative position and are symetrically placed with regard to each other." p. 260.

He then compares the various parts of the membra as symmetrical structures, "repeating each other in a reversed manner from before backwards as right and left parts do from side to side, because, though open to grave objections, 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" (p. 246); the objections are the same as were stated by him seven years before, and relate to the thumb and great toe, which are "assumed by most anatomists to be homotypes; first, on account of their relative size; second, 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" (p. 276). The first two objections to a symmetrical homology of the parts, which brings the thumb as homologue of the little toe, are removed by showing first, that "the attribute of *size* loses its value when studied in the lower animals"; and second, that the natural attitude of the hand is a "false position" due to the "rotation of the fore arm in the embryo, but for which the thumb would have been on the outside of the hand, and would consequently have conformed to the position of the little toe." But the third difficulty "forms the greatest in our way and is not so easily disposed of; and we must rest content with the assumption that the thumb with its two phalanges is the homologue of the little toe with its three phalanges." (p. 277.)

The complete removal of this difficulty is one of the chief aims of the present paper, and will be the subject of a section upon the "morphical unimportance of numerical composition."

Prof. Wyman makes a valuable suggestion (p. 274) as to the normal shape of the carpal and tarsal bones, the metacarpals and metatarsals (p. 275), which is capable of application to all the long bones of the membra, and had been even proposed by Mivart, 46,401, with respect to the scapula and ilium; if all the long bones had been regarded as morphically columnar and cylindrical, the theory of "torsion" would never have taken the form it did.

Like Huxley, Wyman lays great stress upon the importance of comparative anatomy and embryology in this connection, but appears not to have seen the former's paper, since he does not allude to the method of comparison suggested by him, namely, by placing the membra parallel with each other and at right angles with the trunk, the convexities of the ancon and genu looking upward as with embryos and many lower vertebrates; and as this is the visual method which now seems to me most likely to lead toward a final solution of the question, the lack of allusion to it and agreement with it, appears to constitute the main defect in the work of my illustrious preceptor as a complete guide to the future study of intermembral homologies.[1]

The same general criticism is applicable to the admirable series of papers by Dr. Coues, which appeared during the past year. The author follows closely in the footsteps of Wyman, "not blindly but unable not to see the validity of his arguments," 70, 195, and therefore with a few minor differences, or doubts respecting details, adopts the osseous homologies of Wyman as the basis for the determination of the "muscular correspondences." In respect to these, although Dr. Coues is led to differ materially upon some points from my own previous conclusions, 45, yet he has generally shown such good reasons therefor, that my approval of this part of his work is unqualified, and I am anxious to go over the whole ground anew in the light of his able discussion. In two other respects, however, I am forced to criticise his work.

In the first place, he has "no acknowledgements to make excepting to three authors,"[2] 70, 149, and therefore, whatever satisfaction may be derived from having so taken up the subject fresh, he has also lost the benefit of the check which an acquaintance with many and different views exerts upon the tendency to the exclusive adoption of any one.

In the second place, he has, in my opinion, adopted a faulty method from each of his predecessors. He has intentionally followed Owen, in the use of many different and often ponderous expressions for the same idea in order to avoid monotony, 70, 193, note; whereas, in homologies, as in mathematics, each object and idea should be known by a single term and by that alone; since of all

[1] It may at first appear that too much stress is laid upon this point, since, as Dr. Coues has suggested to me, the principle is right and the same parts are antitropically compared, whatever be the attitude of the membra ; but it must be borne in mind that this matter, so trivial in the eyes of a zealous antitropist like my morphological brother, is a stumbling block in the way of the confirmed syntropists who constitute the vast majority of anatomists. They deny the law of symmetry at the outset, on the ground that its chief evidences are the natural antagonistic flexures of the membra which exist in a few quadrupeds only, and not in the earlier stages of development. And in vigorously opposing this unnecessary corollary of our theorem, they get into a frame of mind wholly unfit to receive sounder evidence of the theorem itself ; like 'binary composition' the 'quadrupedal attitude' is an uncalled for, though natural, amendment to the measure of antitropy which we support.

[2] Owen, Wyman and the writer.

the natural sciences, this demands the closest attention, and the absence of all unessential considerations.

Coues has accepted unquestioned the view of the normal position of the membra, for comparison, which was first proposed by Wyman and adopted by Foltz, Folsom, and myself; this view is based upon the proposition of Wyman, 55,265, that "the knees and elbows in all animals are bent so as to form angles pointing in opposite directions"; if we except the fishes, this generalization is correct, *provided* that the membra are placed in the position they have with most quadrupeds; but Goodsir, Humphrey and Huxley and Wyman himself have shown that this is not their primary position, and it is quite possible that both Wyman and Coues might have followed Huxley in denying that it is their *normal* position, had they read his paper.

Finally Dr. Coues has accepted from the writer a terminology of ideas (antitypy, etc.) which was itself based upon the Owenian phraseology, which was in no way expressive of the ideas designated thereby, and which I now propose to discard for a more significant nomenclature derived from the word which begins this section; of which more hereafter.

I have commented upon Dr. Coues' methods the more freely because, as regards the use of many and lengthy words, and the acceptance of single authors' peculiar views, my own sins have been more and greater than his can ever be.[1]

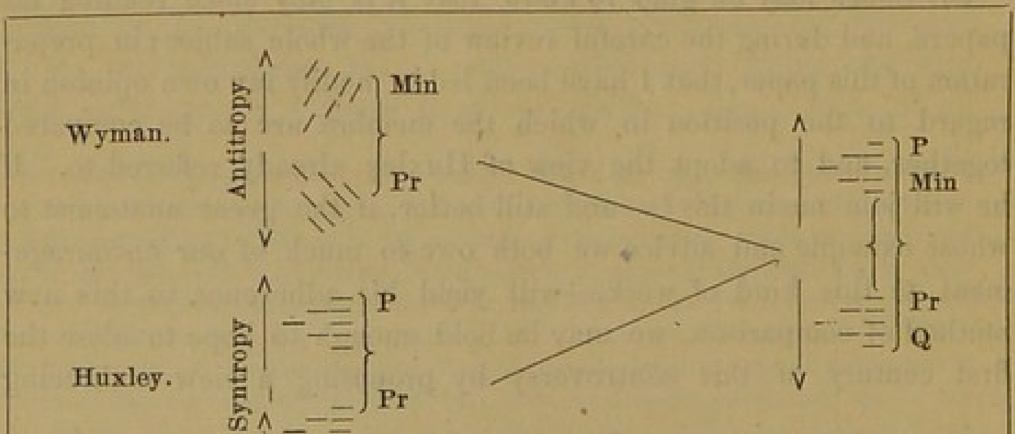
Dr. Coues may be glad to know that it is only since reading his papers, and during the careful review of the whole subject in preparation of this paper, that I have been led to modify my own opinion in regard to the position in which the membra are to be compared together, and to adopt the view of Huxley already referred to. If he will join me in this[2] — and still better, if the great anatomist to whose example and advice we both owe so much of our encouragement to this kind of work,—will yield his adherence to this new method of comparison, we may be bold enough to hope to close the first century of this controversy by proposing a view embracing

[1] Let me here thank my kind preceptor and my other scientific friends for allowing me to be the first to express the opinion that a certain memoir, 45, whereof the writer was rather proud, would have been the better for much cutting and pruning in the above mentioned respects, although I have no reason to regret the general views therein advocated.

[2] Dr. Coues writes me (Dec. 23, 1871) that he sees no valid objection to the neutral position proposed by Huxley.

the best elements of both the two great parties, Syntropists and Antitropists; the Realists and the Idealists they may also be called, since the former based their views upon certain facts to which were given undue prominence, while the latter began with the recognition of a great principle, which they sought to trace in all parts of the body; they may also be called the Peripheralists and the Centralists, since the former began their comparisons at the distal extremities of the membra and made the rest conform thereto, while the latter began with the evidences of symmetry in the body itself, and hoped to find the same law illustrated in the appendages; and finally the two schools are essentially of the Teleologists and Morphologists, since the former always laid great stress upon the functional correspondence of the pollex and primus, while the latter sought for the evidences of an abstract, morphical law of organization, and only failed in that search through lack of discrimination between morphical and telical attitude, form, and composition.[1]

Professors Huxley and Wyman are universally recognized as leaders of these two parties: both are anatomists of the highest rank and the latter has never been known to fully adopt a view which has afterward proved unsound: both admit the difficulties which beset this problem and, unlike some of their predecessors, make no pretence of "cutting the Gordian knot"; finally both have strongly urged the great importance of embryology and comparative anatomy.



[1] Among the notes made about the time of giving a course of University Lectures in Cambridge, Mass., I find the following: "It will be curious if the matter is finally compromised by adopting the view as to the position of the limbs proposed by Huxley, and making our own interpretation of Symmetry"; dated Feb. 15th, 1868.

It is probable, therefore, that for the final solution of this problem, we must combine the *visual* method of Huxley, as based upon the facts of position in embryo and lower animals, with the *intellectual* method of Wyman, as based upon a great law of organization. This convergence of the two opposing theories of Syntropy and Antitropy is indicated in our first diagram of authors, and may be seen still more plainly in the preceding figure.

In that diagram the arrows represent the longitudinal axis of the body; they look in the same direction in the lower figure, in opposite directions in the upper; in the lower figure the membra of the right side are shown in the *position* suggested by Huxley; but the brace still connects pollex (P) and primus (Pr.), which according to syntropy are homologous parts; in the upper figure the membra are turned away from each other as wholes, but the special flexures could be shown only from the side; here the brace joins the minimus (Min.) and primus (Pr.), which are homologous, according to antitropy. The *position* of the membra in the one, and the *idea* of symmetry in the other of these two figures are united in the third, where the braces can join pollex and quintus, minimus and primus.[1]

II. NOMENCLATURE OF PARTS.

The great activity of workers in homologies demands the repair and, in some cases, the renewal, of their "tools of thought"; our anatomical nomenclature is now as incongruous and unmanageable as zoological nomenclature was before Linnæus; even our highest authorities employ those abominable terms compounded of "fore" (200, 1, 273, and 2, 281), and describe the skeleton of an ape as if in the erect attitude, so as to reverse all the terms of comparison with the vertebrate animal in its normal position (275, 176, note 2). Special inconsistencies and objectionable features will appear in the following synonymy, wherein I have purposely quoted, as far as possible, from high authorities, since upon them we must rely for effecting

[1] Since the above was written I have read such parts of 329 as discuss the relative positions of the membra; but although the author well describes the isotropy which exists in many vertebrates where the membra either project laterally, or are rotated so as to bring the ancon and genu forward, as in tortoises, and the "Heterotropie" which characterizes the membra of most other quadrupeds, no direct light is thrown upon the morphical relations between the membra themselves; perhaps his investigations upon the Torsion of the Humerus and Femur are worth consideration.

a reform. The changes proposed are, as far as possible, in accordance with the following requirements of technical terms: —

1. Classic Derivation; 2. Capacity for inflection; 3. Brevity; 4. Independence of context for signification; 5. Non-ambiguity to the ear as well as to the eye; 6. Previous use in a kindred sense. I cannot hope to have satisfied all the requirements in every case, and ask for corrections and amendments. I admit all the objections which have been urged against new terms; but am convinced that some change must be made before homology can be the exact science which it is capable of becoming; and I would refer to Agassiz (200, 3, 69), Goodsir (237, 2, 83), Owen (63, 1, XIII) and Strauss-Durckheim (331, 1, XV) in support of a correct system of nomenclature.

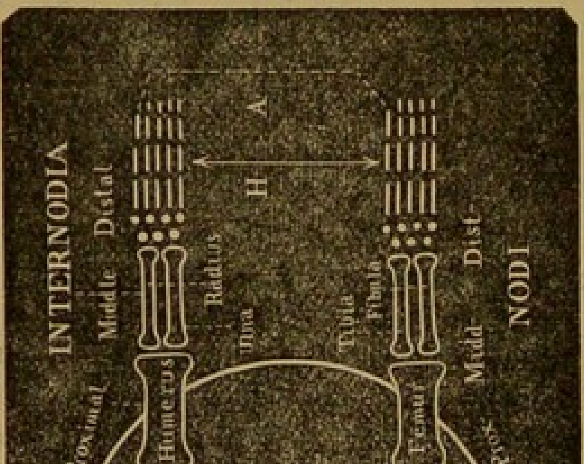


Fig. 1.

The accompanying diagram presents the dorsal surface of a vertebrate animal in what may be called a *neutral* or indifferent condition as to both attitude and structure; although some details are introduced for the purpose of employing this figure in other parts of the discussion. The animal is shown as a circular disk, the "germinative area," at the time it presents the two characteristic and common features of all vertebrates.

First: — A discrimination between the cephalic and the caudal regions by the formation of the cephalic and caudal hoods; and it is of great significance that, (with the Turtle at least, according to Agassiz, 200, 2, 537-539) this occurs prior to the separation into a right and a left half.

Second:— The formation of a groove, the "primitive furrow," which connects the cephalic and the caudal folds and indicates the position of the future longitudinal axis, dividing the ovum into a right and a left half.

The membra also are left in what may be considered their *neutral* position, extending outward at right angles with the longitudinal axis of the trunk and parallel with each other; that this should also be regarded as the "normal position" of the membra in contradistinction to their numerous "natural attitudes" will be shown hereafter. This neutral position of the membra presents the convexities of the knee (genu) and elbow (ancon) corresponding with the so-called "dorsal" or "extensor" or "epaxial" surfaces, the manus being supinated and placed flat upon the earth, and the whole armus having nearly the position it has in a land tortoise or in a man when upon "all fours."

The digits and dactyls are shown of nearly equal length; the premembral digit and dactyl (pollex and primus) are joined by a dotted line (A), to represent the *analogy* which they undoubtedly bear to each other; but the continuous line (H) unites the postarmal digit (minimus) with the preskeleal dactyl (primus) to indicate the *homology* which is held to exist between them by Wyman, by Coues and the writer. The carpal and tarsal bones are shown as parallel rows of similar ossicles, as suggested by Wyman (55, 274).

Omozone (*shoulder girdle*).

Scutula, Lat. —Ὦμος, (?) Gr.— *Ceinture thoracique*, Foltz, 39.— *Schulter-gürtel*, Geg., 230, *fere.*—*Shoulder-girdle*, Park., 292, *fere.*— *Scapulo-coracoid arch*, Ow., 20, 184.— *Hæmal. arch of occipital vertebra*, Ow., 63, 1, 125.—*Scapular girdle*, Goods., 237, 2, 199.— *Scapular arch*, Wym., 55, 260.

Remark. For this and the following name I am indebted to Dr. Coues.

Ischizone (*pelvic girdle*).

Pelvis, Lat. —Ἰσχία, (?) Gr.— *Ceinture pelvienne*, Foltz, 39, *fere.* —*Beckengürtel*, Geg., 230 *fere.*— *Hæmal arch of* (?) *vertebræ*, Ow., 20, 268.—*Pelvic girdle*, Hum., 72, *fere.*—*Pelvic arch*, Ow., 63, 2, 307.

Membra (*the limbs*).

Membra, Lat.—Ῥίθεα, Gr.—*Membres, extremités*, Fr.—*Glieder*, Ger. —*Artus*, Bonap., Tr. Linn. Soc. 18, 248.—*Legs*, vulgo.—*Limbs*, Goods., 240, *fere*.—*Lateral limbs*, Hum., 248, 65.—*Parial limbs*, Ow., 63, 1, 62. —*Appendages*, Miv., 275, *fere*.—*Diverging appendages*, Ow., 63, 2, 581.—*Appendicular parts*, Flow., 71, 219.—*Locomotive organs*, Ow., 63, 2, 280.—*Liberated ribs*, Ok., 285, Par. 2370.—*Archipterygii*, Geg., 68, 400.—*Extremitäten paarigen*, 231, 424.

Membrum, membri, membra, membrorum, membral.[1]

NODUS (*articulus membri*).

Nodus articulus, Lat.—'*Ἄρθρον*, Gr.—*Joint*, *articulation*, Fr.—*Gelenk*, Ger.—*Joint*, Ow. 63, 2, 542, (*internodium*).[2]—*Articulation*, Anthropotomy, *fere*.

Nodus, nodi, nodi, nodorum, nodal.

INTERNODIUM (*segmentum membri*).

Internodium, Lat.—*Τμῆμα*, (?) Gr.—*Internode*, Coues, 70, *fere*.—*Segment*, Ow., 63, 2, 306.—*Joint*, vulgo, (*nodus*).

Internodium, internodii, internodia, internodiorum, internodial.

ARMUS [3] (*membrum anterius*).

Brachium, *ulna*, *lacertus*, Lat.— *Βραχίων*, Gr.— *Bras*, Fr.— *Arm*, Ger.—*Diverging appendage of occipital vertebra*, Ow., 63, 2, Table I.—*Fin*, Ow., 63, 2, 437.—*Leg*, *limb*, *member*, *fin*, *appendage*, with adjectives as follows: *Fore*, Ow., 63, 2, 482.—*Upper*, Macl., 23, 666.—*Anterior*, Hux., 42, 1.— *Pectoral*, Ow., 63, 2, 65.— *Atlantal*, Barclay (quoted by Owen, 20, 334).—*Thoracique*, Foltz, 39, *fere*.—*Sternal*, Vogt, Nature, Jan. 20, 1870.

Armus, armi, armi, armorum, armal.

OMOS (*nodus proximus armi*).

Ὦμος, Gr.— *Épaule*, Fr.—*Achsel*, Ger.— *Shoulder-joint*, *scapulo-humeral articulation*, Anthropotomy.

Omos, omou, omoi, omon, omal.

[1] Here and hereafter are given nom. and gen. singular and plural, and the adjective form of the word; the first number after an author's name corresponds to the number of his work upon the list; the last indicates the page; the second, when it occurs, the volume of the work.

[2] Here and elsewhere a word in parenthesis indicates that the preceding synonym has also been used for the part designated by that word, and thus in two distinct senses.

[3] This word means strictly rather shoulder than arm, but no other term is equally suitable, and the sound of this is in its favor.

ANCON (*nodus medius armi*).

Cubitum, Lat.—'Αγκών, Gr.—*Coude*, Fr.—*Elbogen*, Ger.—*Elbow*, Wym., 55, 265.—*Elbow-joint*, Anthrop.
Ancon, anconos, ancones, anconon, anconal.

CARPUS (*nodus ultimus armi*).

