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XLV.—*Outline of a Theory of the Skull and the Skeleton; being an Epitome of a Paper read before the Cambridge Philosophical Society, Feb.* 26, 1866. By HARRY G. SEELEY, F.G.S., of the Woodwardian Museum in the University of Cambridge.

BY a theory of the skull I mean a way of presenting a set of well-known facts so that they explain themselves; for a theory should ever be a continuity of facts.

The value and homology of bones varies so much with the theoretical views used to interpret them, that, with the number of cranial theories on record, it were hard clearly to describe a skull without attempting to co-ordinate the rival views of its structure. Differing in detail, these all affirm, and some attempt to prove, one side or other of the antithesis, that either the skull is a chain of vertebræ or that it no more consists of a series of vertebræ than the vertebral column consists of a series of skulls. There is much to be said in favour of both these views, from every consideration they involve. Every one is familiar with the beautiful way in which Professor Owen brought together brain and brain-case from the whole vertebrate province, till the conviction dawned on his reader that a skull was but another name for the first four of an animal's vertebræ. Nor will Professor Huxley's lucid demonstration be less remembered, reiterated through one vertebrate class after another till we willingly believe, as he would have us, that a skull is a skull—a complex structure, with three segments forming one organ, a brain-case, and two segments forming a face, while sets of bones for special senses close up the eyes and the ears. To the human anatomist considering the human skull it may be a very trivial matter whether he accept one view or the other; but with the comparative anatomist, ever discovering new animals, and often only guided to their true affinities by the skull, different theories give a very different value to arrangements and bones which are new. And hence, until an attempt is made to discover how far these theories may be different ways of presenting the same truth, and how far they fall short of being true, it will be impossible to compare the facts which they attempt to explain. When one master examines the lowest form of Vertebrate life, the cranium appears to be a continuation of the vertebral column; when another master expounds the highest forms of life, it appears to be a distinct structure, and not to consist of vertebræ. I do not propose to offer anything in this paper which shall be in antagonism with either of these theories.

But it is no less remarkable than patent that, although one Professor has long battled to show that the skull is so many vertebræ, and another Professor battles to show that it is not, no one has discussed the nature of vertebræ, or considered whether it were possible to have a theory of the skull founded in truth before making a theory of a vertebra. In all these speculations a vertebra is regarded as a fundamental principle, as elementary as hydrogen or oxygen to the chemist; and though Professor Owen has classified it into exogenous parts and autogenous parts, no attempt is made to show why it has these parts; and until this is done, I fail to see how it is possible to effect any kind of comparison between a vertebra and a skull; for vertebræ from different animals and from different parts of the same animal vary so much among themselves, that until the principle of the law of variation as well as the law of persistence in structures is known, it will be hard to say whether the elements of vertebræ are or are not modified into skulls, and whether, if so modified, the segments of skulls can in any rational sense be called vertebræ.

Now vertebræ consist of several ossifications, *i. e.* of bones which in various degrees grow. This change and substitution of structure is obviously due to *force*, and must either be of the kind which assists the first development of seeds (in which case it may perhaps at present fitly be called the embryonic or developmental force), or it must be due to the mechanical force of the atmosphere or water, or of one structure or function of the animal modifying another. If it is found, from abstract mechanical principles, that growth *must* take place under the influence of certain mechanical forces, and if it is found, from pathological observation, that growth *does* occur under these influences, then, should it be found in healthy structures that intensity of growth varies with the intensity of the forces, it will be proved that their action is a cause of normal growth. Then it would be possible, from morphology, to show that the same causes which developed the bones originally called them into existence. And therefore, if it is found, in the development of an animal after birth, that the developmental force and the other forces jointly tend to produce growth in the same direction, which depends on the morphology of the animal, coinciding in results, they will be admitted to be different forms of the same force, originally due to the same cause, namely motion. In this way I shall first try to account for the *growth of bone*.

The forces acting on bones must be from within or from without; and therefore every such force will in its effect be either of the nature of an impact or of an explosion. The forces acting *on* the animal are the media in which it lives (as air and water), the air it breathes and the food it eats; while the mechanical forces acting *within* the animal will be the muscles, vessels, viscera, &c. All these can only produce alternations of pressure and tension and rest. These, therefore, are the stimulants to growth. But growth is an enlargement in which the particles expand and increase externally. And as this cannot be favoured, but rather resisted, by pressure, it becomes evident that the actual increase must take place when the pressure is removed. Therefore, since rest must be purely negative as a force, the stimulant to growth is pressure and tension.

