XV. *On the Vertebrate Skeleton.* By ST. GEORGE MIVART, F.R.S.

(Plate LIII.)

Read April 21st, 1870.

THE paper which I have now the honour of submitting to the Linnean Society, is an endeavour to throw, if possible, a little additional light on relations believed to exist between certain subordinate portions of the vertebrate skeleton.

In order to attain this object I am compelled to make certain general observations on the skeleton as a whole, and upon the different ways in which its component parts may be regarded.

The term "skeleton," in its broadest sense, may be considered to denote that system of structures which invests and supports the whole frame; but it is generally and conveniently taken to mean such parts of that system as assume (at least occasionally and in some animals) a cartilaginous or osseous condition.

The skeleton, so restricted, is generally considered to be divisible into two categories, namely:—one external, comprising dermal and epidermal structures—the *exoskeleton*; the other internal, and thence termed the *endoskeleton*.

The endoskeleton consists of a greater or less number of temporarily and permanently distinct parts; and these parts may be distinguished, grouped, and classified in as many distinct ways as there are distinct modes of regarding them. Thus they may be regarded:—

1. Teleologically, or according to the use, object, or application of parts, or groups of parts—as when we say "a wing-bone" or a "brain-protecting part."

2. According to shape and outline of parts—as when we say "a long bone," as in speaking of the tibia.

3. Histologically, or according to structure—as when we speak of "cartilaginous parts of the skeleton," or, again, of bones ossified from membrane (like the frontal), or from cartilage (like the basioccipital).

4. Developmentally, or according to the way parts arise—as when we speak of "skeletal structures developed in the dorsal plates of the embryo."

5. Specially, or according to the relation parts in one animal bear to parts in another animal—as when we speak of the alisphenoid of a bird and of a reptile.

6. Genetically, or accordingly as the resemblance between similar parts in different animals is due to inheritance from a common ancestor, or has arisen independently through similarity of conditions.

7. Serially, or according to the relation parts of an animal bear to other parts, in front of or behind them, in the same animal—as when we speak of "the last rib but one."

8. According to relations of bilateral symmetry—as when we speak of “the right clavicle.”

9. According to relations of vertical symmetry—as when we speak of “the upper and lower arches of the tail of a flat fish,” e. g. of a sole.

10. According to radial symmetry—as when we speak of “the processes diverging in various directions from a single vertebral centrum.”

11. Generally, or according to the place or rank occupied by a part, or series of parts, in an abstract ideal vertebrate skeleton—as when we speak of “a centrum,” or “a neural arch.” Such an abstract ideal, to be a suitable typical conception, should be the “simplest possible generalized expression of observed facts”*.

Now it is to a certain extent of special, but more of serial and general relations that I have to speak; and these have been so well defined and described by Professor Owen † under the happily chosen terms *special homology*, *serial homology*, and *general homology*, that little more, I think, need here be said with regard to them.

In investigating the special homology of skeletal parts, the test employed must be the connexions or contiguity existing, at first or ultimately, between the parts in question and other structures in the two or more animals compared.

In investigating serial homology the test employed must be the resemblance at first or ultimately existing between a certain skeletal part of some animal and other parts, in the same animal, in front of or behind that certain part. No other test than that of parts being or not being “in series” is, I believe, possible in questions of serial homology.

In investigating general homology, both the foregoing tests must be employed, and applied to the several parts of all the more divergent vertebrate animal forms.

The endo-skeleton is, at least conveniently, divisible into, 1, the *axial* skeleton, and, 2, the *appendicular* skeleton. Such a division I believe to be not only convenient but also natural.

THE AXIAL SKELETON.

The parts which together make up the axial skeleton are not yet all satisfactorily grouped and classified, as regards their general homology; and this remark especially applies to some of the inferior arches. Before, however, the general homology of these arches can be investigated with any chance of success, it is necessary to determine relations of special and serial homology.

The uncertainties which hang over these inferior arches have been forcibly brought home to my mind in studying the skeleton as it exists in tailed Batrachians—animals presenting such interesting resemblances to Fishes on the one hand, and to Reptiles and Mammals on the other.

To endeavour, if possible, to contribute towards the removal of some of these uncertainties, I have been led to review the labours of previous writers, and to reexamine and reconsider observations of my own. The results I venture now to present, in the hope

* Prof. Huxley's Croonian Lecture, 1858.

† Archetype and Homologies of the Vertebrate Skeleton, pp. 1 & 72.

that, if they cannot be deemed to supply what has been felt as a desideratum, they may yet provoke such investigation and criticism as by their refutation to elicit truth, and thus occasion, indirectly, what they may fail directly to accomplish.

In studying these tailed Batrachians I have been especially perplexed as to how it may be best to regard the hyobranchial apparatus on the one hand, and the subcaudal arches and processes on the other.

This perplexity has resulted in an endeavour to obtain, if possible, satisfactory answers to the following questions.

1. What is the best way to seek *à priori* a general view of the axial skeleton, or in what way may the axial skeleton as a whole be most reasonably regarded *à priori*?
2. What is the essential nature of ribs, transverse processes, and sternum?
3. What is the essential nature of branchial arches, and in what relation do they stand to ribs?
4. What is the essential nature, as compared with branchial arches, of the hyoidean arch, mandible, and more anterior structures?
5. What relation exists between "chevron bones"* and other parts of the vertebrate skeleton?

1. *As to the best way in which the axial skeleton, as a whole, may be regarded à priori.*

The more morphology is prosecuted, the more it becomes plain and evident that trustworthy views cannot possibly be arrived at without the study of development. Of late years this truth has been more or less recognized and acted on by almost all who have investigated the nature of the vertebrate skeleton. The most reasonable way, then, to endeavour to understand the skeleton is to recur to its earliest embryonic condition.

Dr. Cleland, in his interesting paper† on ribs and transverse processes (read at the Meeting of the British Association at Cambridge, in October 1862), differs from most of his predecessors in declining to regard the skeletal structures which envelope the cerebro-spinal centres as primary elements corresponding to those which embrace the trunk below, but rather as secondary offshoots from the latter. He says, "But the laminæ of the vertebræ are at right angles to the main direction of the dorsal plates and the layers of the embryo; and even as the elevations of blastema in which they are developed are processes from the middle layer of the embryo, so do the laminæ diverge from the main circle of the skeleton; and in that respect they are to be compared with the various processes directed outwards to the skin in fishes, and with the epicostal bones in birds"‡.

Although I think many of the ideas put forth by Dr. Cleland in the paper quoted exceedingly valuable, nevertheless I cannot follow him in this view as to the subordinate and secondary character of the neural arch; for though in estimating the nature and importance of structures as parts of a system we must carefully study their mode of origin, yet we must nevertheless consider fairly the outcome and the result of that process, in order to get the most complete general conception of that system as a whole. Now though "the cylinder which the cerebro-spinal axis forms" may be "the product of only

* By "chevron bones" I mean those detached Y-shaped ossicles so often found beneath the caudal vertebræ of animals above the class of Fishes.

† Nat. Hist. Review, 1863, vol. iii. p. 116.

‡ Loc. cit. p. 125.

a small portion of the external layer of the embryo," while the inferior cylinder is composed of "the whole internal layer of the embryo," yet in all vertebrate animals, when developed, the importance of the contents of the former is not inferior to that of the latter. The neural laminæ come to be of primary consequence, even if of secondary origin—just as the spinal nerves and their roots in the myelon come to be single and continuous structures in spite of the contrast presented by their several modes of development.

The nervous system, indeed, can hardly be considered as ranking below any other in the body. The special homologies of the cranial bones are best determined by taking the places of exit of the cranial nerves as fixed points; and it is certainly probable that the relations of the skeleton generally closely resemble those existing between different parts of the nervous system.

The mode of regarding the embryo which has been adopted by Professor Huxley seems to me to be the most simple and natural. According to that the embryo is developed from three pairs of antero-posteriorly extending laminæ, which radiate from the chorda dorsalis.