Carpus, Lat.—Καρπός, Gr.—*Carpe, poignet*, Fr.—*Handgelenk*, Ger.—*Wrist-joint*, Ow., 63, 2, 310.—*Knee*, Ag., 200, 1, 361, (*genu*). Maynard, Nat. Guide, p. 40.—*Radio-carpal articulation*, Anthrop.

STETHOS (*pseudo-internodium proximum manus.*)

Metacarpus, Anthropotomy.—*Stethos*, Str. Dur., 331, 1, 116.
Stethos, stethou, stethoi, stethon, stethal.

REMARK. This term was really applied by Strauss-Durckheim, not to the whole metacarpus, but to the second metacarpal bone; but upon the ground that the Greeks applied the term to the whole metacarpus.

BRACHIUM (*internodium proximum armi*).

Lacertus, Lat.— *Bras, or bras supérieur*, Fr.— *Oberarm*, Ger.— *Brachium*, Fl., 71, 219, (*armus*).—*Arm*, Fl., 71, 239, (*armus*).—*Upper arm*, Fl., 71, 219.—*First segment*, Ow., 63, 2, 306 (*meros*).—*Proximal segment*, Hum., 36, *fere*, (*meros*).
Brachium, brachii, brachia, brachiorum, brachial.

CUBITUM (*internodium medium armi*).

Cubitum, (?) Lat.— Πῆχυς, Gr.— *Avant bras*, Fr.— *Vorderarm*, Ger.—*Cubit*, Macd., 255, *fere*.—*Fore arm*, Fl., 71, 219.—*Middle segment*, Hum., 36, *fere*, (*crus*).—*Second segment*, Ow., 63, 2, 306 (*crus*).—*Antebrachium*, Fl., 71, 219.
Cubitum, cubiti, cubita, cubitorum, cubital.

MANUS (*internodium ultimum armi*).

Manus, Lat.— Χείρ, Gr.— *Main*, Fr.— *Hand*, Ger.— *Manus*, Fl., 71, *fere*.—*Hand*, Wym., 55, 273.—*Foot*, Ow., 63, 2, 484, (*pes*).—*Fore-foot*, Ow., 63, 2, 283.—*Fore-hand*, Ow., 63, 2, 541.—*Distal segment*, Hum., 36, *fere*, (*pes*).—*Terminal segment*, Fl., 71, 252, (*pes*).
Manus, manûs, manus, manuum, manual.

Digiti (*digiti manus*).

Digiti manûs, Lat.— *Δάκτυλοι*, Gr.— *Doigts*, Fr.— *Finger*, Ger.— *Fingers and thumb*, Ow., 63, 2, 544.—*Toes*, Ow., 63, 2, 488 (*dactyli*). —*Digits*, Ow., 63, 2, 539, (*dactyli*).—*Fingers*, Ow., 63, 2, 328.

Digitus, digiti, digiti, digitorum, digital.

Pollex (*digitus radialis*).

Pollex, Lat.—*'Αντίχειρ*, Gr.—*Pouce*, Fr.—*Daumen*, Ger.—*Pollex*, Fl., 71, *fere*.—*Thumb*, Wym., 55, 276.—*First digit*, Fl., 71, 255, (*primus*). —*Outer digit*, Hum., 34, 389; 326, 112.—*Inner digit*, Ow., 63, 2, 509, (*primus*).—*Radial digit*, Fl., 71, 255.—*Preaxial digit*, Fl., 71, 337. *First toe*, Goods., 237, 1, 450, (*primus*).

Pollex, pollicis, pollices, pollicum, pollical.

Index (*digitus a pollice proximus*).

Digitus index vel salutaris, Lat. — *Λίχανος*, Gr. — *Indicateur*, Fr.— *Zeigefinger*, Ger.—*Index*, Ow., 63, and Fl., 71, *fere*.—*Second digit*, Ow., 63, 2, 428, (*secundus*).—*Fore-finger*, vulgo.

Index, indicis, indices, indicum, indical.

Medius (*digitus medius*).

Digitus medius vel famosus, vel infamis, vel impudicus, Lat.— *Doigt du milieu*, Fr.—*Mittelfinger*, Ger.—*Middle toe*, Ow., 63, 2, 456, (*tertius*).—*Middle finger*, *vulgo*.—*Medius*, Ow., 63, Fl. 71, *fere*.—*Third digit*, Wym., 55, 276, (*tertius*).— *Second digit*, Sandwith, letter to Owen, Mem. on Aye-Aye, Trans. Zool. Soc., (*index*). — *Verpus*, Str. Dur., 331, 1,117.

Medius, medii, medii, mediorum, medial.

Minimus (*digitus ulnaris*).

Digitus minimus ; digitulus auricularis brevissimus, Lat.—*Doigt auriculaire*, Fr.—*Ohrfinger*, Ger.—*Little finger*, Wym. 55, 276.—*Outermost digit*, Ow., ? (*quintus*).—*Fifth digit*, Ow., 63, 2, 307 (*quintus*).—*Minimus*, Ow., 63, Fl. 71, *fere*.—*Wing-finger*, (of the Pterodactyle) Ow., 289, 273. — *Micros*, Str. Dur., 331, 1, 117.

Minimus, minimi, minimi, minimorum, minimal.

Annularis (*digitus a minimo proximus*).

Digitus annularis, medicus, medicinalis, Lat.—*Doigt annulaire*, Fr.— *Ring finger*, Ger.— *Annularis*, Ow., 63, Fl., 71, *fere*.—*Third finger*, (Eng. Lat. Lexicon).—*Fourth digit*, Ow,. 63, 2, 306 (*quartus*).—*Ring-finger*, vulgo. — *Paramèse*, Str. Dur., 331, 1, 117.

Annularis, annularis, annulares, annularium, annularial.

Skelos (*membrum posterius*).

Artus, Lat.—Σκέλος, Gr.—*Jambe*, Fr.—*Schenkel*, (?), Ger.—*Diverging appendage of pelvic arch*, Ow., 63, 2, 429.— *Sacral limb*, Barclay (quoted by Ow., 20, 334. note).—*Hind limb*, Ow., 63, 1, 191.—*Lower limb*, Macl., 23, 666.—*Pelvic limb*, Macl., 23, 664.—*Membre pelvien*, Foltz, 39, *fere*.—*Membre inferieur*, Richaud, 15, *fere*.—*Leg*, vulgo, (*crus*).

Skelos, skeleos, skelea, skeleon, skeleal.

Coxa (*nodus proximus skeleos*).

Coxa, Lat.—'Ισχιόν, Gr.—*Hanche*, Fr.—*Lende*, *Hüfte*, Ger.—*Hip joint*, vulgo.—*Innominato-femoral articulation*, Anthrop.

Coxa, coxæ, coxæ, coxarum, coxal.

Genu (*nodus medius skeleos*).

Genu, Lat.—Γόνυ, Gr.—*Genou*, Fr.—*Knie*, Ger.—*Knee*, Wym., 55, 265.—*Knee-joint*, vulgo.—*Femoro-tibial articulation*, Anthrop.

Genu, genûs, genua, genuum, genual.

Talus (*nodus ultimus skeleos*).

Talus, Lat.—Σφυρὸν, Gr.—*Coude-pied*, Fr.—*Knöchel*, Ger.—*Ankle*, vulgo.—*Ankle-joint*, vulgo.—*Tibio-tarsal articulation*, Anthrop.

Talus, tali, tali, talorum, talar.

Meros (*internodium proximum skeleos*).

Femur, Lat.—Μηρός, Gr.—*Cuisse*, Fr.—*Schenkel*, Ger.—*Proximal segment*, Hum., 36, *fere* (*brachium*).—*Thigh*, Fl., 71, 281.

Meros, merou, meroi, merōn, meral.

Crus (*internodium medium skeleos*).

Crus, Lat.—Κνήμη, Gr.—*Jambe*, Fr.—*Unterschenkel*, Ger.—*Middle segment*, Hum., 36, *fere*, (*cubitum*)—*Cnemion*, Ow., 63, 1, 170.—*Leg*, Fl., 71, 281, (*skelos*).

Crus, cruris, crura, crurum, crural.

Pes (*internodium ultimum skeleos*).

Pes, Lat.—Πούς, Gr.—*Pied*, Fr.—*Füss*, Ger.—*Distal segment*, Hum., 36, *fere* (*manus*).—*Foot*, Wym., 65, 276, (*manus*).—*Hand*, Ow., 63, 2, 294.—*Hind hand*, Ow., 63, 2, 542.—*Hind foot*, Ow., 63, 2, 487.—*Pes*, Ow., Fl., Miv., Rol., *fere*.—*Terminal segment*, Fl., 71, 306.

Pes, pedis, pedes, pedum, pedal.

Podium (*pseudo-internodium proximum pedis*).

Metatarsus, Anthropotomy, *fere.—Podium*, Str. Dur., 331, 1, 12.

Podium, podii, podia, podiorum, podial.

Remark. This term was not really applied by Strauss-Durckheim to the metatarsus, but the vowel variations of podion (padion, pedion, pidion, podion, pudion) were applied to the metatarsal bones of the primus, etc., respectively.

Dactyli (*digiti pedis*).

Digiti pedis, Lat.— *Δάκτυλοι ποδός*, Gr.—*Doigts postérieurs*, Fr.—*Zehen*, Ger.—*Digits*, Ow., 63, *fere*, (*digiti*).—*Toes*, Ow., 63, 2, 362, (*digiti*).

Dactylus, dactyli, dactyli, dactylorum, dactylic.

Primus (*dactylus tibialis pedis*).

Allex, Lat.— *Gros orteil*, Fr.—*Grosse Zehe*, Ger.—*Hallux*, Ow., 63, 2, 553.—*Great toe*, Ow., 63, 2. 553.—*Thumb*, Ow., 63, 2, 544, (*pollex*).—*Inner toe*, Rol., 234, 1, viii.—*Tibial digit*, Fl., 71, 306.—*Preaxial digit*, Fl., 71, 337. —*First digit*, Fl., 71, 306.— *Hinder thumb*, Ow., 63, 2, 512.—*Tibial toe*, Ow., 63, 2, 362.—*Protos*, Wild., 67, *fere*. —*Pollex*, Hum., 34, 576.

Primus, primi, primi, primorum, primal.

Secundus, (*dactylus a primo proximus*).

Digitus secundus pedis, Lat. — *Hellux*, Str. Dur., 331, 1, 125. — *Index*, Rol., 284, L, (*Index*).—*Second toe*, Ow., 63, 2, 553, (*Index*).—*First Hind-finger*, Tenney, Man. of Zoology, 22.—*Second digit*, Ow., 63, 2, 290, (*Index*). — *Second finger*, Van der Hoeven, 307, 743.—*Deuteros*, Wild., 67, *fere*.

Secundus, secundi, secundi, secundorum, secundal.

Tertius, (*dactylus medius*).

Digitus tertius pedis, Lat.—*Hillux*, Str. Dur., 331, 1, 125.—*Middle toe*, Ow., 63, 2, 309 (*medius*).—*Third toe*, Ow., 63, 2, 553.—*Third digit*, Ow., 63, 2, 308 (*medius*). —*Main toe*, Ow., 63, 2, 309. — *Tritos*, Wild., 67, *fere*.

Tertius, tertii, tertii, tertiorum, tertial.

Quartus, (*dactylus a quinto proximus*).

Digitus quartus pedis, Lat.—*Hollux*, Str. Dur., 331, 1, 125.—*Outer toe*, (with Birds) Ow., 63, 2, 83, (*quintus*).—*Fourth toe*, Ow., 63, 2, 309.—*Fourth digit*, Ow., 63, 2, 308.—*Tetratos*, Wild., 67, *fere*.

Quartus, quarti, quarti, quartorum, quartal.

QUINTUS (*dactylus fibularis*).

Digitus quintus pedis, Lat.—*Hallux*, Str. Dur., 331, 1, 125.—*Fifth digit*, Ow., 63, 2, 309, (*minimus*).—*Fifth toe*, Ow., 63, 2,309.—*Little toe, vulgo.*—*Outer toe*, Wym., 55, 277.—*Pemptos*, Wild., 67, *fere.*

Quintus. quinti, quinti, quintorum, quintal.

There remain for consideration the terms used to designate the following internodia; in the *armus*, the *carpus*, the *metacarpus*, and the *phalanges*; in the *skelos*, the *tarsus*, the *metatarsus*, and the *phalanges*; also the nodi which separate them and which are called carpo-metacarpal, metacarpo-phalangeal (or knuckle) and inter-phalangeal articulations of the armus, and tarso-metatarsal, metatarso-phalangeal and inter-phalangeal articulations of the skelos; there are obvious objections to all these terms, chiefly on the score of length, and the shorter terms of Hippotomy (cannon-bone, great and little pastern, and coffin-bone, etc.), are not available for our purpose. I am not prepared to suggest the technical terms which are needed, excepting in the case of the phalanges or digital and dactylic internodes. These are variously termed proximal, middle and distal, or first, second and third (proximal phalanx of the index, etc.), but all these terms are objectionable as to length, and the latter in that they do not indicate whether *first* is counted from the proximal or the distal extremity of the digit or dactyl. I would therefore suggest that the terminal phalanx of a digit or dactyl be called α (alpha), the middle one, β (beta), and the proximal, γ (gamma); the corresponding metacarpal bone may be called delta (Δ).[1] For the present, however, the above nomenclature should be employed *only when there are three* phalanges in the digit or dactyl; for when the number is less, we are not yet sure which is the missing one;[2] and when there are more, as with Cetacea, the homologous phalanges are undetermined.

To show what a reduction of labor and space is gained together with the greater definiteness, instead of saying that the Extensor indicis (of man) is inserted into the third phalanx of the fore-finger, we may now say that it is inserted into "α indicis."

There seems to be an ideal, if not a real, difference between the above mentioned segments of the manus and pes and those three primary segments which have been generally recognized; the same may be said of the articulations between these segments. And although upon strict anatomical grounds we must designate them also as "internodia"

[1] This is less complex and artificial than the nomenclature of the metacarpals and metatarsals proposed by Strauss-Durckheim, 331, 1, 116 and 124.

[2] This problem will be discussed hereafter.

and "nodi," yet for morphological purposes, we may indicate their nature as subdivisions of primary segments by calling them "pseudo-internodia" and "pseudo-nodi."[1]

III. NOMENCLATURE OF IDEAS.

During the early part of the present century all kinds and degrees of relationship between organisms and parts of organisms, were expressed by the single term *Analogy*, or by phrases which were even more indefinite; Swainson used the expression "immediate and remote analogy,"[2] but the distinction between these two relations was not at that time fully recognized even by the authors who have since done so much toward making it clear;[3] since 1846, however, these relationships have been generally admitted to be of two kinds, *homology*, or *affinity*, or *internal* or *structural resemblance* and *analogy* or *external* or *functional resemblance.*[4]

These two kinds of organic relationship have seemed to be the result of the operation of laws or principles, which, whether regarded as of material or divine origin, may be not irreverently called the two great commandments of Nature; the first is variously termed, the principle of *adherence to plan, type, pattern, or idea*; the second is called *adaptation to ends, to special uses, to final causes, etc.*; and by degrees the second has come to be included under the single term Teleology; the first under the less appropriate term Morphology; so that, speaking in the most general way, organisms which are *morphologically* or, for short, *morphically similar*, are *homologous*, and those which are *teleologically* or *telically similar*, are *analogous.*

But it is evident that each of these general terms includes several special kinds and degrees of relationship, and that these cannot all be equally manifested in the same organs, or attributes of organs; we should therefore endeavor to ascertain the respective criteria by which these degrees of relationship may be recognized. In short there remains to be done for Comparative Anatomy the kind of work which Agassiz has begun for Zoölogy; and we must aim to discover the morphic or taxonomic *values* of organs and systems of organs,

[1] A distinction between morphological and teleological joints was proposed by me in 45, 28, with respect to the radio-ulnar articulation; and this has been accepted by Coues, 70, 370.

[2] Cuvier; Anat. Comp.; t. VII, p. 164.

[3] Agassiz; Proc. Zool. Soc., 1834, p. 120; Owen; P. 1, s. 1830, p. 28; 1838, pp. 12, 109, 145, 146; 1842, pp. 36, note, and 143.

[4] Strickland, 343, Owen, 20, Agassiz, 325.

whether central or peripheral; of organisms which are low or high, ancient or recent, immature or adult; and of their various attributes, such as relative position, mode of development, chemical composition, size, form and color.

The following diagram (p. 179) is an attempt to indicate in concise form the work that has to be done in order to reduce our present confused notions of zoölogical and anatomical relationship to something like a logical coördination; it is essentially similar to one which was presented three years ago, 58, Lect. 1, and I have not attempted to incorporate in it the new and valuable ideas of Lankester, 257, and Mivart, 278. I am not now ready to state my grounds of difference from some of their views; and will merely express my gratification at this sign of the recognition of what is to be done, by the new and vigorous school of English anatomy.

For analogy and the categories thereof, see Agassiz, 201, chap. 2, sect. IX, 203, and the chapter on Morphology and Nomenclature, 200, 3, chap. 2, sect. IV. I shall confine myself to the discussion of homologies.

Plural or Relative Homology.

This is the relation between corresponding parts of *different* individuals; Geoffroy proposed to retain the term "analogie" for this relation and to employ "homologie" only for what is here named single or absolute homology; but the two terms were used indiscriminately until 1846, when Owen, 20, 175, proposed the name "special homology" for this relation, and "serial homology" for the other. Of course the correspondence between the zoölogical criteria of Agassiz, 201, 261 and 272, and the anatomical criteria, is provisional until the relative value of these criteria themselves is fully ascertained; but it appears to me that some good may follow their simultaneous presentation upon a diagram, even if it lead merely to a more general admission of the principle of subordination of characters.

I also venture to suggest that since the three higher groups are based upon *internal* structural features and the three lower groups upon *external* features, and since both *plan of structure* and *relative position* of organs, which are *branch* characters, and *outline* as determined by structure, and *relative size* of organs, which are family characters, are all alike displayed upon a transverse (vertico-lateral) section of the whole body, we may hereafter be able to say how the other two sections, (latero-longal and vertico-longal) correspond with the criteria of the class and genus, the order and species, respectively. Some other questions in this connection will be discussed hereafter.

TABLE OF THE SUB-DIVISIONS OF HOMOLOGY.[1]

PLURAL OR RELATIVE HOMOLOGY.