The first and most obvious source of these powers is the muscles; while the more they are used to propel the animal through the resisting air or water, the greater will be the equivalent of general pressure on the bones.

Thus if we take a limb-bone (the humerus, for instance), it will be found most extended in the direction between the radius and the scapula, in which it has to support the weight of the carcase; and if the ends of the bone are examined, where muscles are attached or press tightly, it will be found that growth has extended outward more rapidly than in the body of the shaft, where there is no direct tension, but only a lateral pressure.

But the resistance of the atmosphere produces a different series of modifications. It appears to be a mechanical principle, that if pressure be applied to the outside of a cylinder, it will in effect be relatively equivalent to reducing the pressure within. And it is found, from observations in paralysis and other affections, and in the aged skeleton, that when, from failing vitality, motion is less and the muscles become less powerful (that is, when the pressure is reduced), the bone to some extent dies, and, from the dead part being carried away, becomes smaller and lighter. Now, the effect of motion through the air is relatively to diminish the pressure in the interior of the bones. And therefore it is found, in the sluggish Sloth, that the limb-bones are solid, that the active Mammals have large medullary cavities, while in the more active class of Birds the cavities become larger still. In this class, as in the subclass Saurornia, founded on the Pterodactyles, the process goes on till even the marrow disappears in the bones most used in motion, and their wonderfully thin walls become filled with hot air from the lungs.

Now it becomes necessary to consider in what manner pressure from muscles and other internal forces can act on the bones so as to produce growth; and here I would draw the illustration from pathology. Inflammation, in effect, is pressure; and whenever inflammation extends to the periosteum, that structure is excited to a morbid rapidity of action, and the bone immediately beneath is thickened: hyperostosis is defined to be a thickening and condensation of the shaft from inflammation. Nor is the pathology of the heart and the lung less suggestive where it shows, as is well known, that muscle may be inflamed, indurated, and changed into cartilage, which undergoes a partial change into bone, though, from the nature of the case, the last change can never advance very far, except in the lung, which may be replaced by muscle and well-developed bones.

Therefore, seeing that the effect of motion is a succession of falls, every one of which gives a powerful blow to the bones, and that no muscle can be moved without both pulling and pressing bones, we have an irritating cause, similar in kind though less in degree to that which results in abnormal growth. And accordingly it is found that the greater the activity (that is, the nearer the approach to an inflammatory condition) the more extensive will be the ossification.

Thus in the wild animal, which uses its muscles more vigorously than the tame animal, the ridges and processes for the attachment of muscles are more developed. In the limbs a trochanter appears as a separate ossification, where powerful muscles are attached. The marsupial muscles, which are small in man, become largely developed in the Didelphia, and create the marsupial bones.

Now it remains to show that the intensity of growth depends on the amount of the pressure and tension in the direction of the increase. Dr. Humphrey tells us that bones are densest in those parts which are subject to the greatest mechanical stress, and hardest in those persons who are strongest and most active. Here the intensity of ossification clearly depends on the pressure. And, again, it is observed that bones are most curved in those persons whose muscular strength is greatest—that is to say, where the pressure resulting from muscular action is the greatest; while weak persons, on the contrary, have comparatively straight bones. And thus it is seen that, even in the individual, the form of the bone varies with the relative power of the muscles. And so when the humerus of an active burrowing animal, like the mole, is compared with a humerus where the limb is merely used as a prop and does not meet with the like lateral resistance, it is found that it is so enormously expanded laterally as to be nearly as broad as it is long, instead of presenting a simple cylindrical shaft. But the best examples will be found in animals which use the limbs differently. Thus in the frogs, which use the hind limbs chiefly in leaping, it is found that they are longer than the fore limbs: this, too, is characteristic of the kangaroo and jerboas, of struthious birds, and of man; nor can an example be cited where an animal uses its hind limbs more than the fore limbs without their attaining to a greater length,—because, as we saw at the outset, to use a limb is to bring to bear on it the pressure of all its muscles and the carcase, which were seen to be the stimulants to growth. Thus, too, birds of powerful flight have the fore limbs developed enormously; while in those which do not fly, and therefore where but little pressure can be brought to the bones, these limbs are extremely small.