The first pair of laminæ, the dorsal plates, ascend and form the enclosure of the cerebro-spinal centres.

The ventral plates descend; and each bifurcates, the space formed by the bifurcation constituting the pleuro-peritoneal cavity. The outer walls of this cavity (formed by the outer bifurcation of each ventral plate) constitute the second pair of laminæ, or external ventral plates.

The parts within the internal wall of the pleuro-peritoneal cavity (except the lining membrane of the alimentary canal, which is formed by the mucous layer of the embryo) are formed by the third pair of laminæ, or internal ventral plates.

Now "such being the case, we might expect *à priori*, that a branch from each nerve-root would ascend into the dorsal lamina, that another would pass directly outwards, and two others would follow the laminæ formed by the bifurcation of the ventral plates—one passing along the body-wall (or external ventral plate) the other going down the mesentery to the alimentary canal (the internal ventral plate); and this is what we find to be really the case"*.

For the so-called sympathetic appears to be no separate system distinct from the spinal nerves, but merely to consist of those branches of the latter which descend into the third pair of laminæ (or internal ventral plates) together with commissural fibres.

This striking and original suggestion was made by Professor Huxley in the twelfth lecture of his last Hunterian course. Such being the conditions of the embryonic laminæ, and the spinal nerves being each arranged in this, at the least, triradiate manner on each side, we might expect *à priori* some parallelism as to arrangement to exist in the skeleton. In endeavouring to obtain a good general idea of the vertebrate skeleton, it seems reasonable, then, to look, in the most completely developed skeleton, for three longitudinal series of parts in addition to, and on each side of the common axis. I say "in the most completely developed skeletons," because we may expect in many forms a certain coales-

* British Medical Journal, for May 15th, 1869, No. 437, p. 445.

cence and indeterminateness of skeletal parts—just as nervous structures run together or fail to be differentiated. These series of parts may be expected, then, to be:—

I. Parts related to the first pair of laminae (that is, in the ascending or dorsal plates of the embryo), which may be spoken of as “dorsal” or *epaxial* parts (Plate LIII. fig. 2, E).

II. Parts related to the second pair of laminae (that is, in the external ventral plates), which may be spoken of as the “outer ventral” or *paraxial* parts (fig. 2, P).

III. Parts related to the third pair of laminae (that is in the internal ventral plates), which may be spoken of as the “inner ventral” or *hypaxial* parts (fig. 2, A, B, C).

Epaxial parts will be parts embracing the cerebro-spinal axis, or parts serially homologous with parts which embrace that axis.

Paraxial parts will more or less embrace externally the pleuro-peritoneal cavity (or at least lie without it), or be serially homologous with parts which do so in the trunk. These parts may be also expected to include skeletal elements tending to pass directly outwards, just as certain of the nerves pass directly outwards.

Hypaxial parts will be parts situated between the skeletal axis and some part of the pleuro-peritoneal cavity, or serially homologous with parts so situated.

Now between the skeletal axis and the pleuro-peritoneal cavity we find in the trunk:—

1. The great dorsal aorta.
2. The alimentary tract.
3. The heart with the great vessels springing from it.

It is conceivable then that we might have in a skeleton developed to the most complete possible degree, three kinds of hypaxial parts (Plate LIII. fig. 2, A, B, C):—

- A. Some embracing, or tending to embrace the dorsal vessels (fig. 2, A).
- B. Some embracing, or tending to embrace the alimentary canal (fig. 2, B).
- C. Some embracing or tending to embrace the heart and the great vessels springing from it (fig. 2, C).

These hypaxial skeletal structures might be defined, *à priori*, as skeletal parts either, on the one hand, intervening between the skeletal axis and the pleuro-peritoneal cavity together with any prolongations of it (if such there be), or else skeletal parts serially homologous with others which do so intervene,—or, on the other hand, as skeletal structures placed within the inner wall of the pleuro-peritoneal cavity together with any prolongations of it, or else skeletal parts serially homologous with others which are so placed.

Putting aside, then, all exoskeletal parts, with which we have, in this paper, nothing to do, and also putting aside the appendicular skeleton, the rest of the endo-skeleton (that is to say, the axial skeleton) may, from the mode of development of the embryo, and from that of the nervous system, be expected to appear (in its most developed condition) as a longitudinal axis whence three longitudinal series of more or less developed parts diverge on each side for a greater or less extent, namely:—1, epaxial; 2, paraxial; and 3, hypaxial parts. But a certain coalescence or connation of these parts may also be expected to occur more or less frequently, especially in lower forms.

So much for the *à priori* view; it remains to test its value by-and-by by *à posteriori* considerations.

2. *What is the essential nature of ribs, transverse processes, and sternum?*

Dr. Cleland, in the paper before referred to, has, I think, thrown much light upon this question; and with many of his arguments and determinations I fully agree. I do so especially as to the subordinate importance, in questions of serial or general homology, of the mode of ossification of parts or of their points of attachment to the vertebral column. With him, I believe that "ribs" are parts of the skeleton the primary office of which is to support the outer wall of the trunk, and I think the degree of segmentation of such structures is of very little consequence morphologically.

As to the significance, however, which is to be attached to the fact of parts being or not being "in series" I cannot at all agree with him; for I am at a loss to know what better or other guide we have in matters of serial homology.

All will admit that that part of the rib which intervenes between its head and tubercle in one animal is the general homologue of the part which so intervenes in another animal; and yet the researches of Rathke and Professor Huxley seem to show that sometimes it is a primary part of the rib, sometimes a mere outgrowth. Again, all will admit that the rudimentary neural arches of the tail of the dog are the serial homologues of the fully developed ones of the trunk; yet, as Dr. Cleland himself tells us*, the former are merely exogenous structures. These, and many other instances it would be easy to bring forward, show that diversity as to mode of development is no bar to the legitimacy of serial or general homologies.

Just as little can relations of functions claim a preference as a mode of determining such homologies. Otherwise the neural rudiments of the os coccygis could not claim to be serial representatives of those of the trunk, or caudal transverse processes to represent parts of the viscera-encircling girdles in front of them. Thus the fact of parts being "in series" is most important in determining serial homologies, and, when carefully used and checked by comparing results obtained in many different forms, is the best available guide.

I believe that all transverse processes, ribs, and sternal structures are elements of one system of parts, the primary office of which is to surround the visceral cavity (fig. 2, *p*, *t*, *tr*, *tr'*, *c*, *cr'*, *vr*, *sr*, & *s*), that they are essentially parts belonging to the external lamina of the ventral plate of the embryo, and that their serial relationships, as whole arches and as component parts of such arches, are revealed by the fact of serial position in such arches or parts of arches.

As to the conditions presented by the hard parts forming these arches, we find commonly in the highest animals a rib with a head and tubercle, the latter articulating with a transverse process.

In many of the *Amphibia* we find a rib bifurcating proximally and more or less distally also, and articulating, by the branches of its proximal bifurcation, with two superimposed transverse processes (Plate LIII. figs. 14 & 15, *t*, *c*).

In many fishes we find two series of ribs, one placed above the other; and sometimes these are attached to two more or less distinct, superimposed, transverse processes (Plate

* *Loc. cit.* p. 120.

LIII. fig. 9, *t, c*). There are also in many fishes additional bony rays (as notably in the Herring), generally admitted to be of quite subordinate importance, and which, as far as I know, are not represented, at least by hard structures, in any higher class.

In all the higher Vertebrata the ribs, and in fishes the lower series of ribs, lie, in the trunk, in close proximity to the outer wall of the pleuro-peritoneal cavity. These then are hard parts developed in the layer of a membrane enclosing that cavity. Another layer of membrane extends from the skeletal axis outwards, above the former; and in this layer (in fishes, at all events, if not also in higher vertebrates) hard parts are also sometimes developed.

It occurs forcibly to the mind, then, that the paraxial system of each side may be of an essentially duplex nature; and I venture to suggest for inquiry whether the facts of comparative anatomy, as regards these parts, may not be well and conveniently grouped together by some such conception as the following.