Zoölogical criteria.[2]		Anatomical criteria.	Characteristic section.	Kind of homology.	Examples: organs of
Plan of structure.	Inter-nal.	Relative position.	Vertico-lateral.	Branch.	Dog and Bird
Mode of execution.		Histological composition[3]	Latero-longal?	Class.	" " Bat
Complication of structure.		Chemical composition.[3]	Vertico-longal?	Ordinal.	" " Cat
Form determined by structure.	Exter-nal.	Relative size, natural attitude.	Vertico-lateral.	Family.	" " Lycaon
Ultimate structure.		Numerical composition.	Latero-longal?	Generic.	" " Wolf
Size, ornamentation, habit, etc.		Size, color, etc.	Vertico-longal?	Specific.	" " Dog

SINGLE, ABSOLUTE OR TROPICAL HOMOLOGY.

	Criteria.	Planes.	Kind of Homology.	Examples.
Serial homology or Syntropy.	Morphical parallelism on *same* side of planes.	Vertico-lateral.	Mekesyntropy.	Two thoracic ribs.
		Vertico-longal.	Platesyntropy.	Brachium and cubitum.
		Latero-longal.	Hypsesyntropy.	A rib and its cartilage.
	do. with *telical* antagonism.		Pseudantitropy.	Dorsal and ventral arches.
Polar homology, or Antitropy.	Morphical antagonism on *opposite* sides of planes.	Latero-longal.	Hypsetropy.	Male and female mammæ.
		Vertico-longal.	Platetropy.	Right and left manus.
		Vertico-lateral.	Meketropy.	Armus and skelos.

[1] For spherical homology, see the text, p. 180.

[2] According to Agassiz, 200 and 201, Chap. 2, Lect. vii.

[3] I am in doubt respecting the relative value of these attributes, and even whether some other should not be substituted for one or both of them. The mode of yolk segmentation should perhaps have place here, but that it is not a branch character; see Agassiz, 300 and 101, Chap. 3, Lect. i. See the text for full admission of the provisional nature of this table.

Single or Absolute or Tropical Homology.

Although the detailed comparison of the membra with each other was first made by Vicq d'Azyr, yet the germ of tropical homology existed in all recognitions of the correspondence of the right and left sides of the body; many and vague terms were employed (parallelism, analogy, homology, correspondence, repetition) which did not imply a difference between single and plural homology, or between the different kinds of the former. I hope hereafter to show that the same methods of comparison and argument are as applicable to single as to plural homology; and that cephalo-caudal repetition is comparable to dextro-sinistral repetition.

Spherical Homology.

Radiality, Ag., (Rem. on) 298, 279.—*Radiation*, Ag., 201, 292.—*Radial arrangement*, Rol., 294, CXLIII, CLVI.—*Radial symmetry*, Hux., 251, 46.—*Radiate symmetry*, Ag., 202, 33.—*Radial homology*, Miv., 278, 119.—*Spherical homology*, Wild., 58, Lect. 1.

Definition. The tropical relation between the morphically identical, converging spheromeres of a radiate animal.

Remark. The above definition is chiefly based upon the presentation of the subject by Agassiz especially in 200, 3, pp. 79, 260, 261, etc.; but there remains much to be done toward clearing up the confusion in which the whole subject now rests. In the first place two distinct ideas are included in the above list of terms; radiality is a general name for an *abstract idea* involving the plan of structure of a branch of the animal kingdom; Agassiz admits, 200, 3, 209, 210, 211, that upon this essential plan of radiality may be superinduced an apparent bilateral symmetry, but that he does not regard this as constituting a true bilaterality is shown by his contrasting the Radiates with bilateral animals, 200, 3, 260.[1]

But the very existence of such a radiate idea, is questioned by Morse, 281, 163, Clark, 211, 128, Huxley, 251, 47, and Rolleston, 294, CXLIII, who hold that the bilateral symmetry which is quite prominent in the larvæ of echinoderms is equally, if not more characteristic of the branch; some join the echinoderms with the worms, Rolleston, 294, 152, note; indeed so widely do they differ from Agassiz in respect to the classification of the invertebrates, that anything like

[1] Also by his remarks in the Report of the Trustees of the Mus. of Comp. Zool. 1868, p. 9.

a compromise upon a ground between the two extremes seems quite impossible.

I do not pretend to offer an opinion here, but have not yet seen reason for denying the existence of the radiate idea, and would refer to 45, 14, for suggestions as to a distinction between the morphical term "radiality" and the telical term, "radiation."

Agassiz evidently includes within the abstract idea of radiality, the existence of a real homology between the several spheromeres; but it is not clear whether the term "radiate" or "radial symmetry" means that each spheromere is symmetrical in itself as is believed by Pittard, 293, 850, or with its immediate neighbor, or "antitropically," as implied by Agassiz, 200, 3, 260; in short, when any two contiguous spheromeres are compared, do the inner and outer surfaces correspond together, as with two eyes, or does the inner surface of one correspond with the outer surface of the other, as with two successive thoracic ribs? is the homology antitropical or syntropical or only general?

Syntropy.

Serial homology, Ow., 20, 176; 63, 1, xiii.—*Symmetry*, Ow., Proc. Zool. Soc., 1831, p. 67.—*Homology*, Gervais, (?).—*Unreversed seria repetition*, Pitt., 293, 845.—*Homotypy*, Ow., 63, 2, 361.—*Irrelative repetition*, Ow., 63, 1, xiii.—*Reihenfolge oder Nachfolge*, Pagens., 54, 162.—*Serial symmetry*, Miv., 277, 292.—*Serial actinology*, Miv., 278, 120.—*Homoplastic serial homology*, Miv., 278, 119.—*Homogenetic serial homology*, Miv., 278, 119.—*Similar parallel repetition*, Coues, 70, 149.[1]

Syntropy, syntrope, syntropous, syntropic or syntropical.[2]

Definition. The morphotropic relation between parts upon the same side of a structural plane.

Example. See Mekesyntropy, Platesyntropy and Hypsesyntropy.

Mekesyntropy or Syntropy (μῆκος, length, and syntropy).

Irrelative or vegetative repetition, Ow., 20, 176, (1846), 63, xiii, (1866).—*Unreversed serial repetition*, Pitt., 298, 845, (1850).—*Serial homology*, Ow., 63, 1, xii (1866).—*Longiserial homology*, Wild., 58, Lect. 1, 1867.—*Homogenetic serial homology*, Miv., 278, 119 (1870).

[1] With few exceptions, the synonyms for the names of ideas are given in chronological order.

[2] The other terms may be similarly inflected.

Definition. The syntropical relation between parts upon the same side of the vertico-lateral plane.

Example. Two thoracic ribs or vertebræ.

Remark. Since this is the kind of syntropy which is most apparent and most commonly treated of, it may be allowable to use the shorter term syntropy for the longer one when no misunderstanding can arise.

Platesyntropy (πλάτος, breadth).

Actinology (*serial*, *correlated*, *etc.*), Miv., 278, 118.—*Latiserial homology*, Wild., 58, Lect. 1.

Definition. The morphotropical relation between parts upon the same side of the vertico-longal plane.

Examples. Brachium and cubitum; two right maxillary teeth; two dermal scuta of right side of armadillo.

Hypsesyntropy (ὕψος, height).

Vertiserial homology, Wild., 58, Lect. 1.
(Other synonyms will be included under Pseudantitropy).

Definition. The syntropical relation between parts upon one side of the longo-lateral plane, which, in vertebrates at least, I am inclined to believe should not bisect the body of a single individual into a dorsal and a ventral region, but should pass between *two individuals of opposite sexes*.

Examples. A rib and its cartilage; two muscular bundles of the same muscular segment (myocomma, Owen; myotome, Good s ı).

Remark. Probably no objection exists to giving the name proposed to the relation between a rib and its cartilage; for both lie ventrad of the vertebral axis; but so general is the impression that the vertebrate body presents a "dorso-ventral symmetry" (Macl., 23, 671; Pittard, 293, 851; Wyman, 55, 253; Spencer, 299, 2, 186; Coues, 70, 150), that it is not easy to show that this relation between organs lying upon *opposite* sides of the vertebral axis is really one of syntropy rather than of antitropy; yet I am convinced that this "symmetry" which is so striking in some fishes, is one of appearance chiefly and affects the external form only; certain it is that nothing like a real homology has ever been shown to exist between the internal organs of the dorsal and ventral regions; and the development of the ovum results in a differentiation of dorsal from ventral, which is not suggestive of any such homologous relation as is so apparent between right and left, or between cephalic and cercal, regions.

This important question will be hereafter indicated as one of the problems to be solved. At present, I will only state my conviction that the complete vertebrate *animal* consists of two *individuals* of different sexes placed face to face;[1] there then results a true antitropical homology in all three directions corresponding with the three diameters of a solid; a lateral homology or "platetropy" between two right and left halves of this compound individual, a longal homology or "meketropy" between its cephalic and cercal regions, and a vertical homology or "hypsetropy" between the dorsal regions of the two individuals and between the ventral regions in like manner, as in fig. 2. Such a homology of three directions might be exemplified in a perfect double monster by "anterior duplicity," described and figured as "Zipophage" by St. Hilaire, 235, Pl. XIV, fig. 3.[2]

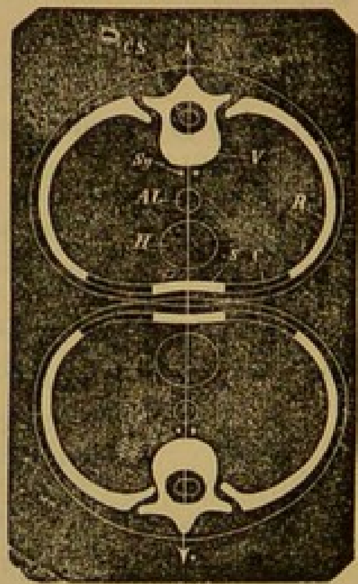


Fig. 2.

PSEUDANTITROPY.

Polar relation of back and belly, Oken, 285, Par. 2093, (1810).—*Dorso-ventral symmetry*, Macl., 22, 667, (1849).—*Antero-posterior symmetry*, Pitt., 293, 851, (1850).—*Tergality* (in part), Ag., (Rem. on) 298, 279, (1861).—*Dorso-ventral polarity*, Dana, 218, 351, (1863).—*Verticality* (in part), Wild., 45, 14, (1865).—*Bipolarity*, Clark, 211, 265, (1865).—*Vertipolar homology* (in part), Wild., 58, Lect. 1, (1867).—*Vertical homology*, Miv., 278, 120, (1870).—*Dorso-abdominal*

[1] Prior suggestions of this idea are contained in Par., 2955 of 285: but indeed, there are few morphological ideas of the present day, germs of which cannot be found in the extraordinary work here cited; and although it is not altogether satisfactory to find one's most valued conceptions thus ambiguously anticipated, no worker in homology should try to lessen Oken's just fame, or hold any other than the opinion which one of his greatest pupils has given us concerning his work. Agassiz, 200, and 201, chap. III, Sect. V.

[2] This would be a *Dicephalus tetrabrachius tetrapus*, in the nomenclature of Fisher, 229, 61.

symmetry, Coues, 70, 150, (1870).—*Supero-inferior symmetry*, Coues, 70, 150, (1870.)— *Correlated serial secondary actinology*, Miv., 278, 120, (1870).—*Vertical symmetry*, Miv., 279, 165, (1871).—*Intrinsic bilateral symmetry* (of membra), Fols., 40, (?),[1] (1864).—*Antitropy*, (?) (with Radiates), Ag., 200, 3, 260.

Definition. The *apparently antitropic* relation between parts which are *telically opposed* to each other, but lie upon the *same* side of a structural plane.

Examples. Of *vertical pseudantitropy*, the dorsal and hæmal arches and the dorsal and anal fins; of *longitudinal pseudantitropy*, corresponding maxillary and mandibular teeth; the anterior and posteror ends of the sternum in many quadrupeds; the prearmal and postarmal borders of manus (as of *Chelydra serpentina*, Flow., 71, 253); of *lateral pseudantitropy*, the inner and outer canthi of the eye; the opposite sides of an apparently bilateral radiate, (Ag., 200, 3, woodcuts 88–91).

Remark. The question involved here has been indicated under hypsesyntropy and spherical homology.* No doubt it will appear to many that it is a question of words rather than of facts; but until I am convinced that *ideas* are not embodied in material forms, I shall aim to at least show what confusion we are now in respecting the nomenclature of both the ideas and the forms.

Antitropy.

Homologie symmetrique, Foltz, 39, 51, (1863).—*Symmetrie*, Flour., 228, *fere*, (1844). —*Duplicity*, Ok., 285, Par. 78, (1810).—*Polarity*, Ok., 285, Par. 76, (1810).—*Antitropy* (?), Schimper and Braun, (?).—*Symmetry*, Ok., 285, Par. 2096, (1810).—*Respective symmetry*, Architecture.—*Antitropic relation*, (?), Ag., 200, 3, 260, (1860).—*Laterality*, Ag., (Rem. on), 298, 279, (1861).— *Anatomical symmetry*, Fols., 40 (?), (1864).—*Antitypy*, Wild., 45, 15, (1865).—*Polar homology*, Wild., 45, 14, (1865).— *Opposition oder Spiegelwilde*, Pagens., 54, 162, (1867).— *Polar antitypy*, Coues, 70, 372, (1870).— *Reversed repetition*,[2] Coues, 70, 152, (1870).—*General antagonism*, ib., 193.—*Antitypical correlation*, ib., 222.—*Repetitive homology*, ib., 398.—*Opposite reversed repetition*, ib., 149.—*Symmetrical repetition*, ib., 149.—*True symmetrical antagonism*, ib., 149.

[1] Here, as generally elsewhere, when an interrogation point stands for the number of the page, it is because I have only manuscript copies of the papers referred to.

[2] These are rather definitions than real synonyms.

DEFINITION. The morphotropic relation between parts upon opposite sides of structural planes.

EXAMPLE. See *hypsetropy*, *meketropy* and *platetropy*.

No better evidence of the need for a uniform and simple terminology of ideas could be asked, than is given by the above synonomy; but it will be observed that the third and fourth terms mean something more than the rest; it is difficult to say just what Oken meant by *duplicity* and indeed many of the great physiophilosopher's expressions are beyond strict logical interpretation, although it is evident that he inwardly perceived much more than he was able to express in definite terms; his Physiophilosophy "was written in a kind of inspiration," (as he admits in the preface to the English translation), and inspiration is only suggestive in science, never conclusive; his term *polarity* too is used in many different senses, and Wyman has well said, 55, 257, that "it does not appear precisely what he meant by the word "pole.'"

At any rate polarity (and, perhaps duplicity) is the name for a general law of organization which is analogous to the physical polar force, Wyman, 55, 254; the result of its undisturbed action would be an absolute symmetry; the one is a *cause*, the other the effect of its *action*; and all the other terms given in our list are synonyms of symmetry, and not of polarity; I do not propose a name for the force for it is not yet understood; but I would urge that symmetry is ineligible as a technical term on account of its common use in several other senses; of all the other terms antitropy seems to express most clearly the idea we wish to convey, a respective symmetry of structure and not necessarily of external form; for this latter is early and most extensively modified by the telical antagonist of our hypothetical "polar force," the so-called "vital force." See Wyman, 55, 258.

But while antitropy seems best adapted for our purpose, it is not quite clear that those who have already employed it have meant to convey the precise idea which we have under consideration; I have not been able to obtain the works of Schimper and Braun, but I judge that they used antitropy to designate any antagonistic relation between parts of the plant embryo, and between opposite leaves upon the stem, although I am not sure that they always included an idea of real homology in this antagonism of position; Agassiz has used the term antitropy to express the relation between spheromeres upon opposite sides of a radiate, 200, 3, 260; and here, of course, the general homology is perfect, but as he discriminates between the radiates and the bilateral animals of the other branches, it would seem better to call this relation of opposite spheromeres, simply *symmetry*, or perhaps *pseudantitropy*, and to confine antitropy to the three higher branches; for otherwise, we should have to devise another and different term for the relation in them; laterality does not seem quite suitable, because, as used by Agassiz, (Rem. on 278, 279), "it relates to the disposition of organs upon *any two sides* of the body, without reference to symmetry"; and it is not evident that the idea of real homology is included in this laterality.

Platetropy.

Symmetrie, Fr.—*Symmetrie*, Ger.—*Symmetria*, Lat.—*Symmetry*, (in part), Most authors.—*Respective symmetry*, Architecture.—*Lateral symmetry*, Ok., 285, Par. 2114, (1810).—*Bilateral symmetry*, Ag., (Rem. on) 298, (1861).—*Homologie symetrique laterale*, Foltz, 39, 51, (1863).—*Bilaterality*, Clark, 211, 265, (1865).—*Latitypy*, Wild., 45, 14, (1865).—*Right and left symmetry*, Wy., 55, 254, (1867).—*Latipolar homology*, Wild., 58, Lect. 1, (1867).—*Lateral homology*, Miv., 278, 119, (1870).—*Lateritypy*, Coues, 70, 151, (1870).—*Transverse symmetrical repetition*, Coues, 70, 150, (1870).—*Transverse polar antagonism*, Coues, 70, 150, (1870).—*Latitropy*, Wild., 74, *fere*, (1871)

Definition. The antitropical relation between parts upon opposite sides of the longo-vertical plane.

Example. The relation between the right and left ear, nostril or kidney.

Remark. This kind of symmetry is so evident with the majority of vertebrates and articulates, and with many mollusks and apparently with some radiates, that it is generally recognized and even thought to be absolute in some cases. But the perfect symmetry of crystals is never realized, according to high authorities, and Wyman, 55, 247, says "it may be doubted whether absolute symmetry exists anywhere." In 312, I have given instances of deviations from symmetry from many groups of animals, and have thus tried to bridge over from one side the gulf which is generally supposed to wholly separate lateral symmetry (platetropy) from longal symmetry (meketropy); the corresponding work from the other side will consist in the presentation of evidence of the close homology which, in many cases, exists between parts at the two ends of the body; and the first step toward this is to recognize that *morphically*, as shown upon the diagram, these two regions are to each other, as are the right and left sides.

Hypsetropy.

Sexual homology, Wild., 58, Lect. 1.— *Dual homology*, Wild., 58, Lect. 1.

Definition. The antitropical relation between parts of the two sexes, when facing each other.

Example. The male and female mammary glands; sterna, etc.

Remark. This kind of homology often but not necessarily includes the idea of inserted development; the difference between it and the apparent dorso-abdominal homology within a single individual has been already indicated, [p. 183].

Meketropy.