Thus it has been attempted to prove by various arguments that pressure and tension is a cause of growth in bones.

To show that the same cause which developes bones originally calls them into existence, it is only necessary to reverse the argument, and show that the less the pressure the less the ossification, until at last, where pressure and tension cease, the bones are lost.

But there are a few simple facts which, exhibiting the formation of osseous particles where they are normally absent, are worth mentioning: one is ossification of the heart, and another the union of fracture in the costal cartilages by bone, just as in birds they become ossified normally; and a third is the significant fact that ossification in the fœtal cartilage first appears around the artery which supplies it—that is, at the first place where pressure can be exhibited. And it seems indisputable that if there had been no inflammatory pressure the heart would never have ossified, and that, but for the pressure of the artery, the fœtal cartilage would not have been converted into bone. This, therefore, I take to be proved; and we shall presently see, when considering the ribs, that pressure is capable of producing not only growth, but new bones also.

It remains now to show that the developmental force (if such a power exist distinct from vitality, of which I see no easy proof) is the same in effect as pressure, and must be regarded as only an inherited result of pressure and tension. Thus Dr. Humphrey tells us that in the fœtal cartilage the curves and processes are already modelled which afterwards characterize the bones. Now this may either be a result, as by all analogy would seem natural, of the formation of the fœtal muscles which are attached to it, or may be referred to the same force (if such is assumed to exist) which gives the individual his form. But the fœtal cartilage is a minute model of the adult bone. I therefore cannot but conclude that the same forces which developed the adult bone also developed the fœtal cartilage, and that the pressure of the uterus and the tension of the muscular fibres could not have failed to produce the same result at one period of life as similar pressure and tension do at another.

Having thus glanced at the nature of growth in the abstract, as seen in a single ossification, we will now briefly examine the conditions exhibited by the more complex bones, which show several distinct osseous parts. Thus, as is well known, the humerus or femur or the bodies of vertebræ consist, as a rule, of three pieces, each of which ossifies from a distinct centre, and is therefore in that sense a distinct bone. Now, since it has been seen that all ossification takes place under the influence of pressure and tension, we have no other forces at command to which to attribute the formation of these terminal parts called epiphyses.

The turtle shows no epiphyses in its limbs; and in a section of a femur of a young crocodile, kindly made for me by Mr. J. W. Clark, I was unable to distinguish epiphyses; and it is well known that these sluggish animals do not subject the bones to enormous pressure in their crawling motion: but when the activity becomes greater and the pressure is increased, then epiphyses appear, as in the frog, where they long remain separate. And in the case of a limb-bone, it is worth considering that when the limb comes to the ground, it receives a blow at each of its ends, equivalent to the weight it supports, and varying with the power with which the limb strikes the ground. Here, then, it is seen that special pressure, if powerful enough and maintained, developes special ossification, just as the ordinary pressure of the atmosphere, the muscles, and the weight of the body developed the original bone. And hence it is found that in the phalanges, metatarsals, and metacarpals there is commonly but one epiphysis, because, from the way in which the bones are applied to the ground, the pressure takes place at one extremity only.

Moreover there can be no doubt that atmospheric pressure, which holds the bones together so well, must also be a powerful stimulant to ossification.

The ligaments, too, by their resistance all help the epiphysial formation.

And when it is seen that the trochanters appear under the influence of the muscles, it is obvious that those muscles which are inserted at the extremities of bones must exercise a powerful influence on the formation of epiphyses. Therefore epiphyses and processes are to be looked for wherever the pressure and tension on a bone become more than sufficient to continue ossification. Now just as ossified epiphyses are not to be found in bones where the pressure at the ends is small, so it would be expected that in cases where the pressure and tension of the bone is almost entirely at the ends, and the shaft does not support the animal, the epiphyses should be enormously large, while the shaft would be small. And in Plesiosaurs this is actually found to be the case; for the large limbs, swimming powerfully through the yielding water, have experienced an enormous lateral tension at the ends of the long bones without any greater pressure in the direction of length. And therefore it happens that the ends of the epiphyses which are attached to the shaft become conical and penetrate down the girdling shaft till they meet in the middle of the bone; and, as might be anticipated, that of the distal end is much the larger one. Therefore it would seem possible, if the muscles attached were small, and the bones so placed as only to experience tension and no direct pressure, that the shaft might altogether disappear, and only the two epiphyses remain, as I am inclined to suggest may be the case with the bones which are called tarsal and carpal—a conclusion to which I am led by a consideration of the bones called the tarso-metatarsus in birds, which may be a case in which the tarsus does develope a shaft; and if so, then the metatarsals, like the phalanges, as is usual in the other Sauropsida, will be applied to the ground. There can be no *à priori* reason for supposing that the tarsals and metatarsals should unite together to form one bone; and all the facts of osteology point to their remaining separate; while an erect position for the metatarsal bone in a clawed animal is unusual, and only partial even in *jumping* jerboas, which it characterizes.