That there are really two series of paraxial elements on each side of the body :—

1. An upper series, which, leaving the central axis, tends outwards towards the skin (corresponding with the nerves passing directly outwards), and which may be termed *upper paraxial* or (making use of a name employed by Professor Owen) *diapophysial elements* (fig. 2, *t, tr, tr'*);

2. A lower series, which, leaving the central axis, tends downwards (corresponding with the abdominal nerves) to embrace the visceral cavity, or is serially homologous with other parts which do so, and may be called *lower paraxial* or (again after Professor Owen) *parapophysial elements* (fig. 2, *c, cr, vr, sr, & s*). And :—

That these two series of parts frequently coalesce (before or after solidification) for a longer or shorter distance, and by so doing give rise to double (superimposed) transverse processes with ribs bifurcating at each end (Plate LIII. figs. 14 & 15), or to ribs with the proximal bifurcation modified into “head” and “tubercle,” and with the distal bifurcation disguised by having only one limb of such bifurcation ossified, the other remaining membranous, or, finally, to bifurcating transverse processes simply (figs. 12 & 13).

According to this conception, the root of each upper paraxial element (when a solid structure) is the cartilage or bone (however ossified or wherever situated) connected with the tubercle of the rib of higher vertebrates; and it may be termed the upper transverse process, or the tubercular process, or the diapophysis* (fig. 2, *t*, & fig. 14).

This is continued outwards, in many fishes, by an upper series of ribs (fig. 9, *t, tr'*),—in other vertebrates by entering for a certain extent into the composition of the ribs, and thence onwards by a bifurcation of the rib, in *Amphibia*† (figs. 14 & 15), or, in the highest vertebrates, possibly by membranes passing upwards from the ribs external to the *erector spinæ*, or outwards from the ends of the caudal transverse processes.

The root of each lower paraxial element (when a solid structure) is the cartilage or bone (however ossified and wherever situate) which is connected with the head of the

* Professor Owen originally instituted this term to denote a process essentially *exogenous*. See ‘Archetype and Homologies,’ p. 82.

† Are the costal processes of Birds and Crocodiles similar?

ribs in certain vertebrates; and it may be termed the lower transverse process, or the capitular process, or the parapophysis (fig. 2, *c*, & fig. 14)*.

This (according of course to the same conception) is continued outwards by the ribs, and is often completed inferiorly by skeletal structures which, when ossified or chondrified, are termed sternal, *i.e.* sternal ribs and sternum proper (fig. 2, *sr* & *s*).

Thus we may have complete coalescence proximally of the upper and lower paraxial elements, and then we have a simple transverse process; or we may have a simple transverse process essentially diapophysial, because in series with the tubercular processes of vertebræ in front, as in *Delphinus*; or we may have an apparently quite similar transverse process essentially parapophysial in nature, because in series with the heads of the ribs of vertebræ in front, as in *Physeter*.

These distinctions, as they exist in the *Cetacea*, were pointed out by Professor Flower in his recent Hunterian Course.

Very often, as in so many fishes, the parapophyses and ribs of the trunk are represented in the tail by a single continuous ossification which answers to both. Thus the ribs of most vertebrates, according to this view, would be of essentially complex nature, and consist of an ossification which has taken place in the line where the upper and lower paraxial elements have coalesced. Amongst fishes, the Carp appears to have a single series of ribs into which both elements enter. It must be recollected that this conception is thrown out only as a *suggestion*.

It might be objected that the parts here treated as more or less distinct are often merely outgrowths one from the other. But this is no objection to the view that the form described is the one that the skeleton tends to assume, and actually does assume more or less completely. However solidification be attained, the tendency to solidify *in these particular lines* must preexist in the soft tissues. From the frequent point of origin of the diapophysis it is manifest that we often have coalescence or connation between paraxial and epaxial parts, *i. e.* between the transverse process and neural arch; yet they are accounted distinct.

The "*chevron bones*" and *caudal hæmapophyses* of Professor Owen belong, I believe, to an altogether different skeletal category.

3. *What is the essential nature of branchial arches, and in what relation do they stand to ribs?*

These arches have been regarded by Carus and Professor Owen as forming part of the splanchno-skeleton, and therefore as altogether distinct in nature from the vertebral and sternal ribs, and, indeed, constituting no part of the true endo-skeleton.

Professors Goodsir† and Huxley‡, on the other hand, take them to be the serial homologues of the thoracic or abdominal ribs, and therefore consider them what I call

* Though Professor Owen originally employed this term to denote a process essentially autogenous, now, however, he regards it as normally exogenous. See 'Anatomy of Vertebrates,' vol. i. p. 28.

† See 'Edinburgh New Phil. Journal,' vol. v. New Series, p. 131.

‡ "Hunterian Lecture" for 1869, see 'Brit. Med. Journal,' No. 443, June 26, 1869, p. 589.

paraxial elements—that is, parts which embrace externally the pleuro-peritoneal cavity, or serially homologous with other parts which so embrace it.

I venture to assert, on the other hand, that they are rather hypaxial elements; consequently I agree with Carus and Professor Owen in considering that they belong to a different category altogether from that to which ribs and hæmal arches belong; while at the same time I differ from these authors, and agree with Professors Goodsir and Huxley, in taking them to be certainly portions of the true endo-skeleton.

My reason for so considering them—for counting these hard parts as belonging to the internal laminæ of the ventral plates, or as belonging to those parts (of the undifferentiated ventral plates) which correspond to the internal laminæ of those portions of the ventral plates which *are* differentiated into internal and external laminæ—is the relation which they (*i.e.* the branchial arches) bear to the root-vessels of the arterial system (Plate LIII. figs. 3 & 20, *v*).

The pericardium, with its serous lining (derivations from the primitive pleuro-peritoneal sack), is continued for some distance along the great vessels which leave the heart. These continuations probably indicate the primitively greater extent of the pleuro-peritoneal cavity, and that parts embraced by such pleuro-peritoneal extension belong to the internal laminæ of the embryonic ventral plates. Moreover the parts which spring from and are directly continuous with the parts so embraced may fairly be reckoned (in the absence of any proof to the contrary) as belonging to the same category. I mean that if the roots, so embraced, of the great vessels belong to the inner portion of the ventral plates, then the parts of such vessels, just beyond the point to which such investment can be traced, also belong probably to the same portion of the ventral plates.

This is the more probable as the pericardium is continued on to the large blood-vessels so as to “form tubular prolongations, which become gradually lost upon their external coats”*.

Now in osseous fishes the heart and aortic arches lie *outside* and extend along the *external* margins of these branchial arches (Plate LIII. fig. 20, *v*); and consequently these arches must belong to the inner portion of the ventral plates, and therefore cannot correspond to ribs or other hard parts which embrace the pleuro-peritoneal cavity on its outer side.

Professor Goodsir† long ago called attention to the fact that “in Fish and Amphibia the heart and the branchial artery and its branches are situated below and external to the skeleton of the branchial apparatus.” He further expresses his wonder “that those who refer the branchial and pharyngeal arches to a splanchno-skeleton, have not adduced the external position of the hæmal axis to these arches as an argument in support of their opinion;” but he rejects the argument himself as involving consequences (concerning the mandible &c.—points which will be considered further on) which he regards as fatal, but which are not at all so in my eyes.

I have been much strengthened in my confidence as to the correctness of this view by finding that my friend Mr. W. K. Parker has independently arrived at a similar result, at least as far as regards the non-correspondence between branchial arches and ribs.

* Quain and Sharpey's ‘Elements of Anatomy,’ 5th edit., 1848, vol. ii. p. 1101.

† *Loc. cit.* p. 129.

The branchial arches of osseous fishes and of Amphibia appear, then, to me to be most probably hypaxial elements belonging to the category B—hypaxial elements because they are hard parts either placed within the inner wall of the pleuro-peritoneal cavity or serially homologous with parts so placed, and belonging to the category B because they embrace or tend to embrace a portion of the alimentary tube. They are thus considerably different in nature from the parts (chevron bones, hypapophyses, &c.) which constitute the category A of hypaxial parts. The latter are essentially in close connexion with the skeletal axis. The hypaxial parts of category B, on the other hand, are essentially related to the alimentary tube and its prolongations. Thus, when these latter hypaxial parts exist without corresponding solidifications of the category A, it is evident, *à priori*, that they may be quite detached from the skeletal axis, may arise* independently, and may have not only primitively but even ultimately, no solid connexion with it.