Symmetry in length, Ok., 285, 2114.—*Anterior and posterior symmetry*, Wy., 35, 317.—*Fore and hind symmetry*, Wy., 49, 176.—*Antero-posterior symmetry*, Wy., 55, 277.—*Fore and aft polarity*, Dana, 218, 351.—*Antero-posterior polarity*, Dana, 218, 351.—*Cephality*, (?), Ag., (Rem. on), 298.— *Longitudinal homology*, Wild., 45, 14.—*Longitypy*, Wild., 45, 15.— *Anterior and posterior repetition*, Wild., 45, 17.— *Longitudinal polarity*, Wild., 50, 194.—*Longitudinal symmetry*, Coues, 70, 149.—*Longitudinal antitypy*, Coues, 70, 151.—*Symmetry at opposite ends*, Ogilvie, 283, 156.—*Longitropy*, Wild., 74, *fere*.—*Symmetry of superior and inferior regions*, Gerdy, 9, (?).—*Homologie symmétrique du meme côté*, Foltz, 39, 420.—*Homotypy* (*implied in homotype*), Wy., 55, *fere*.

Definition. The morphotropical relation between parts upon opposite sides of a vertical lateral plane.

Example. The cephalic and caudal regions of an embryo; the armus and skelos; a double-ended ferry-boat offers a familiar example of meketropy.

Remark. Vague suggestions of a polar or symmetrical relation between the anterior and posterior regions of the vertebrate body are contained in the writings of Oken. "The idea underlying his statement that the two ends of the body do repeat each other, is we believe, correct;" Wyman, 55, 257. Duges (Traité de Phys. Comp.

2, 204), seems to have noted the antagonistic relation of the ancon and genu and Humphrey, 36, 14, admitted a functional antagonism of the proximal parts of the membra; Gerdy, 9, (?), had already taken an artistic view of the symmetrical relation of the two ends of the body which he called "superior" and "inferior," which, like Humphrey, he traced in the proximal parts of the membra. Agassiz probably included under the term cephality an idea of homology, but it is not distinctly expressed by him or by Dana; and the idea of a symmetrical homology between parts at the two poles of a longitudinal axis has been evolved into something like clearness by Wyman and his pupils. All the arguments in favor of the generic term antitropy, apply with even greater force to the specific term meketropy, for otherwise a compound term would be required.

IV. THE MORPHOLOGICAL UNIMPORTANCE OF NUMERICAL COMPOSITION.

The familiar fact that with most Mammalia the pollical and primal phalanges are only two in number, while the other digits and dactyls possess three, forms the chief difficulty with those who are asked to consider pollex the meketrope of quintus and primus that of minimus; and it forms the only difficulty with those who have already recognized the fallacy of the objections generally urged upon the ground of the *size* and *natural attitude* of the parts; evidently then, the removal of this difficulty is of the utmost importance.

Here, as generally throughout this paper, the facts and conclusions will be given with reference to the Mammalia; partly because that class has afforded me the most material, but chiefly because the three grand difficulties already mentioned are especially manifest in the higher vertebrates; and I am convinced that they never would have prevented our recognition of meketropy in the membra, had we been lizards or turtles instead of primates.

It cannot be denied that some significance must attach to numerical composition of organs; since, aside from the symbolic character which many believe them to possess, the very constancy of numbers is a remarkable fact in Natural History. But for the general rule that the mammalian cervix consists of seven vertebræ, it is probable that no effort would be made (as by Thomas Bell, Trans. Zool. Soc., vol. I)to show that *Bradypus tridactylus* has but seven, instead of nine, as believed by Turner and Owen; and there would be nothing strange in the fact that *Cholœpus Hoffmanni* has but six cervical vertebræ; on the other hand, the value of this as even a generic character seems to be destroyed by the fact, that another species of the same genus (*C. didactylus*) has the usual number.

Again, it is stated by Mosely and Lankester, that the mole is the only placental mammal with eight intermaxillary teeth; and the exception is equally inexplicable with those of the vertebræ, since that, animal shows comparatively little more affinity with the marsupials, than the sloth shows to the birds.

Again, it is stated by Argyll (204. 223) that the number of tail and wing feathers is constant throughout the Trochilidæ, although 430 species are already known.

Finally, the constancy in the number of mammalian digits is so absolute, that not only do we exclude from the category all "sixth fingers and toes," but we give no heed to the ossicle which projects from the ulnar border of the carpus in Chelone (63, 1, 173) and in many Cetacea (63, 2, 427), and call it "pisiform," although it looks as much like a digital metacarpal as some which are generally accepted as such; and, indeed, so convinced are we that five is the maximum normal number of these parts, that we hardly wonder to find that the required expansion of the manus with the mole and the Yapock opossum is gained, not by the addition of a sixth digit, but by the excessive development of a carpal ossicle.

We must admit, therefore, that numerical composition means *something*; perhaps more in some cases than in others; *how much* it means is difficult to determine; probably, however, not as much as relative normal position.

The following citations from authors are sufficient to show the present obscurity of this subject.

"The examination of the skeleton (of fishes) has led to the conclusion that the number of vertebræ is another character of great importance for the distinction of families; but whether it has any bearing of still greater import, cannot be exactly determined at present."[1]

Owen says, (63, 1, 42), "The number of trunk vertebræ is useful as a specific character in Icthyology."

Agassiz writes as follows (200, 4, 64), respecting the zoological importance of this attribute with radiates; "I would remind the reader of the little value which *numerical differences* undoubtedly have in this question, notwithstanding the constancy of the number of parts in most of the radiates; for though the number five is the typical number among echinoderms, there are crinoids and starfishes and even echinoids, with four and six spheromeres, and others with

[1] Gunther; Cat. of Acanth. Fishes, 1861, Preface.

an unusually large number; and though the number four and its multiples are the typical numbers of acalephs, we find those which have five or six spheromeres and other numerical combinations. We need not therefore hesitate to compare an Aurelia with a quadripartite and an Echinarachinus with a quinquepartite arrangement of parts;" again, (200, 4, 379) "as soon as we can free ourselves from the belief that histological complication and structural differentiation are positive tests of homological relationships, and as soon as we allow full weight to embryological evidence, the close affinities of the echinoderms and the other classes of radiates becomes self-evident."

Spencer uses the following very suggestive language, which I accept as true, omitting his conclusion as to the *cause* of the superinduced segmentation, (299, 2, 110) ; "The parts composing the supposed archetypal vertebræ" (of Owen) "are constant neither in their number nor in their relative" (natural) "position, nor in their modes of ossification, nor in the separateness of their several individualities when present; . . . . everything goes to show that the segmental composition which characterizes the apparatus of external relation in most vertebrates is functionally determined or adaptive."

Finally, Thomas Bell remarks, "the laws which regulate the numerical variations in the different systems of organs in an animal, are perhaps less defined or at least less understood than those which relate to many other conditions of their existence." [1]

Coming now to our special point, we may enumerate the morphical relations of the digits as follows, taking the medius for an example, since there has never been a doubt respecting its homology with tertius, and both these are present in every known manus.

1. Its special or plural homology with the medius of other Mammalia. (Fig. 2, A-B)

2. Its single, serial and longal homology or *mekesyntropy*, with its fellow-digits of the same manus. (C-D).

3. Its single and vertical homology, *hypsetropy* with the medius of an individual of the opposite sex. (E-F).

4. Its single and lateral homology, *platetropy* with the medius of the opposite side. (G-H).

5. Its single and longal homology, *meketropy*, with the middle dactyl, tertius. (G-I).

Now although all these five relations are between a single digit and another digit or dactyl, yet the relations of the several regions

[1] Trans. Zool. Soc., vol. I, p. 133, 1833.

or surfaces of the digits compared are quite distinct, as shown by the figure. In plural homology and in mekesyntropy, the premembral surface of the one corresponds to that of the other, the dorsal surface of the one to that of the other as if both occupied the same place, or were merely superposed, as with geometrical comparisons of similar figures; but with the three antitropical homologies, corresponding parts look in opposite directions; so that with platetropy, the right and left digits are as if placed base to base, or tip to tip, with hypsetropy as if placed back to back or palm to palm, and with meketropy as if placed side by side; but the two *contiguous* surfaces then correspond. In case the normal position of the membra should be determined to be other than it is here assumed to be, a corresponding change would be made with the surfaces compared together; for instance, if the digits were made to point backward and the dactyls forward, their bases and tips would be related meketropically instead of platetropically, while their opposite sides would be related platetropically instead of meketropically; and although this would be a matter of little consequence as regards a single and simple part like a digit, yet when we have to compare such parts as tarsus and carpus, and muscular organs, misunderstanding can be avoided only by regarding the membra as always in the same normal position.

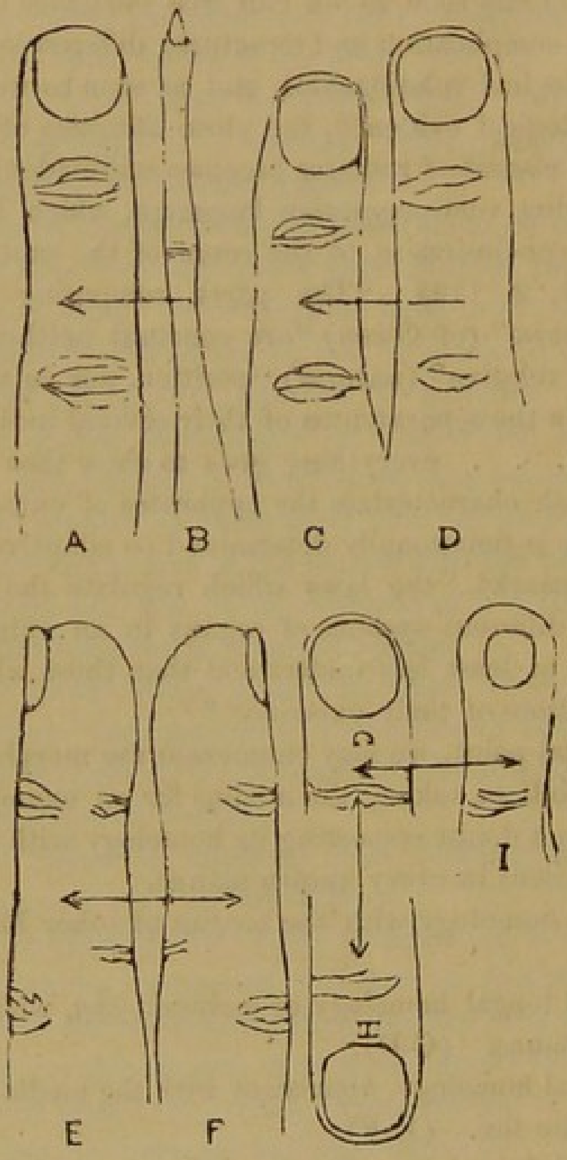


Fig. 3.

Now since these five relations above described, however they may differ among themselves as to the particular regions of two parts which are compared together, are all relations of *homology*, it may probably be taken for granted that whatever criteria are accepted for one kind of homology, are equally applicable to the rest; excepting, of course, the tropical relations which depend upon the position of the parts with reference to the axis of the body. If this is granted, then, we are entitled to employ the arguments used in deciding any one of the relations upon which there is now no dispute, in determining those now under consideration.

For instance, the tertius of a seal is determined to be the plural homologue of the middle dactyl of a rhinoceros, not from its size or function, but from its relative position in the pes; the tertius of man is held to be the meketrope of the medius, from their similar relative position, although the one is a short dactyle, and the other is the longest digit; again, the primus of man is held to be homologous with the primus of a bat, although they differ not only in size and function, but in their apparent relative position, since the human primus is on the inner border of the pes, and that of the bat becomes the "outer toe" through the complete eversion of the skelos; we here see that relative normal position is of superior morphical value to size, function, and natural attitude; finally, the homology between the human primus and that of an orang has never been questioned, although the latter often, if not generally, consists of but a single phalanx; the homology between the minimus of an ordinary mammal and that of a bat has never been denied, although the latter rarely, if ever, consists of the usual number of phalanges; no one has even doubted the entire homology of the five digits of many tortoises, (Ow., 63, 1, p. 173) with those of the Mammalia, as is shown by the use of the same names (pollex, etc.,) yet none of the former have more than two phalanges; a like discrepancy exists with the birds; and, if, as I am willing to admit, it is better to confine the comparisons to the Mammalia, an even more striking case is offered by many Cetacea, where the digits are enumerated from one to five, (or styled pollex, etc.,) and where the subdivisions of the digits are invariably called phalanges, although in some cases, as in the round-headed dolphin, (*Globiocephalus melas*), the medius may possess eight and the index twelve of them, and although the form, function, and attitude of the entire manus be unlike that of man.

It appears therefore, that in the determination of all kinds of homologies, the relative normal position has been found to be of greater morphical value than size, than function, than natural attitude, and finally than even numerical composition; and yet, when we ask anatomists to consider the other evidences of meketropy, which are presented by the development and structure of the body, and show that even the adult membra offer no difficulties in their proximal portions, and that in the embryo, no difference of size or segmentation exists in the manus and pes, they hold to the syntropical comparison, partly because of its antiquity and general acceptation; partly because of the similarity of pollex and primus in that morphological anomaly, the human body; partly because in the natural attitude of the manus with quadrupeds, the pollex becomes the inner digit like the primus; but chiefly because with many Mammalia pollex and primus differ in numerical composition from the other digits and dactyls : and this in spite of the fact that for the determination of every other case of homology, all these considerations have been set aside in favor of the single character, relative normal position.

In reference to this question, some other facts and arguments should be considered.

1. That with most members of the group called Perissodactyla, (Ow., 62, 2, 283; Fl., 71, 3,) including the existing genera Rhinosceros, Hyrax, Tapirus, and Equus, and many extinct genera, the pollex and minimus, the primus and quintus are wanting,[1] so that, were the problem to be decided for them alone, no objection would arise respecting these outer digits and dactyls; and the argument that such a question cannot be decided upon evidence drawn from a single group, applies with equal force to the consideration of the Mammalia alone out of all the vertebrate branch; and, as has been already stated, the objection derived from the numerical composition of certain digits and dactyls, would never have arisen among the members of the lower classes of vertebrates.

2. That it is not yet determined whether the so-called pollical metacarpal (⊿ pollicis) and primal metatarsal (⊿ primi) should not be regarded rather as proximal *phalanges* of the pollex and primus, as Oken (284, Par. 2382) and Maclise (23, 663) are inclined to believe; this view is not obviously inconsistent with the observations of Thomson and Humphrey (305) upon the mode of ossification of these parts, and Flower admits (71, 255) that the question is not decided.

[1] Tapirus retains the minimus and Hyrax the minimus and a rudimentary pollex.

3. That in a few cases, the human pollex has consisted of three phalanges, and so resembled the other digits and the quintus; such a case figured by Annandale,[1] who adds that he has met with others; Dubois describes a case[2] which is referred to by Fort[3]; and in the Cabinet of the Boston Society for Medical Improvement, is a plaster cast of another case which came under the observation of Dr. B. E. Cotting, and was described by Dr. J. B. S. Jackson.[4] Dr. Fort mentions other instances of an unusual increase or decrease in the number of digital phalanges.

4. That all the digits and dactyls may possess less than three phalanges, as in Chrysochloris, while in Cetacea all of them may possess more than that number.

5. That in many Mammalia the number of minimal and quintal phalanges is less than three; which removes, so far as those species are concerned, the objection to homologizing minimus and quintus with primus and pollex; the following list gives the species, the number of phalanges, and the authority for the statement; no reference is made to the many species in which the minimus and quintus are wholly wanting, or represented only by a metacarpal or metatarsal. The Cetecea are enumerated in a separate table, since their digital phalanges generally vary from the usual number with Mammalia.

	POLLEX.	
Ateles.	1 or 0	Fl., 71, 258.
Colobus.	1	" "
Elephas.	1	Hum., 36, 5.
	INDEX.	
Perodicticus.	2	Fl., 71, 258.
Arctocebus,	2	Miv., 276, 325.
Cheiroptera (generally).	2	Fl., 71, 262.
Chrysochloris.	2	Miv., Journ. of Anat. and Phys. 2, 133.
	MEDIUS.	
Chrysochloris.	2	Miv., Journ. of Anat. and Phys., 2, 133.
Pteropinæ.	2	Fl., 71, 262.
	ANNULARIS.	
Cheiroptera, (generally).	2	Fl., 71, 262.

[1] Malformation of fingers and toes; p. 29; pl. ii, fig. 19.
[2] Archives de Medicin, Apr., 1826.
[3] Difformités des doigts, p. 59, 1869.
[4] Catalogue of Museum of Med. Imp. Soc., p. 871.

MINIMUS.

Cheiroptera (generally)[1].	2	Fl., 71, 262.
Chrysochloris.	2	Miv., J. of A. and P., 2, 133.
Rhynchocyon.	2	Ow., 63, 2, 390.
Hyrax dorsalis.[2]	2	Fl., 71, 293.
Periodontes (Dasypus) sexcinctus.	2	Ow., 63, 2, 408; Fl., 71, 277.
Megatherium Americanum.	2	Ow., 63, 2, 412.
Myrmecophaga jubata.	2	Ow., 63, 2, 410.
" didactyla.	2	Fl., 71, 275.

Table giving the number of digital phalanges with some species of Cetacea.

Species.	P.	I.	M.	A.	Min.	*Authority.*
Balæna mysticetus	0	3	4	3	2	Esch. and Reinh: Ray Soc. Mems., 129.
Balænoptera Bonærensis	0	4	3	2	2	? Proc. Zool. Soc., 1867, 712.
" musculus	0	5	6	7	4	Lillej. Ray Soc. Mems. 260.
" laticeps	0	3	6	5	2	" " " " 271.
" rostrata	0	4	7	6	3	" " " "
" "	0	3	7	6	4	" " " "
Physalus antiquorum	0	4	5	5	3	Flow. Proc. Zool. Soc., ? 1864, 413.
" "	0	2	7	6	3[3]	Flow. Proc. Zool. Soc. 1864, 413.
" sibbaldii.	0	4	5	5	3	Flow. Proc. Zool. Soc. 1865, 473.
Sibbaldius ?	0	3	3	6	3	Flow. Proc. Zool. Soc. 1864, 398.
Catodon macrocephalus	3	4	4	4	3	Gray, P. Z. S. 1864, 233.
Physeter "	1	5	5	4	3	Fl. T. Z. S. v. pl. 61.
" (euphysetes) simus	3	6	4	3	3	? T. Z. S. vi., pl. 2.
Euphysetes ?	0[4]	7	5	5	4	Burmeister, P. Z. S., 1865, p. 712.
" grayii	2	5	4	4	2	Owen, T. Z. Soc. vi., p. 43.
Delphinus orca	2	6	4	3	2	Esch. Ray Soc. Mems., 173.
" sinensis	0	6	5	2	1	Flow. T. Z. S., vii., 158.
" leucas	1	5	4	3	3	Lillej. Ray Soc. Mems., 243.
" griseus	2	8	7	2	1	Cuv; qu. in Ray Mems., 214.
Globiocephalus (?)	4[5]	14	10	3	2	Reinh. Ray Soc. Mems., 213.
" mellas	3	12	8	2	0	Flower, 71, 271.
Clymene similis	2	7	3	7	0	Gray, P. Z. S. 1868, 148.
Inia Geoffroy ensis	0	5	4	2	2	(?) T. Z. S. VI, pl. 25.
Orca (?)	2	7	4	3	2	Reinh. Ray Soc. Mems., 214.
" gladiator	1	6[6]	4	3	1[7]	Lillej. Ray Soc. Mems., 234.
" schlegellii	1	5	3	2	1	Lillej, Ray Soc. Mems., 237.
Pseudorca crassidens	2	7	6	3	2	Reinh. Ray Soc. Mems., 213.
Pontoporia Blainvillii	0	6	6	3	2	Burm. P. Z. S. 1867, 487.
Hyperodon rostratus	1	6	5	2	1	Lillej. Ray Soc. Mems., 248.