The careful dissections of the leg in the ostrich and crocodile &c. by Dr. S. Haughton enable me to add a little evidence from the muscles. The gastrocnemius muscle in the crocodile, as is usual, is inserted in the os calcis (and tarsal bones). It weighed 0·14 oz., while the tibialis anticus and extensor digitorum communis weighed 0·11 oz. But in the ostrich the gastrocnemido-solæus is inserted into the middle of the so-called tarso-metatarsal bone, and weighs 115½ oz., while all the other muscles of the limb and those attached from it to the body only weigh 220 oz., the tibialis anticus and extensor digitorum communis weighing 14 oz. Now there is nothing to induce us to expect that the gastrocnemius would be inserted in the *metatarsal* bone, as it would be if the tarso-metatarsal explanation were accepted; for, terminating in the Achilles tendon, it is eminently the muscle of the os calcis. And, seeing how the os calcis is elongated by it in ordinary mammals, one cannot be blind to the fact that, if the tension were increased to a power many times as great as it is in mammals, the bone would be extended to a much greater length. And therefore, when there is such a great power as this huge muscle present in birds, capable of elongating the tarsal bones, I fail to see any reason for supposing that the laws of osteological development have been departed from in birds. Therefore, when the muscles become of sufficient power, there is every reason to believe that the tarsal bones will follow the same law as other bones, and become elongated, developing a shaft; and hence, and for reasons indicated, under ordinary circumstances they present the condition of epiphyses of bones where the shafts are never formed.

And all these considerations point alike to the same general conclusion, that one ossification may develope another, if sufficient pressure and tension can be applied to its surface. And this law appears to be equally true for the entire animal as for a single bone. Thus in serpents, where the tension on the vertebræ is enormous, the number of vertebræ increases prodigiously; while in the frog, where progression is so carried on as scarcely to affect the spinal column, the vertebræ are surprisingly few. Among birds, too, where the number of vertebræ is extremely variable, it is found that those genera which use their cervical or sacral regions most, have in those regions most vertebræ: thus the emu and cassowary have each nineteen sacral vertebræ, while the emu has as many in the neck. And while the swan has twenty-three cervical vertebræ, and the average of this region in Natatores, Grallatores, and Cursores is much higher than in the other orders, on the other hand, in birds of great flight the number of vertebræ is small. Such facts appear to lead to the conclusion that the different regions of the body most used experience in consequence a tendency to increase in development.

With these remarks on the relation of structures to functions we may now examine the constitution of the vertebræ.

The body of the vertebra, or centrum, follows the law of a typical bone, and is therefore made up of two epiphyses and a shaft. And when it is seen with what ligaments the vertebræ are connected, to what vibrations they are subject in motion, and what muscles bind them together and pull them about, these powers are the forces which develope and account for the epiphyses.

The rib in a typical animal, as a *Plesiosaurus*, whether called pleurapophysis or hæmapophysis, is extremely short in the neck, and supported on the lower part of the centrum. In the pectoral region, where the viscera first enlarge, it becomes a little longer, and by the enlargement of the organs has its articulation forced higher up the centrum. In the back, where the viscera are at their maximum, it is found that the ribs are longest, and that they are entirely attached to the neural arches. In the tail these hæmal arches ultimately disappear, and there the vessels dwindle almost to nothing. Here there appears to be an incontestable demonstration that as the internal pressure increases so do the bones lengthen, and so do they give way before it, changing their articular place; and when the pressure becomes reduced in the tail, the arch dwindles to two lateral eminences, and at last is utterly lost. In other words, it is deducible from observation that the development of the ribs depends on the pressure to which the base of the centrum is subjected by the vessels, counteracted, of course, by pressure from the outer muscles and media. This, indeed, we are led to expect from the fact that the ribs are not developed in relation to the same function in animals where the lungs are rudimentary. Thus the frog has *no* ribs. And thus it is found that *caries* of the ribs is often associated with disease of the lungs; while the deformity of the chest called *ectopia cordis* consists in a partial or complete absence of the sternum and ribs with more or less deficiency in the pericardium, pleura, heart, and lungs. In serpents the ribs are functionally innumerable limbs. The rib in many animals terminates at its head in an epiphysis, which articulates with another epiphysis on the neural arch; while at its distal end, in birds, where the tension of the pectoral muscles on the sternum pulls with great power, an epiphysis is ossified and developed to a great length. Thus the rib appears to follow the same general law as other bones; for the distention of the thorax, both by growth and muscles and function in breathing, performs the office of ever-acting muscles, while other muscles, and the skin, and the atmosphere act as a great opposing power.