If this reading is correct, the nerves which descend beside these branchial arches (Plate LIII. fig. 20, *l*) cannot answer to the abdominal branches of the spinal nerves, but are rather hypertrophied representatives of the sympathetic. Now the branches of the vagus which descend in the posterior mediastinum should also be considered sympathetic, as that space is the upper portion of the internal laminae, *i. e.* within the pleuro-peritoneal cavity.

Moreover Professor Huxley in his last Hunterian course supported the view of the essentially sympathetic nature of the vagus; and, as regards the branches supplying the branchial arches, he said “it is probable that these are distinct nerves, the true origins of which have become quite inconspicuous, while their antero-posterior commissural fibres have become exceedingly developed”†.

It remains to notice the branchial arches of the Elasmobranchs and of the Lamprey.

In the Elasmobranchs (Plate LIII. fig. 3) it is manifestly the internal cartilages (within the arterial branches) which correspond to the branchial arches of osseous fishes. To what, then, do the external cartilages correspond? I should suggest that they are paraxial parts, and really do correspond to the ribs and hæmal arches of posterior segments of the trunk (fig. 3, *p*).

In the Lamprey, on the other hand (Plate LIII. fig. 4), the vessels are internal, and therefore the cartilaginous basket cannot at all answer to the branchial arches of osseous fishes; it answers only to the external branchial cartilages of the Elasmobranchs, and so is probably also paraxial in its nature (fig. 4, *p*).

This view is confirmed by its line of suspension, which runs along the *side* and *outer wall* of the skeletal axis. The branchial arches, on the other hand, are suspended, as manifestly in certain Elasmobranchs, to the *under* surface of the spinal column (Plate LIII. fig. 5).

The cartilaginous protection of the heart of the Lamprey is thus no part of the hypaxial

* If the resemblance to Vertebrates lately discovered in larval Ascidians be a resemblance due to genetic affinity, and not, as is quite possible, to some similarity of conditions, then this part of the hypaxial system may turn out to have originally arisen in a different mode from the rest of it. But the generalized expression of facts here adopted will none the less apply to the skeleton as it exists in the five vertebrate classes; as was before said, the outcome and result of development must have its weight as well as the mode by which that result is attained.

† *Loc. cit.* May 22, 1869, p. 466.

system, but is a median inferior portion of the paraxial system, and is thus a representative (and, as far as I know, the only true representative in Fishes) of the sternum.

4. *What is the essential nature, as compared with branchial arches, of the hyoidean arch, mandible, and more anterior structures?*

The hyoid arch and mandible have both been considered by Professor Owen to belong to the true endo-skeleton, and therefore to differ radically in their nature from the branchial arches, the latter, as has been said, appertaining to the splanchno-skeleton according to the same Professor.

Carus has taken the same view of the hyoidean arch, but not of the mandible.

Professors Goodsir and Huxley concur in thinking that the mandible and hyoidean arches are both endo-skeletal structures, and similar in essential nature to the branchial arches behind them.

I agree in these opinions with the distinguished Professors last named; but, as they (as before mentioned) have considered the branchial arches essentially similar to ribs, while I do not do so, there is, of course, a similar divergence in our estimation of the hyoidean arch and mandible.

As to structures in front of the mouth, Professors Owen and Goodsir both believe that there is a maxillary hæmal arch serially homologous with the mandible; while Professor Goodsir counts the palatine arch as a separate hæmal segment.

Professor Huxley, in his last Hunterian course, threw out a very original and striking idea as to the præ-stomal serial homologues of the mandible. He said*, "May not the maxillo-palatine processes and the trabeculæ cranii be the most anterior members of the same lateral series?"

I am inclined to fully accept this view as regards the trabeculæ; and I am again strengthened, in so doing, by the valuable opinion of my friend Mr. Parker, who has described to me the primitive downward-tending position of the trabeculæ cranii of the Frog.

By an elaborate description of the arrangements of the vascular and nervous systems, Professor Huxley supported his conjecture as to the præ-stomal arches, and by the very same considerations he seems to me to have conclusively and unanswerably demonstrated the essentially similar nature of the hyo-mandibular and branchial arches. He showed how the serial homologues of the branchial arteries were represented, or their course indicated, by the pseudobranchiæ of *Heptanchus* and *Lepidosiren*, and by the "so-called" carotid gland of the Frog. He stated that the external carotids were the continuations forwards of the ventral aortic roots, and that the internal carotids were the representatives of the most anterior part of the dorsal aorta.

He also showed that as the branches of the vagus (Plate LIII. fig. 2, *l*) skirted the branchial arches, so the ninth nerve, or glossopharyngeal, divided and then skirted the adjacent sides of the hyoidean and first branchial arches—that similarly the seventh nerve divided to go to the adjacent sides of the hyoidean arch and mandible respectively—that, in the same way, the fifth nerve supplied the adjacent sides of the mandible and

* See 'British Medical Journal' for June 26, 1869, p. 590.

palato-quadrate arches, while, finally, the ophthalmic division of the fifth skirted the adjacent sides of the palato-quadrate arch and the trabecula cranii of the same side.

Thus, then, if I am right in believing the branchial arches to be hypaxial skeletal elements, it follows that the mandible and hyoidean arches, and most probably the trabeculæ cranii are hypaxial also.

Are there, then, any solid parts belonging to the paraxial system—*i. e.* answering to the external branchial cartilages of the Elasmobranchs, and to the cartilaginous branchial skeleton of the Lamprey (figs. 3 & 4, P)?

On this point I am not prepared to absolutely affirm any thing; but I am inclined to believe that the labial cartilages of Sharks (the nature of which has been so much disputed) will be found to belong to the paraxial and costal category. Some of the complex labial cartilages of the Marsipobranchii may possibly also be of the same nature essentially; and it does not seem to be impossible that even some of the cartilages of the nose may be modified representatives of the true hæmal arches of the anterior extremity of the axial endo-skeleton.

5. *What relation exists between the "chevron bones" and other parts of the vertebrate axial skeleton?*

By "chevron bones" I mean those subcaudal arches which exist in many Mammals and are so largely developed in the Cetacea, and the serial homologues of these arches, supposing such homologues to exist. To inquire, therefore, into the relation of these bones or processes to other parts of the axial skeleton as it exists in all five classes of the vertebrate subkingdom implies the asking of two important questions.

1. What is the nature of the mammalian "chevron bones"?
2. What is the nature of the analogous subcaudal arches of Fishes?

Professor Owen* regards the distinct bony arches beneath the tail of Cetaceans and other Mammals, and of Crocodiles and other Reptiles, as the serial homologues of the hæmal arches embracing the trunk, while the small arches beneath the cervical vertebræ of the Pelican belong, according to him, to another category altogether—namely, to that to which the inferior median processes of Serpents and Lizards belong, together with the processes to which the chevron bones are sometimes attached, as in *Myrmecophaga*†.

In this view of the chevron bone as a hæmal arch removed from its normal costal attachment and articulating with the centrum, Professor Owen has not been followed by many; and it is an interpretation I can by no means accept, believing as I do that the distinction between autogenous and exogenous parts is of quite subordinate importance‡.

* 'Archetype and Homologies,' and Part I. of Memoir on the Megatherium, Phil. Trans. for 1851.

† See Memoir on the Megatherium, plate liii. fig. 60, *hy*.