[1] Mystacina has three according to Tomes.
[2] *Hyrax capensis* has the usual number.
[3] These digits were articulated artificially, so the observer had some doubts respecting the number of phalanges.
[4] The figure (from a photograph) does not show clearly whether there is a phalanx attached to the metarpal pollicis.
[5] The left pollex had three phalanges.
[6] The index may have had seven and the minimus two.

The foregoing tables are suggestive of some other considerations bearing more or less directly upon intermembral homologies.

1. From the nature of the parts, especially in Cetacea, and also from the admissions of some observers, it is not always easy to ascertain the number of digital phalanges; it appears also, that the possible morphical value of such information has not always been recognized by observers, by reason of the slight telical importance of the individual phalanges; but on the other hand, some have been so accurate as to note a difference in the numerical composition of the same digit upon the two sides of the body: (as with the Globiocephalus described by Reinhardt).

2. The distinctions between metacarpals and phalanges, in respect to length and mobility, which exist with the higher Mammalia, do not appear with the Cetacea; with *Glob. swineval*, according to Macallister, (P. Z. S., 1867, p. 481), the exact "number of phalanges could not be reckoned," and the only synovial capsule was at the omos; and in describing the armus of *Balæna mysticetus*, Eschricht and Reinhardt state that the minimus "is in direct contact with the ulna," . . . and they are led to suppose that "not only the carpus and digits, but also the bones of the forearm have all been formed in the beginning from one continuous cartilage, and that, at all events, we cannot here expect fixed or quite immutable relations between individual bones." (Ray Soc. Mem., p. 131.)

3. While there seems to be no objection to admitting the special homology of the cetacean *digits* with those of other Mammalia, there appears to be no way of determining the special homology of individual phalanges even within the Cetacea themselves; for, allowing a margin for inaccuracies of observation and statement, there is nevertheless a considerable discrepancy in this respect between members not only of the same order and family, but also of the same genus (*Delphinus*, for instance) and species (*Physalus antiquorum*).

4. The taxonomic value of the numerical composition of the digits must be regarded as very low with the Cetacea; it may be said that this conclusion would not necessarily apply to the other Mammalia, but it would not be easy to prove this, since they are members of one and the same class; the Cetacea do not present exactly the case of the Cheiroptera, because the usual number, three, is never exceeded in this group, and although it is not now certain which of the phalanges is missing, yet there appears to be no reason why this matter may not some time be decided; but I see no way of ascertain-

ing the special homology between the twelve indical phalanges of *Globiocephalus melas* and the three of an ordinary mammal.

5. It might be thought that such lack of special homology between the cetacean digits and that of other Mammalia, indicated the propriety of regarding the former as forming a subclass; but this at once brings up another consideration.

NUMBER OF VERTEBRÆ.

The number of vertebræ (excepting the cervical), differs greatly among the ordinary Mammalia, as is stated in all works upon comparative anatomy; from various authorities, chiefly Owen, 63, 2, and Flower, 71, I have prepared a table showing the number of cervical, thoracic, lumbar, sacral and caudal vertebræ of many species of Mammalia, (105 species representing 91 genera) ; the cervical vertebræ are seven in all excepting in *Manatus* (6) and *Cholœpus Hoffmanni* (6) and *Bradypus tridactylus* (9); but there is evidently room for different interpretations of the facts in these cases.

The same is the case with the enumeration of the sacral and caudal vertebræ, but the variations in their number are so great and so generally recognized that a tabular statement is not required in this connection. I wish here, however, to ask whether the immense elongation of the tail in many species is primordial or secondary; and if the latter, whether the increase is by gradual development of new segments or by the increase in size of some which are formed all together at the front; upon the answer to this question, might be based a discrimination between the segments which immediately succeed the sacrum, and have the *structure* of vertebræ, and those more simple cylinders of bone which have no claim to the title of vertebra beyond their serial relation to the former.

In any case, the numerical variation of a peripheral part like the tail, would not have a greater morphical significance than that of the phalanges.

But with the so-called *trunk vertebræ* the case is very different; they are the central portion of the skeleton, whether from side to side, from back to belly, from head to tail; and there is no obvious reason why their number should not be constant, or at least as much so as that of the cervical vertebræ, since the degrees of mobility required of the latter in different species, are far more numerous and decided than appear to be required from the trunk; yet no such constancy exists, even with species of the same family and genus, as is shown by the following table of the thoracic and lumbar vertebræ. The conflicting statements of different authorities may be due to a different interpretation of facts, but I am quite prepared to suppose that in some cases, really individual differences existed between the specimens examined.

Table showing the number of trunk-vertebra with Mammalia.[1]

LEMURIDÆ.	D.	L.		
Tarsius spectrum.	13	6	19	Owen.
Perodicticus Potto	16	6	22	" (or 15-7,—22).
Stenops gracilis	15	9	24	"
" tardigradus	16	8	24	"
Otolicnus peli	13	7	20	"
" crassicaudatus	13	6	19	"
Lichanotus Indri	13	8	21	" (or 12-9,—21).
Loris	14	9	23	Miv. (or 15-9,—24).
Cheiromys madagascariensis	13	6	19	Owen.
Arctocebus	15	?		Mivart.
Nycticebus	16	8	24	"
Hapalemur	12	7	19	"
Microcebus pusillus	13	7	20	"
Cheirogaleus millii	13	7	20	"
Lemur (?)	13	6	19	Owen.

CARNIVORA.	D.	L.		
Canis (lupus, rufus and familiaris)	13	7	20	Owen.
Ursus (generally)	14	6	20	"
" labiatus	15	5	20	"
Hyæna vulgaris and crocuta	15	5	20	"
Felis (generally)	13	7	20	"
Procyon lotor	14	6	20	Flower.
Nasua	14	6	20	"
Meles	15	5	20	"
Phoca grœnlandica.	15	5	20	Owen (or 14, 5,—19).
Stenorrhynchus serridens	15	5	20	"
Otaria	15	5	20	Flower.
Crystophora	15	5	20	"
Callorrhinus ursinus	15	5	20	Allen, J. A.
Eumetopias Stelleri	15	5	20	"
Putorius erminius	14	6	20	Owen.
Mustela zibellina	14	6	20	"
Trichecus rosmarus	15	5	20	"
Mephitis	16	6	22	
Mellivora	14	4	18	

[1] The materials are drawn chiefly from four works; Owen, 63, 2; Flower, 71; Mivart, Osteology of the Insectivora, Journ. of Anat. and Phys.; and Mivart, Ost. of Lemuridæ, Proc. Zool. Soc., Dec. 12, 1867.

INSECTIVORA.

	D.	L.		
Erinaceus	15	6	21	Flower.
Talpa europæa	16	6	22	"
Sorex	15	6	21	Mivart (or 13-5—18).
Centetes	19	5	24	Owen.
Tupaia	13	5	18	Flower.
Macroscelides	13	7	20	Owen.
Chrysochloris	19	3	22	Flower.
Potomogale	16	5	21	Mivart.
Echinops	16	6	22	" (or 17-5—22).
Rhynchocyon	13	8	21	" (quot. Peters).
Gymnura	15	5	20	"
Scalops	14	5	19	"
Urotrichus	13	7	20	"
Myogale	13	6	19	" (or 14-5---19).
Galeopithecus [1]	14	5	19	"
"	14	6	20	Owen (or 13-7—20).

CHEIROPTERA.

	D.	L.		
Vespertilio murinus	12	7	19	Owen.
Pteropus fuscus	14	5	19	"

ARTIODACTYLA.

	D.	L.		
Sus scrofa	13	6	19	Owen.
Dicotyles	14	5	19	"
Hippopotamus amphibius	15	4	19	"
Camelus bactrianus	12	7	19	"
" dromedarius	12	7	19	"
Auchenia	12	7	19	"
Bos taurus	13	6	19	"
" europæus	14	5	19	"
" americanus	15	4	19	"
Moschus moschiferus	14	5	19	"
Ovis	13	6	19	"
Cervus tarandus	14	5	19	"
Camelopardalis giraffa	14	5	19	"
Antelope equina	14	6	20	"
Chousingha	13	5	18	?

PERISSODACTYLA.

	D.	L.		
Equus caballus	19	5	24	Owen.
" zebra	18	6	24	"
" quagga	19	6	25	"
" asinus	18	5	23	"
Tapirus americanus	18	5	23	"
Rhinocerus indicus	19	3	22	"
Elephas indicus [2]	20	3	23	"
Hyrax capensis	22	8	30	"

[1] The place of this genus appears yet undetermined.

[2] Huxley (78) and Gill regard this genus as forming a distinct *order*.

RODENTIA.

	D.	L.		
Hystrix cristata	15	4	19	Owen.
" alopha	14	5	19	"
Lepus timidus	12	7	19	"
Castor fiber	15	4	19	"
Fiber zibethicus	13	3	16	Flower.
Capromys	17	6	23	"
Loncheres	17	8	25	"
Hydromys chrysogaster	14	7	21	Owen.
Myoxus	13	7	20	Cuvier.

BRUTA.

	D.	L.		
Dasypus peba	10	5	15	Owen.
Bradypus	17	3	20	Flower.
"	15	5	20	"
" tridactylus	16	3	19	Owen.
Manis	13	5	18	Flower.
" pentadactyla	13	4	17	Owen.
Myrmecophaga jubata	15	3	18	"
Orycteropus capensis	13	8	21	"
Megatherium	16	3	19	"
Cyclothurus	15	2	17	Flower.

MARSUPIALIA.

	D.	L.		
Most genera	13	6	19	Owen.
Phascolomys wombat	15	4	19	"
" latifrons	13	6	19	Flower.
Phascolarctos	11	8	19	"
Petaurus macrurus	12	7	19	"

After making due allowances for differences in the interpretation of facts by different observers, the preceding tables are very suggestive.

1. The different groups are seen to be unlike as regards the constancy of the vertebral formula; the adherence to 20, among the Carnivora (with but two exceptions so far as I know) is as startling as is the adherence to 7 with the cervical vertebræ; the number 19 is equally characteristic of the Artiodactyla; while in striking contrast to these two groups are the Perissodactyla and the Insectivora, which certainly do not differ widely enough in their habits from the Artiodactyla and Carnivora, to give a clue to the reason for these discrepancies.

2. Although in most cases, the species of a genus differ only by the greater or less development of the rib-process, so that the total number of thoracico-lumbar vertebræ is the same, yet in some cases, (Equus, Otolicnus, Loris, Sorex), this number varies by a single verte-

bra; it appears, also, that even individuals of the same species may vary in this manner, (*Phoca grœnlandica*); and this recalls a suggestion already made by me (45, 15), which ought to be considered, although, at present, its importance may seem rather ideal than real; "it does not seem possible that the head and pelvis can be as strictly homologous in animals having a different number of vertebræ as in those with the same number; in other words, the heads or the pelves of two animals may be cephalic or pelvic modifications of *vertebræ*, without being such modifications of the same identical vertebræ." Even if we exclude the skull from the category of vertebræ, the difficulty is not removed; for if the atlas of Hyrax is homologous with that of Elephas, then the sacrum of Elephas is the homologue of the twenty-fourth vertebra and its successors, with Hyrax; or if we also assume that the sacra of the two are homologous, we must homologize 29 vertebræ in the one with 22 in the other; and, *practically* at least, this seems to be our only course.

I trust that the foregoing considerations will aid in removing the stumbling block of numbers, from the path of those who would otherwise accept the meketropy of pollex and primus. To my own mind they were hardly needed, so decided was the conviction formed in 1866, and expressed in 51, 52 and 57, that no difference in the numbers of phalanges ought to affect our recognition of a profound morphological law affecting the membra.

NOTE. Dr. Coues has kindly placed at my disposal the MS. of some unpublished investigations bearing upon this subject, which so nearly accord with my own views, that I add them here. April, 1872.

Susceptibility of variation in numerical composition he believes to be, *a*, in direct ratio of number of parts composing an organ, and *b*, in inverse ratio of morphical differentiation and telical specialization of the parts of an organ; and that, consequently, the *value* of numerical composition as a morphological or taxonomic datum can be estimated with reasonable confidence of at least approximate accuracy. Value is inversely as variability.

"It is notorious," he continues, "that an organ (whether central or peripheral — whether indispensable to the integrity of an animal, or merely a useful adjunct to its economy) composed of a few parts, does not exhibit the same percentage of variation in the number of these parts, as the same or a similar organ does when it is composed of many parts. For instance, the *normal* variation in the bones of the coccyx of Primates is at a minimum, if it be not, indeed, *nil*; whilst the ordinary individual variation in the coccyx of a longicaudate mammal, such as the *Jaculus hudsonius*, for example, amounts to four or five coccygeal vertebræ. The few dermal scutes of armadillos are sufficiently constant in number to afford specific characters, while the essentially similar but numerous dermal scales upon the belly of a serpent may vary widely in number in different individuals of the same species. The rays of a small, sharply-outlined dorsal fin of a fish have no such variation in number as those composing a fin that extends the greater part of the length of the animal. The very numerous teeth of a serpent cannot be rendered with the certitude that attaches to the dental formula of a few-toothed mammal. In the lower families of birds possessing more than twelve rectrices, the number is fallacious even as a specific character, since it varies one or two pairs, at least, in different individuals of the same species, whereas in birds with eight, ten, or twelve rectrices these numbers mark whole familes, and the slightest variation is properly regarded as an anomaly. The few digital phalanges of birds are so constant (much more constant than their vertebræ) that deviation from the ordinary number becomes a character marking families.

"But it is unnecessary to dwell upon this obvious point, the more so since it is simply one part of the main proposition, that variation is greatest in organs composed of the most similar parts—parts that are essentially either morphically or telically *repetitive*, and conversely, that the variation in numerical composition is least in the structures made up of more perfectly differentiated or specialized parts. Any structure the essence of which admits of what is called 'vegetative repetition,' is susceptible of enlargement or curtailment by the development of more or fewer segments or moieties, and variability is a necessary result of such plasticity of organization. The examples adduced may be here cited again in illustration. Most of the caudal vertebræ of a long-tailed mammal are precisely similar in form and function—positive duplicates of each other, and in such a mammal as the house-rat, the coccygeal formula can only be given approximately, while the still more numerous dermal annuli of the tail, though corresponding in a general way with the bones themselves, must be enumerated simply in round numbers. The vertebræ of a serpent, essentially similar throughout the long series, represent no such fixed number as those of a mammal where they are differentiated in several groups, each with its own character. And even surveying organs composed of few parts, we find striking differences in variability. The presence, in an animal possessing five digits, of a supernumerary one, is in frequency out of any calculable proportion to the appearance of two functional digits in an animal that, like the horse, has normally but one—perhaps the improbability of the latter is on a par with that of the appearance of ten digits in a man. I am not informed as to the individual variability in the number of phalanges of cetaceans, and probably too few of these animals have been dissected for correct estimation, but there is every reason to suppose that the liability to variation here is as much greater than it is an ordinary mammal, as the increase in the number of phalanges.

"The abrupt and marked increase in the number of phalanges of cetaceans as compared with ordinary mammals, and the imperfect discrimination of phalanges, metacarpals and carpals in these mammals, seem to be explicable upon the same principles that account for the great number, small size and mutual resemblance of the vertebræ of prehensile tailed mammals, and those that use a long flexible tail as a balance. There is the same teleology in either case—it is the production of perfect pliability; and in both, the increase seems to be simply a matter of repetition. It is probably as impossible to homologize individual bones of a cetacean manus with those of an ordinary mammal, as it is to homologize the immense number of caudal vertebræ of the genus Mus, for instance, with the few of a neighboring genus, Arvicola. In all such cases as these, where variability is at a maximum, the importance of numerical composition, either as a taxonomic or as a morphical character, is obviously at a minimum. If the Cetacea agreed with ordinary mammals in other respects, the composition of the manus would afford no better grounds for these wide separation than the number of caudal vertebræ in certain other families.

"If we take the other extreme, of a solidungulate animal, we find such strong differentiation of the osseous elements of the manus, that every single one of the few bones has its own shape and size, and each of the distal segments, at least, performs a perceptibly distinct function ; even a sesamoid is elevated, functionally, almost to the rank of a phalanx. Here the variability is virtually *nil* ; if it occur at all, it would be entirely abnormal ; and the slightest normal difference in numerical composition, either in number of digits or of their phalanges, has a generic, if not a higher, value.

"The value of numerical composition of the pollex and primus as a morphological character, has been estimated by different anatomists at its two possible extremes—some considering it an insuperable objection to the antitropic homology of pollex with quintus, and others finding it little or no obstacle to such a view. Two considerations have had great weight with me, in reducing my estimate of its value so low, that it presents itself as no valid objection, when taken in connection with the strong evidence derived from other sources. In the first place, the question can only arise in respect to five-fingered mammals, a part, at least, of the digits of which have three phalanges each ; and since here we have the maximum known number of digits, and the next to the maximum known number of phalanges (Cetacea alone having more) the susceptibility of variation in numerical composition is nearly at a maximum, according to the principles already laid down, and hence the value of numerical composition is nearly at a minimum so far as the manus is concerned.