And in accordance with the same general law which produces the simple ribs, it is found that between their distal ends there is usually developed a common epiphysis, called the sternal arc. In *Plesiosaurus* and animals where the exterior force acting on them was not great, they are arranged one behind another like the rounds of a ladder; but in *Saurornia* and birds, where they came to give attachment to an enormous overgrowth of the pectoral muscles, all are cemented together and modified into a sternum, the greater muscular force having produced a larger amount of ossification. The epiphyses of ribs appear only to be developed when the costal girdle is large and somewhat complete. And therefore, while cervical ribs may well be regarded as epiphyses of the body of the centrum, dorsal ribs, though the same in origin, assume the appearance of separate bones. And thus to alternations of pressure and tension and rest, growth of all kinds seems to be due.

If the upper arches of the vertebral column are now examined, they will be found united by a much more elaborate system of ligaments than the ribs. There is the posterior common ligament at the base of the arch, the supraspinous ligament above the neural spines, the interspinous ligament, the capsular ligament, and the ligamenta subflava; and hence it is not surprising to find that the neural arches often come close together and underlock each other, and that the neural spines are much more expanded in antero-posterior extent than is generally the case with the ribs. But the neural arches present no correspondence with the ribs in size, remaining small and singularly constant in character. Development shows that they grow upon the first appearance of the film of the nervous column, which growing within and resisted by structures without produces the conditions under which epiphyses are developed. Hence I conclude that the lateral halves of the neural arch are also of the nature of epiphyses. But the neural spine, in those animals where I have had an opportunity of examining it, seems to be quite as fortuitous an element as, and less constant than, the sternal arc. That bone was seen only to be developed under the combined expansive and contractile action of the thorax or an equivalent force; and therefore its homologue is not to be looked for in connexion with an organ of such fixed character as the spinal column. But separated bones for the neural spine unquestionably occur, and seem rather to owe their existence to the spinalis dorsi muscle and the supraspinal ligament.

It has been already remarked that in certain ribs of some animals, as the buffalo and rhinoceros, there are well-marked epiphyses at the ends. Now I conclude from this, that just as these ribs behave themselves like separate bones in this circumstance, so we are justified in believing that, like the centra and limb-bones, they would have produced epiphyses in any other direction if the forces had favoured it; and, indeed, the lateral processes of the ribs of birds may be cited as examples of such a modification. And it is quite possible to explain the formation of the Chelonian carapace by regarding the plates as external epiphysial overgrowths of the vertebral elements. And I suppose that the neural arches do not develope such structures between each other only because, owing to the weakness of attachment to the centrum and the absence of ligaments and muscles of sufficient power, the strain was never great enough to produce active ossification and the vibrating tension in which the epiphysis takes its origin. But if it were possible that the tension on the neural arches were ever sufficient to produce an impact, then we might reasonably expect that the neural arch itself, like the centrum, should have epiphyses, as, indeed, appears sometimes to be the case between the zygapophyses. And in fishes, where the head is very large and the connexion with the body powerful, there appears sometimes to be such an epiphysis developed, though it is, as perhaps was to be expected, rather an epiphysis of the skull than of the atlas. Thus we are told, by Mr. Robertson and others, that in the carp, for instance, if the bar of bone which bounds the posterior extremity of the exoccipitals be traced from above downwards, distinct traces of sutures will be seen between it and the exoccipitals on which it rests; and following it upwards another suture is found dividing it from the supraoccipitals, so that the bars do not meet above to form a complete arch, the supraoccipitals being prolonged back between these two plates and forming the upper part of this neural arch, which has no centrum of its own, but rests on the basioccipital. Thus it is seen that epiphyses are not limited to the limb-bones and centra of the vertebræ, but that they may be developed on any bone if it is subjected to the requisite tension and pressure.