‡ Dr. Cleland is of a similar opinion, which he thus supports in a passage before referred to:—"There are caudal vertebræ in many mammals, the Dog for example, entirely ossified from the centra, which send upwards very small pairs of processes forming the rudiments of neural arches, and outwards small transverse processes. Whatever we may think of the latter, we cannot fail to see that there is a greater amount of correspondence between the former and neural arches than can be counterbalanced by the fact of their being productions of the centrum and not autogenous." "So also the anterior part of the upper jaw in man indubitably corresponds to the intermaxillary bone in any other mammal, although, except in cases of cleft palate, it is ossified, as M. Em. Rousseau has shown, from the

The learned Professor himself has modified the views he first put forward on the subject, as he himself states; for at first he was disposed to regard even the subcervical canal of the Pelican as the homologue of the thoracic hæmal arch*.

This change of opinion is so far an approximation to the view which I venture to believe is correct—namely, that neither the subcervical nor the subcaudal arches are homologous with hæmal ones, but are hypaxial and not paraxial parts.

Professor Goodsir† differs from Professor Owen, and, while he deems it probable that the chevron bones are similar in nature to such parts as the subcervical canal of the Pelican, at the same time considers the hæmal arches (vertebral and sternal ribs) quite distinct from either. The true representatives in the tail of these hæmal arches of the trunk he takes to be the transverse processes with the aponeuroses extending down from them. In a note he says:—"In dissecting lately a large Crocodile, I found that an aponeurotic membrane extended outwards, and curved downwards on each side from the extremities of the caudal transverse processes. These aponeuroses met one another in the mesial line below the tail, and were there joined by a mesial aponeurosis which extended down from between the chevron bones. A layer of fat one-third of an inch in thickness lay on the outside of the lateral aponeuroses; and imbedded in it the hæmal divisions of the spinal nerves extended outwards, downwards, and backwards, like a series of intercostal nerves. The lateral muscular mass of the tail, arranged in myotomes with metamyotomic fibrous laminae nearly as distinct as in the fish, lay on the outside of the layer of fat. Each of the lateral aponeurotic cavities was occupied by the 'fémoro-péronéo-coccygien' muscle of Cuvier‡, which arose from the under surfaces of the transverse processes, the sides of the chevron bones, and mesial aponeurosis, and passed out of the cavity through a space left in its outer wall behind the ischium to be inserted into the thigh bone. The mesial membrane divided above, its two laminae corresponding to the limbs of the chevron bones, and passing in front into the walls of the pelvis." He adds, "This arrangement appeared to me to indicate that the transverse processes and the lateral aponeuroses and the hæmal divisions of the spinal nerves, were in the position of the proper hæmal arches of the tail—that the two aponeurotic chambers constituted in fact, together, the abdominal or visceral cavity, divided by the mesial lamina, and occupied by a pair of muscles referable to that group of muscles which in the trunk lie on the inner surface of the visceral chamber—and that therefore the chevron-bones are not real hæmal arches, but subcentral developments."

Dr. Cleland appears to take a similar view. He says§, "In Saurians the inferior caudal arches are only in series with structures projecting into the interior of the visceral cavity: those in the anterior part of the tail so project; and further forwards, in series with

maxillary. August Müller also demonstrates the small importance of the division or non-division of the costal element into 'rib,' and 'transverse process.'"

Professor Huxley in his Hunterian Lectures has brought forward numerous instances of diverse modes of ossification of similar parts; and Professor Flower has done the same in his recent and first course of the same lectures.

* Geol. Trans. vol. v. 2nd Series, p. 519, pl. 44, figs. 2 & 3.

† *Loc. cit.* p. 128.

‡ My femoro-caudal in *Iguana*, *Menopoma*, and *Menobanchus*, Proc. Zool. Soc. June 27, 1867, and April 22 and June 24, 1869.

§ *Loc. cit.* p. 130.

them, there are, in certain species, imperforate processes projecting in the middle line, and not even forking to enclose the great vessels."

Professor Huxley, speaking of the chevron bones of the Amphibia, says, in his last course of Hunterian lectures *, "These processes certainly, however, do not answer to ribs, as they coexist with transverse processes to the extremities of which moveable ribs are articulated." This is well seen in *Menobranchus*.

Now, reverting to the condition of the embryo, and the bifurcation of the ventral plates into the external and internal laminae, I think it is most probable that median azygos processes beneath the centra of the trunk vertebrae belong to the common root of the internal laminae. Such processes are, *e. g.*, those in the lumbar and last dorsal vertebrae of the Hare, the last cervical vertebrae of the Great Auk and Penguin (Plate LIII. fig. 11, Hy.), the trunk vertebrae of the Rattle-snake or Cobra, &c. &c.

Often, *e. g.* in the Penguin, median azygos and quite single processes are in series with others which begin to bifurcate, and these again with others in which the bifurcating limbs reunite inferiorly so as to form a subcentral bony ring.

Such parts in the trunk evidently, if they do not actually belong to the internal laminae, are clearly related to them, and belong to that part of the undifferentiated mass from which those laminae elsewhere proceed; they are therefore what I propose to call hypaxial parts.

Now as, in the series of hypaxial parts forming the hyo-branchial apparatus and jaws, the branchial arches (if any) in front of the bifurcation of the ventral plates into external and internal laminae are most probably similar in nature to those behind (and therefore within) such bifurcation, so the processes, ridges, or arches in parts of the body where there may be no distinct differentiation into external and internal laminae must be held similar in nature to the serially homologous ridges, processes, and arches developed in parts of the body where there is such a differentiation.

Again, just as the aortic arches may be taken as indicating the potential line of such differentiation beyond its actual limit, so the continuation backwards of the dorsal aorta may similarly be taken as a potential (if not actual) division—the parts immediately embracing it in the tail being evidently serially homologous with the parts embracing it in the trunk. Now the dorsal aorta in the trunk belongs surely to the system of the internal laminae and their common root, the external laminae lying altogether without and surrounding the visceral cavity. Therefore any hard parts immediately embracing the caudal continuation of the dorsal aorta must belong to the same system (*i. e.* to the internal laminae), unless, by the atrophy of the visceral cavity, parts serially homologous with ribs are brought into immediate contact with the caudal vessel, and coalesce or are connate with or replace and simulate absent hypaxial parts.

The coexistence, however, in the tail, of the transverse processes of both kinds (tubercular and capitular) with chevron bones, as in *Menobranchus*, proves that the latter bones cannot be the homologues of the paraxial hard parts of the trunk (as has already been said); while the fact of their being embraced externally, in the Crocodile, by the lining membrane of the continued visceral cavity (as observed by Professor

* *Loc. cit.* p. 279.

Goodsir) proves them, in my opinion, to belong to the system of the internal laminae, and to be true hypaxial parts.

If, then, my view be correct that the mode of ossification and the degree of segmentation of skeletal elements is of secondary importance, it seems to me that the subcervical rings or processes, and the azygos or bifold subthoracic plates of Birds, together with their homologues in other Sauropsidans and in Mammals (in fact, all parts in these groups which are termed hypapophyses by Professor Owen), are serially homologous with the "chevron bones" of the same animals, and that they all belong to my category A of hypaxial parts. At the same time it must always be borne in mind that the hypaxial and paraxial parts have a common starting-point, that it is probable *à priori* that they will sometimes coalesce, and that this coalescence may take place before solidification, and that thus we may have a skeletal part which is neither completely paraxial nor hypaxial, but partakes of the nature of both, and may therefore be called *parhypaxial*.

The second question about chevron bones has now to be answered, namely, *What is the nature of the analogous subcaudal arches of Fishes?*

Professor Owen* regards these arches as formed by bent-down paraphyses, *i. e.* by essentially paraxial elements. I have not as yet ascertained what precise view Professor Goodsir held as to the homology of these piscine arches with parts of the mammalian or sauropsidan skeleton.

J. Müller† considers them to answer to the chevron bones, and the piscine and mammalian ribs to be homologous.

A. Müller‡ thinks the ribs of fishes peculiar, and different from those of mammals; and it seems to follow from his views that "chevron bones" are the homologues of the former, the mass of muscles below the lateral intermuscular septum being considered by him to answer to the subvertebral muscles placed within the ribs in higher animals.