"Secondly, it is certain that pollex and primus are telically correspondent (analogous), and no less so that the modification each has undergone in its composition is simply telical. Both have been strongly differentiated from the other digits in the same way, and for the same purpose. It is presumed that no anatomist questions the homology of the whole manus of a bird, a reptile and a mammal ; yet the homology cannot be pushed to the individual osseous elements without recognition of vastly more difference in numerical composition than we are called upon to admit in the present case of pollex and quintus, and hence without tacit depreciation of the morphical import of mere number. The manus and the pes of a bird cannot be homologized with each other, according to any one of the current modes of comparison, without greater allowance still for telical modification in the matter of numerical composition. For myself, if I attempt to recognize any homology between the manus of a man, for example, and that of certain chelonians and of a cetacean, beyond a homology of the members in their aggregate, I must consider that a medius digit, for example, with three phalanges, corresponds to one with several more than three, and believe in telical suppression of a phalanx in one case, and a similar redundancy of phalanges in the other case. If I undertake to compare the manus of a bird with its pes, either antitropically or otherwise, I must admit with every single digit a difference in the numerical composition of its homologue. Until our morphological insight has penetrated far enough for the solution of such problems as these, it seems perfectly reasonable to maintain that the objections on the score of numerical composition that have been urged against the antitropic homology of pollex with quintus, and of minimus with primus, apply with manifold force to a majority of the homologies that anatomists consider determined."

V. GENERAL PROBLEMS.

The radical difference of opinion respecting the morphical relations of membra which the historical sketch exhibits between such Syntropists as Owen, for instance, and such Antitropists as Wyman, is not to be accounted for by any assumption of difference in their knowledge of facts or their intellectual power, but rather, as it seems to me, by a recognition of the dissimilarity of the premises which they have admitted, and the methods of reasoning which they have followed: in the one case, the human body has been chiefly employed in making the comparison, and attention has been early diverted to the correspondence of the pollex with the primus in respect to size, numerical composition and relative position, when the manus is in its natural attitude of pronation, as with many quadrupeds. In the other case, more attention has been given to the telical antagonism of the ancon and genu with many animals, and to the relative position of the membra during the early stages of development.

In more general terms, the idea of Syntropy is based upon the obvious resemblance in respect to *size*, *numerical composition and natural attitude* of certain *highly specialized* parts of *peripheral* organs belonging to animals of *high zoological rank*, and in the *adult* condition; while the idea of Antitropy is based upon the antagonism of *relative position* of *proximal* and *less specialized* parts with animals *lower* in rank or at *earlier* stages of development.[1]

Now, without doubt, the question under discussion is primarily one of *structure* rather than of *function*; it is a *morphological* and not a *teleological* problem. Before it can be solved, it is evident that we must first ascertain which are correct of the two groups of premises above

[1] These ideas were advanced by me in part in 45, 21, and more distinctly in 57, (Props. 9 and 10).

mentioned; and our present inquiry is, therefore, what are the relative morphical *values* of different attributes, different organs, different systems, different species and stages of development?

To fully discuss this question would require many volumes, and I can only attempt at this time to present the conclusions to which I have been led by the material now at my command, and, perhaps, to indicate more definitely than has been done heretofore, the matters which demand especial investigation. For it is clear that some of us upon both sides have been arguing upon false or insufficient premises, and that we have taken some steps upon the "high priori road," which we shall have to retrace in order to reach the truth; still, I must claim that, as a rule, the Syntropists have, in spite of their numbers, fallen into the more serious errors, and have disagreed so decidedly among themselves, as to suggest upon that ground alone that their general view was incorrect; the Antitropists, on the contrary, have at least kept a great idea always before them, although they may have been too eager and confident, and been led astray by un founded fancies.

Morphical Values of Characters.

Admitting then, as an abstract definition, that morphical value is the usefulness of any character in the determination of morphical relations, we have still to ascertain the *relative* morphical value of the various characters already mentioned. So far as I know, the phrase "morphological value" was first employed by Huxley, in 1858 (250, 381); "morphological *importance*" was used by Cleland in 1860 (215, 306), and the former phrase several times by Traquair, in 1865.[1]

In 1867, Wyman suggests that the osseous system is more reliable in the determination of intermembral homologies than the other systems (55,277), and a like comparison is made by Flower (66,239) in 1870; my own convictions of the need of some determination of morphical values, were reached independently, and were expressed in 1866 and 1867 (57 and 58); but, although I am convinced that an approximate estimate of the comparative value of the characters already mentioned might be reached by analogies, and by a careful study of the history of the question, yet there appears to be a more satisfactory method of accomplishing the same end; namely, by ascertaining the value which these characters have for the determina-

[1] On the Asymmetry of the Pleuronectidæ Trans. Linn. Soc., 1865.

tion of the other kind of morphical relations, plural homologies, upon which zoological classification is based; since, although few have spoken of the two halves of a single individual as if they were two distinct individuals and comparable in like manner, yet it is not probable that any one will object to such a view of the case, and such a method of comparison.

May we then conclude that morphical value is essentially equivaent to taxonomic or zoological or classificatory value, and that the only difference is that the former is used when two parts of the same individual are compared, while the latter is used when two different individuals are compared, with a view to ascertain their zoologica relationship; if so, then morphical value is value in respect to single homologies, taxonomic value is value in respect to plural homologies; and since both are morphical relations, it seems probable that the same attributes, organs, systems, species and stages of development which have been found available in the one, should be given a like absolute and relative importance in the other class of morphical questions.

This conclusion seems warranted by the language of high authorities,[1] who either use morphological as if equivalent to taxonomic value, or imply that morphical relations, near and remote, are the true test of zoological affinity.

Assuming then provisionally, and until decided objection is raised by others, that morphical value and taxonomic value are correlative, we are now justified in considering the zoological criteria, which have been admitted, in order to ascertain the relative morphical value of the characters already mentioned; but here, unfortunately, we meet with a most unsatisfactory difference of opinion.

For instance, we find the same high authority making two incompatible generalizations, as follows: "The generative organs, being those which are most *remotely* related to the habits and food of the animal, I have always regarded as affording very clear indications of its true affinities; we are least likely in the modifications of these organs, to mistake a merely adaptive for an essential character." Owen (on the Dugong, Proc. Zool. Soc., vol. I, p. 40.) "Teeth are always most *intimately* related to the food and habits of the animal and are therefore important guides in the classification of animals." (63, 1, 361).

[1] Agassiz (201, *fere*), Huxley (251, 2 and 100), Gill, American Naturalist, vol. IV, Proc. Am. Ass. Adv. Soc., 1870, and Rolleston (294, XXII).

Dr. J. E. Gray "observed that in his opinion internal characters were of little use in Zoology; (Proc. Zool. Soc., Apr. 11, 1867, and Journ. of Anat. and Phys., 2, 371); while Parker admits the value of external characters, but says the mind will not rest in these outward things, and that the skeleton, nervous system, digestive, respiratory and vocal organs are very important.[1] Testimony to the zoological value of the skeleton is given by Agassiz,[2] but Owen speaks again as follows: "Guided by the seldom failing law that distinctive characters are most strongly developed in the peripheral portions of the body," etc.,[3] and further believes that the "form and disposition of the scales of the legs of birds have afforded distinctive characters to the zoologist" (63, 2, 232).

Further reference to the opinions of various authors, respecting the taxonomic value of different systems of organs is given by Rolleston (294, XXI, note), and the matter is briefly discussed by H. Allen[4].

It is quite probable that in practice all the above authors have been more definite than their language would imply, and that they have more or less perfectly discriminated between the value of an organ for one kind of group, and that which it might have for another; this is done by Wyman [5] when he says that the "teeth of mammals afford the surest indication of zoological affinities," because he means that for the determination of groups *within the class* the teeth have a high morphical value. Flower questions this fact,[6] but admits the principle, as had Turner before him,[7] by attaching morphical value to characters of the base of the skull within the order, Carnivora.

Günther likewise discriminates within the order, when he says,[8] "under these circumstances, I still feel satisfied to distribute the fishes on the basis of Müller's ordinal arrangement into minor natural groups, whether called families, groups or genera; and in my opinion, there is no character equal in importance to that of the structure and position of the fins; as they are in immediate connection with

[1] Trans. Zool. Soc., v. 149, 1862.

[2] Anat. des Salmones, p. 1.

[3] Memoir on Dinornis, p. 78.

[4] Outlines of Comp. Anat.. and Med. Zool. p. 13, 1869.

[5] Lectures on Comp. Physiology, 1849, p. 24.

[6] Proc. Zool. Soc., 1849, p. 5.

[7] Turner, H. N., P. Z. S. 1848.

[8] Catal. of Acanth. Fishes. Preface. 1861.

the entire habit of fishes, and with their mode of life, they best indicate their natural affinities, and indeed prove to be the most constant and general characters."

As to generic criteria, Müller and Henle enumerate [1] the characters found by them most useful among Selachians; and Parker is explicit respecting the unimportance of certain characters, for the determination of groups more comprehensive than genera.[2]

Specific characters of the Pycnogonidæ are enumerated by H. D. S. Goodsir,[3] and those of the tortoises by Owen (62, 1, 162.)

Finally, a great part of Agassiz's later works (200 and 201), is devoted to the effort to show not only that groups really exist in nature, but that they are based upon distinct "categories of structure." I quote the following also from my notes of his lectures on Selachians.[4] "Zoologists take very different criteria or different parts as foundation for the same kind of group, or the same criteria for different kinds of groups, so that their results are very diverse. We must have some means of determining the *value of characters*."

Accepting provisionally Agassiz's abstract enunciation of these criteria and their subordination as to value, as summed up on page 261 of 201, and likewise considering the only direct application of these principles to a single group, the Testudinata and its subdivisions (200, 1, Part II), I have endeavored to translate the zoological criteria into anatomical language, and in this way to at least indicate the means by which we may sometime be able to determine the exact morphical value of any anatomical character. The conclusions which I reached are given in the diagram (page 28), and afterward briefly explained; but I must here admit that I feel sure of being right upon only the following points:

1. That both *plan of structure* and *form* are displayed upon a vertico-lateral section of an animal.[5]

[1] Ann. and Mag. of Nat. Hist., 1844, pp. 1 and 4.

[2] Proc. Zool. Soc., 1863, p. 572.

[3] Ann. of Nat. Hist., July, 1844, p. 1.

[4] Given at the Museum of Comp. Zool., 1867 - 1868.

[5] As between Vertebrata and Radiata, or between either of these and the Mollusca and Articulata this is clear enough; but since the relative positions of digestive, nervous and circulatory systems seem nearly identical in the two latter branches, the respiratory and perhaps some other systems must be included in our representation of a vertico-lateral section. See Huxley's diagrams, 151, fig. 30. As to the view that Vertebrata and Mollusca may find connecting links in Amphioxus and the Ascidians (references to which are given in 336), I have not yet seen any comparison of the vertico-lateral sections of these animals, or any statement that they are identical.

2. That plan of structure depends upon the relative normal position of important organs; while form depends upon the relative size of these and other organs. If, then, it is true that the *branch* is determined by the plan of structure, and the family by the form, it follows that relative size is of less morphical value than relative normal position; it seems probable, too, that the natural attitude of organs must be similar within the same family, since the membra of a family have not only the same form, but the same mode of locomotion; if this is true, then this character also is of less morphical value than normal position.

3. I am also convinced that segmentation, or numerical composition, is of less morphical value than either of the characters above named; but this has been already considered.

In support of the general conclusion which is expressed by the diagram (page 28), that internal characters are more valuable in the determination of the more comprehensive groups, while external characters are more valuable for the determination of lesser groups, which would ascribe to the former more, and to the latter less, morphical value, I can bring little direct evidence; but the following passage from an eminent conchologist shows that the idea is not confined to myself; and I am inclined to believe that it must have been in practice, at least, recognized to some extent by all who have sought to reach a natural classification.

"In all attempts to characterize the groups of animals, we find that in advancing from the smaller to the larger combinations, many of the most obvious external features become of less avail, and we are compelled to seek for more constant and comprehensive signs in the phases of embryonic development, and the condition of the circulatory, respiratory, and nervous systems." [1]

The above is in part confirmed by Agassiz's view that the genera of turtles are based upon the voluntary organs of nutrition, the jaws and other muscles (200, 1, 422), and by Owen's view that the primary subdivisions of the mammalia are characterized by the condition of the brain (63, 2, 270 [2]), and further by the general acknowledgement that osteological characters alone are often insufficient for the dis-

[1] Woodward; Recent and Fossil Shells., p. 56.

[2] Flower (Phil. Trans. 1865, p. 647), remarks of the brains of monotremes and marsupials as contrasted with those of other Mammalia. "The appearance of either a transverse or longitudinal section would leave no doubt as to which group the brain belonged."

crimination of species within the same genus; although Owen once held a different opinion. (Trans. Zool. Soc., vol. II., p. 379, 1838).

But how can we reconcile the above generalization with the statement of Dr. J. E. Gray,[1] that with the Balænidæ and Balænopteridæ, "every bone of each genus is peculiar, though not always easy to describe; likewise, almost every bone of each *species*, especially the ribs and phalanges, the skull, tympanic bones, scapula, and cervical vertebræ"? Is it not probable that there *are* not only specific but individual differences between two individuals in each and every part of the body, and in each and every possible attribute of these parts; but that these differences are more *obvious* in some parts than in others, so that certain parts and attributes are more *available* than others? and such a view is by no means incompatible with the result of our experience, and with the analysis of other matters which lead us to believe that for the determination of more important and comprehensive questions, we must look to the central and essential parts, while minor questions may be decided by observation of peripheral and less vital organs. For instance, a single vertebra would enable us to say whether its owner were a reptile, a bird, or a mammal; but it would far less distinctly exhibit the particular genus or species to which it belonged; on the other hand, the manus of the whales and of the Sirenia resemble each other, and even that of the penguin might not be at once recognizable as that of a different class; but within the same order or family, the genus would be at once apparent from the special proportions of the parts.

According to Gray,[2] the long spine which has been described as *Myriosteon Higginsii*, was thought by some to be the tail of a ray, but is probably part of a starfish; certain pointed fossils are thought by Pander to be teeth of selachians, by Owen to be from the borders of the suckers of cuttlefish; the "ichyodorulites" have been regarded as spines of Crustacea by some authors, but as selachian spines by Agassiz[3]; from which the latter concludes that these parts are at any rate not available as either branch, class, ordinal, or perhaps family characters, but rather as generic; the "bird-tracks" in the Red Sandstone of the Connecticut Valley, did not at once indicate whether the feet which made them belonged to birds or to reptiles;

[1] Proc. Zool. Soc., 1864, p. 228.
[2] Proc. Zool. Soc., 1864, p. 168.
[3] Lectures on Selachians, Dec. 1867; (unpublished).

now all the above examples are peripheral parts, and the like questions never would have arisen with such a part as a vertebra.

Putnam [Am. Nat., Jan. 1872, p. 26, note], mentions the slight taxonomic value of air-bladder, head-scales, barbels, ventral fins and eyes, and Agassiz once figured fossil Crustaceans [*Eurypterus remipes* and *Pterygotus*], as fishes on account of their external aspect.[1]

Packard[2] has recognized the unreliability of characters drawn from peripheral and inconstant organs, like the mouth parts and wings; and Owen himself seems to recognize the principle, "Judge not according to appearances," in the following paragraph: "The prominent appearances which first catch the eye are deceptive; and the less obtrusive phenomena which require searching out, more frequently, when their full signification is reasoned upon, guide us to the right comprehension of the whole."[3]

From the unpublished lectures on Selachians I again quote Agassiz: "The Chimeræ are generally separated from the other Selachians on account of a single branchial fissure; but as this is a *variable* character, it should not set aside more *internal* characters."

A zoological illustration of our proposition is given in the great variety and discrepancy of the definitions of the vertebrate type; so long as investigators regarded especially some one group with which they were more familiar, and so long as they included in their definition of an abstract idea, the special structures which characterized those minor groups (see Agassiz, 201, 213), so long they disagreed among themselves, and failed to follow Nature; this is seen in the difficulty which others have found in accepting Owen's archetype skeleton as correct; for it is essentially a piscine skeleton, and although the great anatomist holds that fishes depart least from the vertebrate archetype (63, 1, 102), such a generalization involves reasoning in a circle, and has been adopted by few (as Maclise, 23, 674–676).

The Amphioxus is, without doubt, the simplest known vertebrate; but it cannot be regarded as *the* material manifestation of the vertebrate idea, since its structure presents positive characters by which

[1] Microscopic section of the tooth of Ceratodus has convinced Mr. Bicknell that it is "unsafe to found genera or even species upon the microscopical structure of a single tooth or bone, although it has proved correct in many cases." Proc. Bost. Soc. Nat. Hist., April 19th, 1871.

[2] Guide to the Study of Insects, p. 14.

[3] Palæontology, p. 357.

it is not merely an exception to the generalizations applicable to all other fishes, but which seem to constitute it a distinct class, coëqual with the Myzonts, Selachians, Ganoids, and Teleosts; still there can be no question that this simply organized vertebrate, presenting the fewest organs, and the simplest functions, really does come the nearest to being the realization of the ideal plan of structure of the branch. Now the Amphioxus may be said to be the zoological counterpart of the embryonic state of the higher vertebrates, and to hold within the branch a central position, surrounded by the more specialized organisms, as the central and constant organs of a single individual are encompassed by peripheral and variable ones.

A still better illustration will be furnished by the very question now under consideration, in case it is decided in favor of antitropy; a glance at the manus and pes of most animals indicates a general correspondence between them; but they alone would furnish no sure guide to the principle upon which they are to be compared in detail; at any rate, even if we are not right now, the total disagreement for a century is sufficient evidence of our proposition, and of the need of appealing to more central and reliable parts of the membra, and even to the trunk itself.

From the foregoing considerations, there arises the suggestion that the morphical value of a part of an animal, is in an inverse ratio to its telical importance; that *reliability* is inversely to *variability*; and, that hence, in determining morphical relations, we should regard primarily, those parts which are constant in position and function, and secondarily, those which are variable and inconstant, whether zoologically, physiologically or teratically.

The variability of the two extremes of the vertebral column is remarked by Owen, (63, 1, 94,) and Bell[1] connects peripheral variability with diversity of function in language the more suggestive, as coming from so "untranscendental" an anatomist.

It is generally admitted that multiple organs, whether animal or vegetal, are liable to variation, and many authors have remarked the variability of the membra; Owen refers to it in many places[2]; T. Rymer Jones[3] suggestively associates peripheral position with variability in number and appearance; and Pouchet[4] goes so far as to

[1] On the Hand; close of chap. 2.
[2] Trans. Zool. Soc., 1835, p. 353; 20, 333; 20, 269; 63, 2, 254.
[3] Cycl. of Anat. and Phys., 3, 841 and 843.
[4] Plurality of races, p. 47.

acknowledge that the "law which causes the modifications of organisms, becomes more and more decided and clear *from the centre to the periphery.*" I may here say that the convictions expressed in 58, (Props. 9 and 10) were formed independently of the authors above quoted.