Dr. Cleland§ combats (I think, very successfully) August Müller's view, saying, "In the saurian tail the lateral intermuscular septum is found as in fishes. The muscles superior to it are, as August Müller rightly observes, continued into the muscles of the back; but the muscles below that line cannot be justly described as continued into the interior of the visceral cavity. The superficial ones are attached to the pelvis; and continuous with them, in front of the pelvis, are those muscles of the abdomen which lie superficial to the ribs, among others the rectus, which can easily be distinguished in some fishes. When the fore part of the tail is laid open, we find, indeed, two masses of muscle continued into the abdominal cavity, and which, as has been shown by Professor Goodsir, are enclosed in the continuation backwards of the lining membrane of the abdomen; but that that membrane corresponds not to the lateral intermuscular septum of the first, but to the lining membrane of the fish's abdomen, is proved by the co-existence of the lateral intermuscular septum, which finds its way to the skin in fishes. Forward in the trunk there are both infracostal and transversi abdominis muscles internal

* Anatomy of Vertebrates, vol. i. p. 40.

† Vergleichende Anatomie der Myxinoiden, p. 100.

‡ "Beobachtungen zur vergleichenden Anatomie der Wirbelsäule," Müller's Archiv, 1853, p. 260 &c.

§ *Loc. cit.* p. 127.

to the costal arches; but the main trunks of nerve are outside these, not on their abdominal aspects, as they would have been were August Müller's theory correct."

Dr. Cleland regards the costal arches of fishes as homologous with those of the higher vertebrata; but I do not find a distinct affirmation of any general relationship between the subcaudal arches of fishes and chevron bones or other parts of higher animals. But he does not appear to coincide with my view, as he denies the homology between what I believe to be the same parts in *Menobranchus* and *Naseus fronticornis** and asserts that the subcentral arches of the trunk-vertebræ of the Sole are of essentially the same nature as transverse processes.

Professor Huxley has not, so far as I know, given forth any decided view as to the real nature of the subcaudal piscine arches. For myself, I believe that the facts will not warrant us in saying that they belong altogether to any one category, but that their nature is more or less different in different cases.

A priori we might expect that in these lower vertebrata "differentiation" in some parts of the skeleton would be less complete than in higher classes; and such I believe to be the case as regards the hypaxial and paraxial elements.

In the embryo before the bifurcation of the laminae of the ventral fold is complete, it can only be approximately determined to which category portions of tissue belong which are situated in the as yet undifferentiated part. And if, by arrest of development, the bifurcation never extended further, hard parts so situated could only be so determined during the whole of life. But as the alimentary tube (except of course its mucous lining) is undoubtedly formed from the internal laminae, the parts lying directly above it and beneath the vertebral column may well be taken to belong to the same category, lying, as they do, at least in the roots of such laminae and above their points of suspension.

Such skeletal elements in the trunk, when they coexist with distinct paraxial elements surrounding externally the visceral cavity, being deemed hypaxial, the nature of the subcaudal arches must be determined by examining whether they are serially related to one or the other set of elements.

That they should partake of the nature of both systems and be parhypaxial, or that distinct paraxial ribs should start from undifferentiated parhypaxial root-processes, would only harmonize with what we might expect *a priori* to find in some cases, especially in members of the lowest class. We have seen that in some vertebrates, upon an hypothesis suggested a little back, coalescence or connation takes place between parts which are distinct in other forms (*i. e.* the coalescence between diapophysial and parapophysial elements); it is therefore not improbable that we may find a similar want of differentiation (coalescence or connation) with regard to such skeletal elements as the paraxial and hypaxial ones.

Again, the internal and external laminae of each ventral plate merge one into the other superiorly; and we might expect sometimes to find solid skeletal parts in certain situations, the true and essential nature of which is only be determined by following it serially in the same individual, or by carefully comparing it with other forms.

From the piscine skeletons I have as yet examined, I believe that in the great majority

* *Loc. cit.* p. 131.

of fishes this undifferentiated condition of the paraxial and hypaxial parts obtains. Nevertheless, sometimes both elements coexist in full perfection, as is well shown by Dr. Cleland himself, whose instructive woodcut of *Naseus fronticornis* I have had copied (Plate LIII. fig. 9). In this fish we have on each side a diapophysis (or tubercular process) with an upper rib (fig. 9, *t, tr*), and a parapophysis (or capitular process) from which an aponeurosis (fig. 9, dotted line), in the position of a lower rib, runs down to embrace the visceral cavity while the hypaxial arch plainly and manifestly dips into that cavity (like the caudal chevron bone of a crocodile) in the line of suspension of the primitive embryonic internal laminae. Dr. Cleland declines to recognize a relation of homology between this arch of *Naseus fronticornis* and the chevron bone of *Menobranchus*, because in the latter animal the visceral cavity "lies entirely below the inferior caudal spine, whose top only reaches its upper margin." But this objection, if valid, would destroy the homology between the chevron bones of *Menobranchus* and those of the crocodile, as described by Professor Goodsir, at least of such of them as are quite posterior to the caudal leg-muscles; and it seems to me to imply no more than that the area of the internal laminae has become narrowed for a certain space, certainly not any essential difference in the nature of the parts—nothing being more common than the application of serially homologous parts to diverse uses.

In *Muraena Helena* we have a good example (Plate LIII. figs. 16, 17, 18 & 19) of a rudimentary and undifferentiated condition of these parts. In the vertebræ immediately behind the head (fig. 16) we have a transverse process on each side, and a single median inferior process. This latter process, as it lies directly in the line suspending the viscera, must be regarded as hypaxial (fig. 16 H). Further backward it divides and approximates toward the transverse process, with which it gradually coalesces (fig. 17, PH). This single process is now the serial homologue of both the hypaxial and paraxial parts of the more anterior vertebræ, *i. e.* it is parhypaxial. It is short and does not extend beyond the walls of the groove for the aorta, which groove is formed into a canal by membrane extending transversely beneath it. From the ends of these parhypaxial processes the membrane extends which bounds the pleuro-peritoneal cavity externally, and in which there are no hard parts; but if hard parts did exist there, they would be ribs. Further backward the parhypaxial process becomes again differentiated into its elements (fig. 18); and still further back the hypaxial ones, meeting below, form inferior arches (fig. 19) which are the general homologues of the Mammalian and Reptilian chevron bones, and the serial homologues of the inner parts of the single more anterior processes. Did the transversely extending subaortic membrane of the trunk ossify, then such median ossification would be plainly hypaxial, and would connect together (if it extended completely across) the two parhypaxial processes.

Of such an essentially complex nature are the subcaudal arches of most fishes. These arches are in general evidently the bent-down serial homologues of the paraxial elements of the trunk; but they are often also the serial homologues of the margins of a subcentral abdominal aortic groove, and so far are hypaxial, as also are the transverse bars of bone sometimes extending beneath the caudal vessels.

In certain cases, however, we have (as in *Muraena Helena*) a more complete differenti-

ation; and thus it is that in the Sole (Plate LIII. fig. 7) the subcaudal arches are hypaxial in nature, while in the Flounder (Plate LIII. fig. 6) they are certainly in part paraxial, being, in the latter case (as pointed out by Dr. Cleland), to a certain extent in series with the transverse processes of the trunk, but in the former case with the aortic investment, as they are in *Lophius piscatorius* (Plate LIII. fig. 8), where they are also, to all appearance, simply hypaxial parts.

That the subcaudal arches of the Sole should be reckoned as belonging to a more or less different category from the subcaudal arches of the Flounder, may by some be deemed paradoxical. It is, nevertheless, simply a short statement of facts—namely, that they succeed serially in a certain different manner in one case from what they do in another.

We have already met with a parallel instance in the caudal transverse processes of certain Cetaceans; and the instances are numerous, indeed, in which skeletal parts in one animal closely resemble, in external appearance and function, skeletal parts in another animal, which parts nevertheless have a different origin. Thus the different ways in which the cranial walls are formed in different animals, now by an enlargement of a lateral part, *e. g.* the alisphenoid, now by the greater extension downward of an upper part, *e. g.* the parietal, will supply an example of functional resemblance and genetic divergence.

We have now reviewed, in connexion with the questions proposed, the more important modifications of the axial skeleton as it exists in its fullest development in the five vertebrate classes. And it seems to me that the view thence derivable *à posteriori*, appears to coincide tolerably well with the *à priori* view derived from a consideration of the mode of development of the vertebrate embryo with its three pairs of laminæ; for we have found, beside the neural arches (or epaxial parts), a series of more or less segmented hard parts embracing externally the pleuro-peritoneal cavity (paraxial parts) and also a series of hard parts (hypaxial parts) either situated within the pleuro-peritoneal cavity and its prolongation, *e. g.* the branchial arches, or else placed within the paraxial elements, and related to the dorsal vessels, *e. g.* chevron bones and hypapophyses.

Moreover, as the laminæ start from a common longitudinal axis, so we have found that coalescence or connation sometimes takes place between adjacent series, whether between paraxial parts and epaxial parts, on the one hand, or between paraxial parts and hypaxial parts on the other.

Adopting then the view before mentioned as to the nature of the trabeculæ cranii, the axial skeleton of vertebrates may be shortly described as follows (Plate LIII. fig. 1):—

1. A central axis, terminating anteriorly behind the sella turcica, and posteriorly at the end of the spine itself, and segmented antero-posteriorly or not, but generally so, the segments having a numerical relation to the spinal nerves.

2. A superior cylinder, enlarged (except in *Amphioxus*) at its anterior end to embrace the brain. The cylinder is generally segmented, the segments (except at the anterior end) generally corresponding in number to those of the axis, though sometimes much more numerous—*Epaxial parts*.

3. An inferior cylinder external to the pleuro-peritoneal cavity (or continuous with

parts which are so), in which two longitudinal series of hard parts (having a numerical relation to the epaxial hard parts) may be developed, and may coalesce more or less completely together after or before solidification—*Paraxial parts*.

They are subdivisible into (A) diapophyses and upper ribs, and (B) parapophyses, lower ribs and sternum.

4. An inferior cylinder internal to the pleuro-peritoneal cavity (or continuous with parts which are so), in which hard parts may be developed (having generally a numerical relation to the other, axial hard parts)—*Hypaxial parts*.

These may be of two very different kinds. They may be (A) in close relation with the dorsal vessels—*Hypapophyses*, including “chevron bones;” or (B) they may bound exteriorly the anterior part of the alimentary canal, or be in series with parts so bounding it—*Visceral arches*.

By “visceral arches” I mean the branchial arches, the hyoidean arch, the mandible, and the trabeculæ cranii. On the authority of Mr. Parker, I do not count the palatine structure as a distinct arch, as he informs me it is but a secondary growth.

Hypaxial parts, then, are skeletal structures either, on the one hand, intervening between the axis and the pleuro-peritoneal cavity together with its prolongations, or else parts serially homologous with others which do so intervene; or, on the other hand, parts placed within the inner wall of the pleuro-peritoneal cavity, together with its prolongations, or else parts serially homologous with others which are so placed. Finally, a greater or less degree of coalescence, before or after solidification, may take place between epaxial parts and paraxial parts, or between paraxial parts and hypaxial parts.

In vertebrates generally (Plate LIII. fig. 1) we have, at the anterior end of the axial skeleton, hypertrophied epaxial and hypaxial parts, *i. e.* the brain-case and visceral arches. Further back we have hypertrophied paraxial parts with much diminished hypaxial ones. Finally, towards the hinder end of the body (except in tailless forms) we have, in vertebrates above fishes, a reappearance of hypaxial elements, generally accompanied by coexisting but distinct paraxial parts. In Fishes, in the same region, we have generally paraxial parts in union with more or less of the hypaxial element, or we have paraxial parts only, or, much more rarely, only hypaxial parts.

In this way the much discussed theory of the essentially vertebrate nature of the skull reappears, but in diminished proportions. As suggested by Professor Huxley, we have no vertebral body beyond the sella turcica—the region of the trabeculæ belonging to the system of inferior arches, not of neural ones or of bodies. The anterior end of the neural canal (in an ossified condition) seems to present us with three segments, suggesting three vertebral elements, viz.:—1, the occipital segment; 2, the alisphenoids and parietals; 3, the orbito-sphenoids and frontals. A sense-capsule is at the anterior part of each of these three segments.

All the ossifications of the acoustic capsule belong to a different category. Only two distinct vertebral centres (the basi-occipital and part of the basi-sphenoid), however, correspond now to these three pairs of neural arches; but many others may have at one time existed and since disappeared. Professor Huxley suggested this as possible in his last Hunterian course.

With regard to the descending arches, it may be that more than one pair belongs to each vertebral element, just as in some fishes there are two neurapophyses on each side to a single centrum. But as they are hypaxial and not paraxial in nature, there is no embarrassment in assigning some of them, in fishes, to vertebræ provided with true costal elements.

Such are the results which seem to me to follow from the study of the vertebrate axial skeleton, in the light afforded by the works and labours of the authors before referred to; and if these results are not themselves correct, I trust they may nevertheless contribute (as I before said), by provoking further examination and criticism, to the elucidation of truth on this somewhat puzzling question.

THE APPENDICULAR SKELETON.

That this part of the skeleton is an independent, separate part, and no mere modification of any of the before described axial elements, has, I think, been satisfactorily demonstrated by previous writers.

The serial homology between the parts of the anterior and posterior limbs of the same side* has also been pretty satisfactorily determined. The femur answers to the humerus, the tibia to the radius, the hallux to the pollex, &c. (Plate LIII. fig. 1).

But can the limb-skeleton have a yet simpler expression than a mere statement of their average development in the higher classes? can we reduce it to a form in which it shall correspond to piscine structures also, and reveal genetic relationships?

Professor Gegenbaur, in a recent paper†, has given an affirmative answer to this question.

From a consideration of the limb-bones of *Ichthyosaurus*, *Plesiosaurus*, Amphibia and Elasmobranchs, he comes to the conclusion that a common form may be arrived at, a type at once of both fin and limb, according to the figure which I have had copied (fig. 4).

He conceives that the increasing number of parts as we proceed distad from the root of the limb, is owing to the limb having originally consisted of a fin with a marginal chain of ossicles (H, R, r , c^1 , m^1 , &c.) and with a secondary longitudinal series of ossicles attached to the distal end of each marginal ossicle, all the series ending at about the same level transversely. Thus the root marginal ossicle, H, (the future humerus or femur) would have attached to one side of its distal end a chain of ossicles (U, u , c^5 , m^5 , &c.), the future ulna, cuneiforme, part of unciforme, fifth metacarpal, and phalanges of fifth digit. The second marginal ossicle (the future radius) would have attached to one side of its distal end a chain of ossicles (i , c , c^4 , m^4 , &c.), the future lunare, first part of os centrale, other part of unciforme, fourth metacarpal, and phalanges of fourth digit. The third marginal ossicle, r (the future scaphoid), would have attached to one side of its distal end a chain of ossicles (c , c^3 , m^3 , &c.), the future second part of os centrale,

* That special relationship between the ilium and scapula, with the attached muscles, which I had the honour of suggesting in a paper published in the Linnean Society's Transactions (vol. xxv. p. 395) has been accepted, confirmed, and reinforced by Professor Flower in his recent course of Hunterian Lectures.

† Ueber das Gliedmaassenskelet der Enaliosaurier. Von C. Gegenbaur, Jenaischen Zeitschrift, Bd. v. Heft. 3.

the magnum, the third metacarpal, and phalanges of the third digit. The fourth marginal ossicle, c' (the future trapezium) would have attached to one side of its distal end a chain of ossicles (c^2 , m^2 , &c.), the future trapezoides, the second metacarpal, and the

Fig. 1. Limb-bones of *Ichthyosaurus*.

Fig. 2. Limb-bones of *Plesiosaurus*.

Fig. 3. Ideal fore limb of Amphibian.