The results of a tabulation of cases of sexdigitism and hexadactylism,[1] (as given in 313), have been confirmed by the addition of cases, gathered up to Jan. 1, 1870; at that date, of 242 individuals affected, 152 were males and 90 females; and of the membra, 312 were armi and only 155 skelea; this not only shows the extreme frequency of this malformation of peripheral parts belonging to the highest vertebrate animal, but also indicates that in this respect, the skelos is more constant and reliable than the armus, as it is also the membrum less often and less extensively modified for special purposes throughout the vertebrate type (313, 10); but in respect to the vascular system, particularly, Meckel believes the reverse is the case, (6, English edition, 2, 176); and upon this question more remains to be done.

Another very important question is as yet undecided; is the homology of a muscle to be determined mainly by its place of *origin*, or its point of *insertion?* The latter is the opinion of Mivart (46, 398) Rolleston (61, 620), (with some exceptions), and Humphrey (64, 321). Coues states that the insertion is less frequently changed than the origin (70, 223), and I know of no author who has taken the opposite view[2]; I am not now prepared to do so, and would suggest that we ought first to discriminate between the "sliding up or down the *same* bone" referred to by Coues (70, 223), and the lateral transfer from one bone to another, as of the tendon of insertion of the *biceps brachialis* (Coues, 70, 299); the former transfer would generally be for the purpose of securing greater length of fibre, and extent of motion, and would also occur more frequently with the origin; but the latter would affect the essential function of the muscle, and would perhaps warrant us in regarding a muscle so affected as wholly distinct.

[1] Do cases ever occur of extra digits, or dactyls upon both borders of the manus or pes?

[2] Since this was written, the graduation thesis of W. S. Barnard, "On the Membral Myology of the Orang" has been prepared in my laboratory, and the facts and ideas therein presented have nearly convinced me that the homology of muscles depends far more upon their origins than upon their insertion; the paper has been offered for publication to the Boston Society of Natural History.

Morphical Integers.

This suggests a further and very important enquiry. What is a morphical integer, whether in the muscular or osseous system, or among the digits and dactyls? The phrase "morphological integer" is first used by Coues (70, 222), but the general problem has been considered by Owen and others, with especial reference to the bones. The question of Spencer (299, 2, 526), "How are centres of ossification which have a homological meaning to be distinguished from those which have not?" is not answered satisfactorily by Owen's reference to a "knowledge of the archetype skeleton" (63, 1, XXIV), since the knowledge itself depends upon the prior determination of the question. I do not feel ready to discuss the question, but would call attention to its great importance, and to the need of such investigations as those of Parker; this author (292, 4) thinks that "true and safe landmarks" for the recognition of "morphological territories," may be found in segmentation both by fission of primary cartilage, and by the appearance of two or more separate centres of ossification within the same undivided tract"; but it is evident that much more remains to be done, not only for the bones, but for the muscles, in order to ascertain the morphical integers and equivalents in the osseous and muscular and other systems.

What Constitutes a Digit or a Dactyl?

There do not appear to have arisen as yet any serious discrepancies between the statements of different authors respecting the number of digits or dactyls which may exist in a given animal; but since no one, so far as I know, has given a general rule by which to determine the above question, and it is probable that at some time direct contradictions will appear in different works [1], it is worth our while to inquire into the elements which might form the basis of such a rule.

Among the mammalia, the vast majority of those digits and dactyls about which no question can arise, consist of three phalanges, are visible to the eye as subdivisions of the distal extremity of the member, and perform some obvious function in the economy of the animal; the ordinary mammalian digit or dactyl is then *functional*, *visible*, and *trimerous*. But to this definition are many exceptions.

[1] Leading perhaps to as unfortunate complications as the conflicting accounts of the *hippocampus minor* and the *corpus callosum*.

First: in respect to the *number of phalanges*, which may be increased to 14 (index of Globiocephalus) or, more commonly, reduced to 2, (as with all the digits of Pteropidæ and the pollices and primi of most species), or to 1 (as with the primus of Simia); but all these dimerous or monomerous digits and dactyls are visible and functional, and numerical composition alone is evidently insufficient to determine their right to be included with the rest. But there may be no phalanges whatever, and merely the metacarpal or metatarsal bone; and the question may arise as to the propriety of including that in the enumeration.

Second: in respect to its external visibility. The pollex of Hyæna (63, 2, 306), has a single minute phalanx, supported by an equally minute metacarpal; the *Hyrax capensis* offers a similar structure; these digits are monomerous, concealed, and apparently functionless, and would not be enumerated in a new species by one who confined himself to the external characters which are believed by many to serve for generic and specific distinctions; yet, undoubtedly, an anatomical description of the species would mention the existence of five digits in both these animals, in contradistinction to a new Tapirus, which presents only a rudimentary pollical metacarpal. Again, although the pollices might be concealed from the sight, they might be felt under the skin, and another and distinct element must be taken into account in framing our definition.

Third: a digit or dactyle may be trimerous and visible, and yet, to all appearance, functionless or *atelic*; such are the "dew-claws" of many Artiodactyla, and the slender index and annularis of Hipparion (63, 2, 309, and 63, 3, 825); they are supposed to prevent sinking into soft soil, but there seems no reason why the Camelidæ should be wholly destitute of these organs, if this is their use with the typical Ruminants; such are also the pollices of the Canidæ and Felidæ which have little if any power of motion.

The above are instances of what are generally called "rudimentary organs," to which so much attention has lately been directed, and respecting which such contradictory opinions are entertained; this is not the place for a discussion of the general subject, but the above remarks may indicate the special questions as to the definition of digits and dactyls.

Histological Composition.

The morphical value of this attribute of organs is variously estimated by different authors; Agassiz, in the second passage already quoted, evidently thinks it is not of class value in the determination of homologies among radiates; Parker, 292, 3, associates "histology" and "function" in such a way as to indicate that he regards their morphical value as less than that of relative position. But it does not appear that due attention has been given to the problem suggested by the following considerations:

It is certain that a tendon may ossify, as in the skelea of fowls and the so-called "marsupial bones," so that what was at one time fibrous becomes osseous in structure; the same, however, holds true of the membrane bones of the skull, and of course, no one questions the homology of a bone with its own pre-existing cartilage, or with that of another individual or part of the same indiviudal; and upon this ground alone no objection arises to Owen's view of the mekesyntropic homology of the marsupial bones[1] (63, 2, 356); so, too, the capsule of the eye-ball is generally admitted to be homologous throughout the vertebrate branch, although it is fibrous in man, gristly in the turtle, and bony in the tunny (Thynnus) (63, 1, 26). But is it possible for a muscle to be the true homologue of a ligament? as Duvernoy thinks of the human *subclavius* and the costo-coracoid ligament of the gorilla[2]; and still more, can muscle correspond to bone? as is assumed by Humphrey and Huxley of the clavicle and Poupart's' ligament (72, 77 and 78, 37). Coues alludes to a theory (apparently a notion of his own) that certain omozonic muscles may be antitropically represented in pelvico-sacral ligaments. It might be urged that since in a typical muscular organ, muscle and tendon are continuous parts, and since the belly of a given muscle may be of very different lengths in different species, they are in one sense homologous structures, but evidently there should be a better understanding among homologists respecting the morphical value of histological composition.[3]

Mode of Development.

Respecting the morphical value of this attribute of organs and animals, the most widely diverse opinions have been held. Owen has constantly urged its slight importance in comparison with adult struc-

[1] As to the rudimentary fibro-cartilages of Thylacinus, see Owen, Proc. Zool. Soc., 1843, p. 148.

[2] Archives du Museum, Tome VIII; referred to in 38, 367.

[3] Goodsir alludes to this question (297, 397), when he says, "*Tissue is subordinate to form*," and Huxley mentions without comment, the extraordinary fact that the outer serous stratum, or *epiblast*, of the beginning embryo, gives rise to the two anatomical and physiological antipodes, epidermis and cerebrospinal nervous centres (78, 10).

ture and relative position, and I quote a few passages: "There exists, doubtless, a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions, and very substance of such parts, without their essential homological relationships being thereby obliterated. These relationships are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function, and similarity of development. But the connections must be sought for at every period of development, and the changes of relative position, if any, during growth, must be compared with the connections which the part presents in the classes where vegetative repetition is greatest and adaptive modification least" (20, 174). "So far is embryology from being a criterion of homology" (63, 1, XXVI). "Embryology affords no criterion between ossific centres that have a homological, and those that have a teleological significance" (63, 1, XXV). "No part is, however, absolutely autogenous throughout the vertebrate series, and some parts usually exogenous are autogenous in a few instances" (63, 1, 27). "The developmental phenomena of the head neither supersede nor can supply the better evidences of homology afforded by relative position and connections, any more than do those of the foot; . . . it is neither here nor elsewhere the criterion of homology" (63, 2, 311). Cleland says, "Morphologically, it is of little importance whether cranial bones are developed *in* the primordial cartilage of the skull or *around* it" (215, 305).

The general importance of embryology in the determination of homologies has been urged by Goodsir and Huxley, and in 251 the latter has well indicated the necessity of deciding the general question before attempting to solve minor problems respecting the correspondence of the skull and the vertebral column. Agassiz has constantly presented the taxonomic value of embryology not only throughout his later works, but in the lectures on Comparative Embryology, Boston, 1849; and upon the ground of a difference of development, he in great measure bases his opinion that the Batrachians form a class distinct from the scaly reptiles; but in discussing this, Dana asks[1] "whether, in the determination of *classes* it is not the more correct method to take note primarily of species in their finished or adult state; and whether adults do not express the true nature and idea of species, or the objects to be classified, rather than the special

[1] Am. Journ. of Sci., Mar. 1864, p. 184

series of changes through which the adult characteristics are reached."

On the other hand, Owen based his own nomenclature of the mammalian molar and premolar teeth upon the facts of development; but Flower (227), and Moseley and Lankester (282) have pointed out defects in this system, and the latter even hold that "the existence of any homology at all between upper and lower jaw teeth must be denied; it could only have a theoretical existence in connection with that view of the structure of the vertebrate skull, which placed the upper and lower jaws as homologous parts of a vertebra" (282, 272).

Now all this has no apparent reference to intermembral homologies, but it must nevertheless be considered before any conclusion can be reached satisfactory to all; are, or are we not, justified in comparing the membra together in that condition in respect to both position and structure, which they present when first forming in the embryo? if not, then the utter disagreement between Syntropists and Antitropists will forever remain; but if we are, then the former must simply eliminate from their train of argument, all such criteria as numerical composition, size, shape and function; and both must wholly disregard the telical parallelism or antagonism which exists between the corresponding parts of the membra of some animals, and must endeavor to ascertain first the general laws of organization according to which the trunk is formed.[1]

VI. SPECIAL PROBLEMS.

Since it is probable that the telical antagonism of the membra with some mammals must be eliminated from the discussion of their morphical relations; and since the latest views upon the subject are based upon the primitive condition and position of the membra in the embryo; and since they then do not indicate either syntropy or antitropy, but are capable of interpretation upon either hypothesis; and since, finally, their adult condition points toward syntropy rather than antitropy, so that the majority of anatomists are inclined to regard that as their true and morphical relation; it is evident that we must not merely remove the obvious objections to our way of thinking, but must produce some positive evidence in its favor.

This evidence consists in the establishment of the following propositions.

1. The cephalic and caudal regions[1] of the body are comparable with each other as are the right and left sides.

2. The armus and skelos are appendages of the cephalic and caudal regions respectively.

Whence it follows that the armus is comparable with the skelos as the two armi or the two skelea are comparable with each other.

CEPHALICO-CAUDAL HOMOLOGY.

The evidence in favor of the first proposition is admirably stated by Wyman, 55,249 ; but I think we must eliminate what he regards as "the most striking facts bearing upon the idea of fore-and-hind symmetry," the antagonistic attitude which the *membra* assume during the *third* stage of development, (55,252.); since the syntropists would say that this attitude is only secondary and adaptive with the mammalia, and does not even occur at all with lower vertebrates.

As to the *trunk*, we quote Wyman's statements as follows :

"First. The embryo increases in size, not by a growth from before backward, but from a central, and, as it were, neutral point, both backward and forward, so that the two ends are made to recede from each other in opposite directions."

To this it may be objected, that with the turtle (Agassiz, 200, 2,539 and 543), and probably with most vertebrates, the cephalic fold is *first formed;* and retains throughout a prominence by which it is distinguishable from the caudal fold; but on the other hand we may say, that the turtle is from the beginning a *cephalized* organism, and all its development must have reference to the after existence of a prominent head, so that this priority in appearance of a cephalic over a caudal part is purely telical and no bar to a morphical comparison. I am inclined to doubt whether this objection could arise with Amphioxus.

"Second. The primitive groove of the nervous axis in its earliest stage is nearly symmetrically enlarged at either end, so as to form two opposite dilatations ; one the precursor of the future cerebral vesicles, the other of the rhomboidal sinus."

"Third. When the spinal groove closes up, 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."

To the above it will perhaps be answered that with turtles, (200,

[1] The term region must here be taken to include all in front of, or behind, a middle point, and not merely the head or the tail.

544, and 546), the primitive furrow appears first nearer the cephalic fold, and its closure also begins in that region; but it is probable that both these differences are explicable like the preceding, and that they would not exist in the Amphioxus.

"Fourth. The first traces of 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; the ossification of the bodies of the vertebræ takes place in the same order, beginning in the middle and extending in either direction."

Upon this point Dr. Cleland has written me as follows: "Remak is quite explicit in the statement that the primordial vertebræ are developed *from before backward;* it is quite true that the first three or four which appear, are placed about the middle of the embryo, but that is because the cephalic part of the embryo forms so large a portion of the whole." May 7th, 1868. Upon this I cannot give an opinion, because it is not yet determined where the middle point of the vertebrate embryo lies; indeed, it *seems* to shift position from stage to stage of growth. Agassiz's statements respecting the turtle agree with Wyman's, but if we exclude the head from the length, then the first vertebræ appear to be formed in the neck; and I have observed that in a large adult skate, *Raia ocellata*, the segmentation of the vertebral column appears at some distance behind the occiput, and increases *gradually* toward the middle of the length.

Bischoff's figures, especially in the paper on Kaninchen-Eies (figs. 53 and 54), indicate that the primitive vertebræ begin at some distance behind the cerebral vesicles; but Huxley (78, 11) states that the protovertebræ commence at the *anterior* part of the cervical region and gradually increase *backward.* The matter can only be decided by observations made with the present doubt in view.

But for this as for the previous questions, I believe we must look to Amphioxus.

I quote further from Cleland's letter. "A strong point against primitive antero-posterior symmetry, is found in the construction of the vertebræ; the body of each vertebra, according to Remak, is originally formed, the anterior half from one primordial vertebra, the posterior from another; you have these two parts seen in the shape of two cones placed apex to apex, and if there were primitive symmetry, surely, when the arch and ribs are in connection with the anterior cone in the anterior vertebræ, they ought to spring from the posterior cone in the posterior vertebræ; but it is not so; they always, I believe in all vertebrates, come from the anterior half; . . . . the nerves also, lie *behind* the arches and ribs of the permanent vertebræ, throughout the spinal column." It is evident that these are fair objections, and I call upon others to aid in their removal.

But in my opinion, the most conclusive evidence of a meketropic homology between cephalic and caudal regions, lies in the fact that in the very earliest stages of the vertebrate embryo, no difference whatever can be detected between them; the primitive disk is circular, and homogeneous, and, in the turtle at least (200, 2, 536), the very first step toward the formation of organs is the depression of the surface at two points upon opposite sides, which mark the position of the future head and tail; the primitive furrow appears later; so that if development is given the importance which most now allow it, we can say that the two ends of the body are set off against each other, as homologous and antagonistic parts, even before the right and left sides are separated by the primitive furrow; moreover, at this time, the head and tail are nearer each other than the right and left borders of the embryonic disk, and the subsequent elongation and narrowing is adaptive and not of morphical importance.

Prof. Wyman's fifth kind of evidence embraces the facts of resemblance between the organs at the oral and the anal outlets of the alimentary canal, which was first alluded to by Oken; but it is probable that all determinations of the softer parts must wait until those of the bones are satisfactorily made out. When, however, they are taken up, it ought to be ascertained whether the reversed relative position of the urinary to the intestinal orifices in *Teleostei* as compared with other vertebrates, affects the homology of the parts, or whether it may be regarded as comparable to the differences in the connection of the pneumatic duct of *Lepidosteus* and *Erythrinus*, (Ow. 63, 1, 494), as compared with *Lepidosiren* and the true air-breathing vertebrates.

THE "NATURE OF LIMBS."

Can we now demonstrate the second proposition, that the armi are appendages of the cephalic region of the trunk, and the skelea of the caudal region, and thus find reason for regarding them as similarly related?

The "Nature of Limbs" has been very differently interpreted, and the minor problems involved in the general question are many and complex.

[1] See Hunter's Anat. Memoirs, edited by Owen, vol. 1, p. 196.

1. What is the normal number of membra?

If we could confine ourselves to the adult *Mammalia*, the answer to this would be easy, for no member of this class is known to possess more than two pair of organs which answer to the common idea of "limbs"; the same is true with the reptiles, the birds, and the amphibia, but if we include the fishes, there is room for difference of opinion.

Huxley (251, 61,) and Rolleston, (284, XXXII), state that there are only two pair of "articulated limbs;" and this is the opinion of nearly all anatomists; but Parker, (292, 3), seems to include the ordinary membra in the same category with the median fins; Humphrey, (248, 65,) is more explicit and holds that "each limb of the higher animals corresponds with a lateral factor or factors of the mesial fin of the fish and would, if development had proceeded in a similar manner, have united with its fellow into a mesial organ." Cleland (65), advances the view that "the suspensorium and lower jaw form an arch corresponding with the limb arches, and the opercular apparatus of fishes consists of appendages attached to it;" while Owen (20, 333 and 63, 1, 102), not only includes under the general title of "diverging appendages," the pectoral and ventral fins (or "limbs"), the "branchiostegals," the "operculars" and the "pterygoids," but also (20, 269; 63, 1, 30, and 63, 2, 18) enumerates therewith the slender or flat processes projecting backward from the ribs in some fishes, crocodiles and birds; and further adds that "the true insight into the general homology of limbs leads us to recognize many potential pairs in the typical endo-skeleton," (20, 270).