Fig. 4. Ideal typical limb developing from a fin.

H. Humerus. R. Radius. U. Ulna. r. Scaphoides. i. Lunare. u. Cuneiforme. c. Os centrale (represented as divided). c' . Trapezium. c^2 . Trapezoides. c^3 . Os magnum. c^4 . One part of unciforme. c^5 . Other part of unciforme. m^1-5 . Metacarpal bones. p^1-4 . A sixth chain of ossicles, of which the pisiforme is supposed to be the last rudiment.

phalanges of the second digit,—the fifth marginal ossicle (the future first metacarpal) having attached to it other marginal ossicles, the future phalanges of the pollex in the manus, or of the hallux in the pes.

This view is applied to the limb-bones as they exist in *Ichthyosaurus*, *Plesiosaurus*, and to an ideal amphibian, as the woodcuts sufficiently explain.

The hypothesis is very ingenious and tempting; still, much as one is naturally disposed to accept it, there are yet certain difficulties which it will not do to ignore.

In the first place, the exact nature of some of the ossicles of *Ichthyosaurus*, together with the division of the os centrale, seems yet open to dispute. And again, though the pisiforme is accounted for by reckoning it as the rudiment of a sixth digit, yet there is no way of accounting for the presence of the corresponding ossicle on the radial side; it cannot be similarly explained, because it is on the outer side, and would be external to the series of original marginal ossicles; nevertheless this radial ossicle is very often present even in Primates*, and in the Mole it becomes enormous. Moreover, as I have been reminded by Professor Huxley, some specimens of *Ichthyosaurus* not only have extra ossicles along the ulnar side of the limb, but along the radial side also, and extending far up its radial border. A fine specimen showing this has been pointed out to me at the British Museum by Mr. Davis.

* Phil. Trans. 1867, p. 319.

Thus at present, I think, we are hardly in a position to generalize the expression of the vertebrate limb more than to take it, in our typical form, as a pentadactyle member differentiated as in vertebrates generally, and approximating to what we find in certain amphibians.

Of course, we may be confident *à priori* that the typical differentiation of the higher classes has been evolved from *some* antecedent quasi-piscine condition. But that condition does not seem to me yet to have been made out; and, whatever may be in future determined by further investigations into known forms, or by the discovery of others as yet unknown, I hardly think that the view propounded by Professor Gegenbaur is the one destined eventually to prevail.

Summing up what has been stated, then, the divisions of the vertebrate skeleton may, according to the views here advocated, be conveniently represented as follows:—

The most generalized and simplest expression of observed facts may also, I think, be diagrammatically represented as it is in Plate LIII. fig. 1.

I will conclude in the words of Professor Jeffries Wyman*:—"Such a conception as an archetype involves is necessary in our attempts to study the creative idea which underlies all animal structures, apart from their adaptation to the modes of existence in each species; and just in proportion as such conception is based upon a more and more complete knowledge of the plan of structure and of development, anatomy will, in the same degree, become philosophical."

* "On Symmetry and Homology in Limbs," Proceedings of the Boston Society of Natural History, vol. xi. June 5th, 1867.

DESCRIPTION OF THE PLATE.

PLATE LIII.

- Fig. 1. Ideal generalized expression of the vertebrate skeleton. Descending from the cranium (or expanded, anterior part of the epaxial system) are the enlarged anterior parts of the hypaxial system:—1, the trabeculæ cranii; 2, the mandible; 3, the hyoidean arch; 4, the first branchial arch. The paraxial parts are made to show their generally double origin (tubercular and capitular), and a certain tendency to distal bifurcation. These parts diminish in the caudal region concomitantly with the increase in the hypaxial system. The skull, or expanded anterior end of the epaxial system, is represented as consisting of three segments (I., II., III.), with a sense-capsule (nasal, ocular, auditory) at the anterior aspect of each segment. The limbs are supposed to be simplified according to the view before expressed by me in the Transactions of the Linnean Society—namely, a correspondence between the greater tuberosity and the lesser trochanter, and between the lesser tuberosity and the great trochanter.
- Fig. 2. Diagram of a transverse section of the most developed skeletal segment according to the ideal here expressed. From above the centrum the epaxial parts, E (neural arches and neural spine), ascend. From each side of the centrum the paraxial system proceeds outwards and downwards to coalesce in the sternum below.
- t*, tubercular process; *tr*, tubercular part of the rib; *tr'*, its continuation outwards towards the surface of the body; *c*, capitular process; *cr*, capitular part of the rib; *vr*, vertebral rib; *sr*, sternal rib; *s*, sternum. From beneath the centrum the hypaxial system descends.
- A, The part of the hypaxial system which is related to the great vessels; B, part related to the alimentary system; C, part related to the heart.
- Fig. 3. Diagram of the conditions existing in sharks. N, neural canal; B, alimentary tract, surrounded by solid hypaxial parts, H (the branchial arches). V, the aortic vessels, extending up outside the branchial arches and inside the paraxial system (P), here represented by certain external branchial cartilages.
- Fig. 4. Diagram of the conditions existing in the Lamprey. N, neural canal; B, alimentary tract, only bounded by H, a membranous representation of the hypaxial system. V, the ascending vessels; P, the paraxial system or branchial basket.
- Fig. 5. Branchial arches, H, of the Monk fish (*Squatina*), attached to the under surface of the spine; P, ridge representing the root of the paraxial system. Drawn, by permission, from the specimen No. 442 in the Museum of the Royal College of Surgeons.
- Fig. 6. Part of the vertebral column of a Flounder, showing the caudal arches, HP, apparently formed by the bending down of the paraxial parts of the trunk.
- Fig. 7. Part of the vertebral column of a Sole, showing the caudal arches formed by the simple elongation of the hypaxial elements of the trunk—the paraxial elements, P, retaining their independence till they disappear.
- Fig. 8. Under surface of part of the vertebral column of *Lophius*, showing the caudal arches, H, formed by the production of the margins of the subcentral aortic groove of the trunk.
- Fig. 9. Vertebra of *Naseus fronticornis* (copied from Dr. Cleland's article in the Natural-History Review, vol. iii. p. 129). H, hypaxial elements; P, paraxial elements, consisting of:—*t*, tubercular process; *tr*, the rib from it, continuing outward toward the body-wall; *c*, capitular process, which is continued on by membrane only.
- Fig. 10. Part of the vertebral column of a fish, showing the suspension of hypaxial elements, H, to the paraxial parts, P, of the first caudal vertebræ.

- Fig. 11. Side view of four vertebræ of the Great Auk (*Alca impennis*). Hy, hypaxial elements of category A, *i. e.* hypapophyses. From the specimen No. 1151 in the Museum of the Royal College of Surgeons.
- Fig. 12. Under view of four ophidian vertebræ, showing the coexistence of hypaxial elements (hypapophyses) with bifurcated paraxial parts. Specimen, No. 634 A, in the same Museum.
- Fig. 13. Side view of four vertebræ of a Python. Specimen, No. 630, in the same Museum, showing the bifurcating paraxial elements.
- Fig. 14. Vertebra and rib of the Axolotl, showing the bifurcation of the rib both at its proximal end, where it is attached to the superimposed tubercular and capitular processes, and also at its distal end.
- Fig. 15. Rib of a Salamander, similarly bifurcating at each end.
- Figs. 16, 17, 18 & 19. Four vertebræ of *Muraena Helena*, seen from behind. Specimen, No. 36, in the same Museum. P, paraxial element; H, hypaxial element; PH, parhypaxial process.
- Fig. 20. Lateral view of the aortic arches and descending nerves (*external to them*) of *Lepidosiren paradoxa*. Copied from Professor Hyrtl's Memoir, tab. iv. fig. 2. *ch*, the spine or chorda dorsalis; O, part of the œsophagus; V, aortic root, whence diverge the aortic arteries, ascending outside the branchial arches; *b, b, b, b*, the gill-apertures between the branchial arches; *l*, the exit of the nervus vagus—the nerves descending outside the arches, and to the outer wall of the œsophagus.