Now it must be admitted that the facts of development as at present understood, are not wholly opposed to the above views of the "general homology of limbs"; and Wyman, after a most admirable exposition of the case (55, 264) says "we believe there is ground for the hypothesis that limbs belong to the category of tegumentary organs."[1] But it ought also to be considered that this conclusion is based chiefly upon the *apparent identity of the membral buds with the ridges which afterward give rise to the median fins;* and this involves the great question of the relative value of *development* and of *position* for the determination of homologies; in the present case, if we allow that the homology between the median and the lateral appendages of fishes is as complete as that between the two pairs of lateral appendages themselves, upon the ground of primitive identity of structure, then must

[1] Oken, (285, Par. 3337), called them "tegumentary members."

we not likewise conclude that the visceral arches are membra joined on the middle line; that the flukes of cetacea are membra; that the lateral ridges at the root of the tail in some selachians are also membra; and finally that the carapax of tortoises, (Agassiz, 200, 2, 562,) represents a continuous series of *undistinguishable* membra above the ordinary pairs; this is almost a *reductio ad absurdum*, and is to my mind sufficient evidence that in this connection at least, relative position is of greater importance than apparent identity of primitive structure; and that we are entitled to recognize in the vertebrate only two pairs of real membra.

There is one other fact which serves to distinguish the membra from the median fins; the latter always appear as a continuous dorsal and ventral ridge, which may persist in some fishes and batrachians, but which is generally absorbed at intervals so as to leave certain portions to form the permanent fins; now if the membra were wholly in the same category with these median fins, why should they not be formed in like manner? The fact is that they never are so formed, even in the skate, where, as shown by Wyman (317, p. 35 and Fig. 4), the pectoral and ventral fins commence as slight ridges in the same plane and in close juxtaposition, yet *not continuous* with each other.

Nevertheless the opinions of the above-mentioned authorities are entitled to great respect, and it can hardly be assumed that the question as to the number of membra is decided; indeed, perhaps a recognition of three or more "potential pairs of limbs" is not necessarily incompatible with the idea of a meketropic relation between the armus and skelos, which all agree to be homologous in some way; but it is evident that such a conception as Owen's archetype skeleton, (63, 1, 30), in which the diverging appendages all point backward, could not co-exist with a distinct idea of meketropy; and neither he, nor Cleland, nor Humphrey, nor Parker have ever admitted such a principle of organization so far as the skeleton is concerned; it is manifestly more easy to regard the membra as themselves antitropically related if we can show that there are but two pairs, the one belonging to the cephalic the other to the caudal half of the trunk, as seen in Fig. 4.

The early and enormous increase of the head in the higher vertebrates leaves the armal buds at about the middle of the embryo; the balance is only restored when a long tail is formed at the other end; in either case the armi would seem to be most intimately connected with the cervical region, and the skelea with the lumbar; but here arises the question as to the relative value of nervous and osseous associations.

The previous question suggests several others which have already been much discussed.

1. What is the morphical relation between the membra and the omozone and ischizone ?

2. What is the morphical relation between these arches themselves and the skeletal axis ?

3. What relation do these arches hold to each other ?

It is now generally admitted that the scapula and ilium are not properly parts of the membra, although the former, especially, appears to be such in many quadrupeds, which lack the other elements of the omozone; and although the telical antagonism of position between scapula and ilium has led me to include these bones in the presentation of evidence (45, 20,): but I am now convinced that this, like some other considerations (the convergence of the dorsal spines toward the centre of motion, and the antagonism of membral internodes), must be eliminated from the discussion.

The relation between the membra and the membral arches has been ably discussed by Humphrey, (36, 23); also by Wyman, (55, 264), who concludes that "in their primary condition, limbs do not appear to be dependencies of the scapular and pelvic arches any more than . . . . . the teeth are dependencies of the jaws, with which, notwithstanding their totally different origin they become so intimately united at last." Stili, and in spite of the probability that the omozone serves, especially with fishes, as a heart protector, there seems no reason to doubt that both omozone and ischizone are formed with reference to the attachment of the membra, and are shifted in position in conformity with the needs of different species. Upon this point consult also Coues, (70, 194, note).

This leads to the second question as to the morphical relation between the omozone and ischizone and the rest of the skeleton.

The view of Owen that the " scapular arch is normally the haemal arch of the posterior occipital vertebra of the skull" has been endorsed by no real investigator of the subject,[1] and has on the contrary been vigorously combated by Goodsir, (240, 199,) Humphrey, (36, 26),

[1] Prof. Dana has in a letter to me stated that he now regards the relation of the arms to the head as a functional one, not a structural, as admitted in 217, 341; and I here beg to withdraw my own acceptance of what Parker calls the "peripatetic morphology of the shoulder-girdle."

Agassiz, Wyman, (55, 260) Spencer, (299, 522) and Parker, (292, 87); like some other views of the eminent English anatomist, this must be regarded as a motion unseconded, and therefore not open to debate. Upon this question consult Parker, (292), Cleland (65,) and Wyman (55, 260,) who think that "additional evidence, especially from embryology, is needed before definite conclusions can be reached."

Embryology ought to determine whether the forward transfer of the ventrals to beneath or even in front of the pectorals, in some *Malacopteri*, is a real shifting or only an ideal one, and if the former, how it is accomplished ; for evidently our second proposition will not be accepted by the "realists" in anatomy so long as the "legs" are in front of the "arms" with any vertebrate, unless a sufficient account can be given of the matter, enabling us to adduce the somewhat similar displacement of the eye in the *Pleuronectidæ*, which, by the way, could be made to serve in the elucidation of both problems, since Traquair's researches are not so complete as might be wished.

As to the third question, there seems to be no dispute that the omozone and ischizone do, in some way correspond; but both Wyman and Humphrey, who have most ably discussed it, will now doubtless admit that no determination of the special homologies of the constituent bones can be other than provisional until the development of the ischizone has been elucidated as completely as that of the omozone has by Parker; and even then, we must know whether these bones are to be compared syntropically or antitropically; the importance of such determinations is obvious on account of the great number of muscles which arise from the two arches.

We have now to inquire whether the foregoing considerations justify our acceptance of the proposition that the armus and skelos are respectively appendages of the cephalic and caudal regions of the trunk ; it seems to me that they do justify us in accepting it provisionally, and until it is satisfactorily shown, first, that there are more than two pairs of membra, actual or potential, and second, that no such thing as antitropy exists in the body itself. Till then, I think we are entitled to study the membra as if they might be proved to be antitropically related, and to regard our success in such comparison as presumptive evidence of the correctness of our method.

Membral Osteogenesis.

If, as is held by Darwin and others, the morphical value of a character is inversely to its apparent telical importance, I think a very strong argument in favor of the antitropic relation of the membra may be derived from the manner of their ossification as described and figured by Robin.[1]

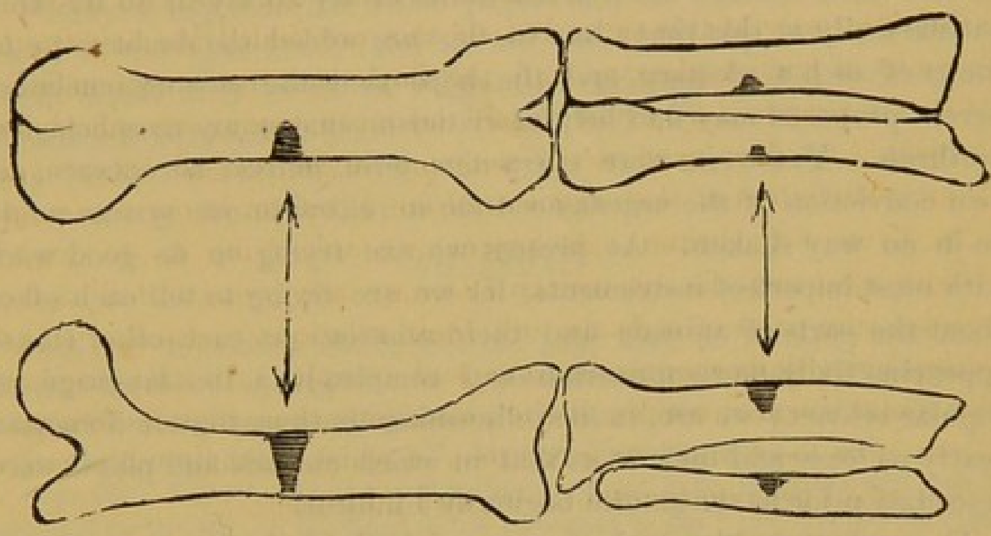


Fig. 5.

I have copied his figures, reversing one of them in order to show the membra in the relative position which they would have when attached to the body, the inside borders (post-armal and pre-skeleal) facing each other. It appears from both the figure and description of Robin, (though he evidently attached no such significance to the fact, and this gives it the greater value for us,) that the long bones of both membra begin to ossify in a strictly antitropic manner, the very shapes of the points of ossification being symmetrically related. If this is the rule with the mammalia, I shall look upon it as a most decided confirmation of the general views advocated in this paper, and would call the attention of embryologists to the statements of Robin, which I have no means of verifying at the present time.

[1] Sur les conditions de l'osteogenié avec ou sans cartilage prexistant; Journ. de l'Anatomie, Tom. 1, 1864, p. 577, Pl. xv.

REMARK.

The delay in the publication of the last part of this paper enables me to offer some general remarks upon it in place of the Glossary of morphological terms, the announcement of which was inserted during publication, but which for various reasons I have concluded to omit.

The chief of these reasons is a doubt of my ability to do the work satisfactorily at this time; but to this are added the doubt as to the limits of such a glossary, and the hope that the new nomenclature herein proposed may find helpful criticism among my morphological brethren. Yet even were every new term refused acceptance, my own conviction of the urgent need for a reform in our system would be in no way shaken. At present we are trying to do good work with most imperfect instruments; for we are trying to tell each other about the parts of animals and their relations to each other (these appearing daily more numerous and complex), in the language of popular science; we are, in fact, discussing these matters in a manner nearly as loose and inexact as that in which animals and plants were described prior to the reform begun by Linnæus.

The various problems which are involved in the general question of intermembral homologies, are rather indicated than discussed; the solution of some requires new information upon *facts*; but it seems to me that a more urgent need is some agreement as to the *value* of different kinds of evidence; together with a logical method in its application. In view of these necessities I venture to suggest the incorporation of systematic instruction upon "logic" and "evidence" into all University Courses in Natural History. I am certain that had logical and legal methods of thought been followed, the acceptance of the symmetrical relation of the membra never would have been hindered by a purely popular superstition, like the correspondence of thumb and great toe; and I claim to have proved in the foregoing pages that the agreement or disagreement of parts in *numerical composition* has never been held to invalidate any homology based upon *relative position* or *mode of development*. Yet even in this section of my paper merely an outline of the evidence and argument is given, and I have to thank my friend Dr. Coues for a forcible amplification of certain points. I may here refer to the intention formed ten years ago, and expressed at the beginning of this paper, to make the elucidation of intermembral homologies a main object through life, and to offer from time to time papers upon the special problems involved. One word as to the historical sketch; I can hardly hope to have done justice to all; especially to those whose works have not been directly accessible; but while the diagrammatic arrangement of the authors will make my errors more apparent, it will also enable every one to find or alter his own proper place, or that of another upon the scheme.

Finally I beg that the whole paper may be viewed as a "topography of our ignorance," and as an effort to map out our future work, rather than as an *ad captandum* attempt to decide the great questions herein presented.

ADDENDA.

Page 161. It is worth noting that the great work of Bourgery and Jacob contains the following suggestion to a symmetrical comparison of the membra, which, however, like many another, fell still-born; "En resume, l'epaule n'est autre chose que le bassin renverse." Anat. de l'homme, tom i, p. 107.

Page 169. I trust that the new technical terms here proposed will not be included by the Rev. J. G. Wood in his reference to the "Cacophonic combinations of syllables" (Ill. Nat. Hist. of Birds, p. 173). Yet his general criticism upon scientific nomenclature is well merited; and would only perhaps be more useful if coming from one whose style was less diffuse than that of the above-mentioned popular writer.

Page 173. Synonyms of Annularis; from Huxley, 78; *Ulnar finger*, p. 266; *Ulnar digit*, p. 270; *Fourth digit*, p. 269.

Page 311. As to the morphical value of numerical composition Mivart says, "I think the degree of segmentation of such structures (ribs) of very little consequence morphologically." Vertebrate skeleton, p. 374.

Page 326. The phrase "morphological value" occurs in Wyman's paper on the Development of Raia batis, 337, 35.

Page 328. As to establishing different kinds of groups upon certain organs, Agassiz says, "No system can be true to Nature which is based upon the consideration of a single part, or a single organ"; 201, 289. And Alfred Newton, in reviewing Huxley's new classification of *Aves*, speaks as follows: "It does seem a question very much deserving of attention, how far any approach to a natural system can be based upon the modifications of one part of an animal's structure, without any reference whatever to other portions of it." Zoolog. Record, 1867, p. 48.

Page 330. Agassiz intimates that orders are based upon *internal* structure, in contradistinction to form upon which families are founded; 201, 213.

Page 332. I greatly regret that Kowalewsky's researches upon the development of Amphioxus were not accessible to me when this paper was written: the little creature is a good illustration of the contrast between teleological importance and morphological value, for I believe it will prove more useful than all other vertebrates together, in deciding the problems indicated in this paper.

Page 337. For representation in fibrous tissue by adult structures of what was cartilaginous in the embryo, see Parker (292, 182 and 197).

Page 338. As to the morphical value of development, the two great English authorities differ further, as follows: Owen (63, 3, 742) speaks of the "low taxonomic value of the placental character"; "development is no ground of homology or homotypy"; while his general repudiation of the criterion is vigorously expressed as follows: "Whenever a false homology has to be maintained, the earliest and obscurest phenomena and embryonal development are usually resorted to in support of such view" (63, 3, 146, note 5). While Huxley, on the other hand, states that "an extensive study of the integumentary organs convinces one at once that mere structure affords no base for homology; . . . these definitions of ecderon and enderon rest wholly upon the mode of growth." Cyc. Anat. and Phys.; suppl., p. 476.

VII. CHRONOLOGICAL LIST OF SPECIAL WORKS AND PAPERS UPON INTERMEMBRAL HOMOLOGIES.[1]

1. Vicq d'Azyr: Memoire sur les rapports qui se trouvent entre les usages et la structure des quatre extrémités dans l'homme et dans les animaux. Mémoires de l'Académie royale des sciences, 1774, p. 254. (Reprinted in Œuvres recueillies par Moreau, 1805; tom. iv, p. 315.)

2. Winslow, J. B.: Exposition anatomique de la structure du corps humain, nouvelle édition, 1775. (First edition, 1732; second, 1763.)

3. Isenflamme et Ferlyrolles: Dissertation des extrémités —— —— Erlangen, 1785.

4. Chaussier: Exposition des Muscles, 1789.

5. Sœmmering: De corporis humani fabrica, 1794.

6. Cuvier: Leçons de l'Anatomie comparée, 1800; tom. i, p. 430. (2d ed. 1832.)

7. Handbuch der menschlichen Anatomie, 1816. (See also the French and English editions.)

8. De Blainville: Nouveau dictionnaire d'histoire naturelle de Deterville, 1818; tom. xix, p. 91. (See also his Ostéographie *Primates*, tom. i, p. 26, 1841; and a citation upon the Muscles in the Appendix to Meckel's Traité d'anat. comp., tom. vi, p. 494.)

9. Barclay: The bones of the human body represented in a series of engravings; explanation of plate XXIV, 1824.

10. Gerdy: Note sur le parallèle des os; Bulletin Univ. de Férussac, Sciences Médicales, tom. xix, 1829.

11. Duges: Sur la conformité organique de l'echelle animale; Ann. des Sci. Nat., 1831. (Printed separately, 1832.)

[1] An asterisk indicates that the work is in the possession of the writer. For others he would be glad to exchange copies of the present and previous papers.

12. Bourgery (et Jacob): Traité complet de l'anatomie de l'homme; tom. i, pp. 132–135, 1832.

13. Blandin: Nouveaux éléments d'anatomie descriptive, 1838.

14. Flourens: Nouvelles observations sur le parallèle des extrémités dans l'homme et les quadrupèdes; Ann. des Sciences Nat., 1838; the same in Memoires d'Anat. et de Phys. Comp., 1844. (With plates.)

15. Richaud: Sur l'homologie des membres supérieures et inférieures de 'homme; Comptes rendus, tom. xxix, p. 130, 1840.

16. Bergmann: Vergl. des Unterschenkels mit dem Vorderarm; Müller's Archiv für Anatomie, 1841.

17. Budd: On diseases which effect corresponding parts of the body in a symmetrical manner; Med. Chi. Trans., Vol. xxv, 1841.

17½. Paget: On the relation between symmetry and the diseases of the body; Med. Chi. Trans., Vol. xxv, 1841.

18. Cruveilhier: Parallèle des membres thoraçiques et des membres abdominaux; Anat. desc., tom. i, p. 340, 1843.

19. Strauss-Durckheim: Traité d'Anat. Comp., 1843, pp. 281, 282.

20. Owen: On the archetype and homologies of the vertebrate skeleton; Rep. of Brit. Ass. for Adv. of Science, 1846; pp, 169–340. (Many figures.)

21. Auzias Turenne: Sur les analogies des membres supérieures avec les inférieures; Comptes rendus de l'Acad. des Sciences, 1846; tom. xxiii. p. 1148.

22. Maclise, Joseph: Comparative osteology and the archetype skeleton; 1847. (With plates.)

23. *Maclise: Article Skeleton; Todd's Cyclopedia of Anatomy and Physiology, 1849.

24. *Jones, T. R.: Article Osseous System; Cyc. of Anat. and Phys., 1847.

25. Rigaud: Sur l'homologie des membres supérieures et inférieures de l'homme; Comptes rendus de l'Acad. des Sciences, 1849, p. 630; the same, Revue et Magasin de Zoölogie, 1849, p. 564.

26. *Agassiz and Gould: Principles of Zoölogy, 1851.

27. Gervais: Sur la comparison des membres chez les animaux vertébres; Ann. des Sciences Naturelles, 1853.

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[1] An apology is due for the inaccuracies, omissions and occasional inconsistencies of the foregoing list of works. The latter defect is mainly the result of my desire to avail myself of the numerical designation of many works before the list was completed; a partial remedy for the others will be the reception of the papers not herein marked as already in my possession.

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