And from these considerations I deduce the following theory of the vertebra—viz., that it consists of a centrum or centre of ossification which normally developes three (or more) pairs of epiphyses, any of which may assume the appearance of separate bones and develope epiphyses themselves. Thus in the majority of animals there are, 1st, one pair of epiphyses at the front and back ends of the centrum; 2ndly, one pair above, to enclose the neural canal; and, 3rdly, another pair to enclose the viscera. The upper epiphyses are observed to change their position a little with function, while the lower epiphyses may ascend the centrum and become articulated to, and seemingly developed from, the upper epiphyses; all of them may be absent, and the simple original osseous centre will still be accounted a vertebra. But, as we shall hereafter see that the whole skeleton may by this law be accounted for and derived from a single ossification, it would be impossible to admit as a vertebra any structure which varied in plan and function from that which is found in the spinal column.

With this conception of a vertebra it will now be possible to determine what the skull and spinal column have in common, and how far they differ.

Amphioxus lanceolatus appears to demonstrate that in certain vertebrata, where the vertebrate structure is scarcely assumed, a skull need not exist, and that there may be nothing in structure to distinguish the more anterior or sensory part of the neural column and canal from the part which is always more or less uniform, and is called the spinal column; it also exhibits the fact that a mouth may exist without having the least connexion with the cranium,—thus showing that just as a skull must be a result of functional development of the organs of sense at one end of the nervous column, so by modification the apparatus around the commencement of the digestive canal takes the form of jaws and facial bones. Thus, however close the jaws may be brought in contact with the cranium, and however the primitive cartilages which form the prehensile end of the digestive canal may be modified by adaptation to other ossifications, they constitute a structure which can only owe its development, like everything else, to the higher requirement, or differentiation, of the function in which it took its rise; and so, though forming no part of the original structure of the cranium in the lowest vertebrata, it constitutes by adaptation in higher forms of life an essential part of the skull. And, on the other hand, since the cranium is sometimes wanting (and in *Amphioxus* there is nothing which can be separated from the spinal cord as a brain), it would be hard to regard any brain as more than a functional overgrowth of the end of the spinal cord, and therefore to do otherwise than believe that its osseous case would be originally formed on the same plan with the vertebræ, yet speedily and enormously modified by the different functions which it subserves. Then, just as the brain, from being inseparable from the spinal cord at first, comes at last to be a structure as distinct as may be, there is here a modification not unlike that which separates the segments of a limb (only greater), so that, though both are parts of the same organ, their structure and functions are very different. And therefore, although the covering of the brain may in some organisms be inseparable from the vertebræ, there can only be expected to be the same degree of correspondence between the skull and the vertebral column that there is between the brain and the spinal cord. If a brain has parts which have no representatives in the spinal cord, it will not be surprising if the brain-case has parts which are not found in the case for the spinal cord.

If a skull is examined, it will be found to be the outlet for, or rather the entrance to, the nervous system; this part is occupied by the brain. Secondly, it is the entrance to the digestive system; and this part is constituted by the jaws. And, lastly, it is the entrance of the lungs, respiration being carried on through the nasal apertures. All these several forces of eating, breathing, and observing and thinking exercise great pressure and tension on the regions they affect; and it is precisely these which we have already seen ossifying the skeleton. Seeing how the small epiphysial elements of the neck in *Plesiosaurus* were observed to put on an enormous and complex development under the increasing pressure of the viscera in the thorax, I cannot but point out that the brain presents to the spinal cord precisely the same sort of relation which the viscera of the thorax do to those of the neck, and therefore to anticipate that the formation of the cranium will follow an analogous law. And it has already been seen how, under the action of the lungs, &c. the ribs elongated and formed epiphyses; and therefore when this force used in breathing comes to be narrowed to a small aperture it accounts for the often osseous condition of the trachea, and, coming in contact with other ossifications, could hardly fail to develope epiphyses: and accordingly we shall see that the nares are generally surrounded by the same set of bones, quite regardless of the place where they open in the skull, whether at the tip of the jaws or near to the brain. And, finally, it would be superfluous to insist on the force manifested in using the jaws; and thus we shall see that the degree of development in the maxillary and premaxillary bones will be entirely proportionate to the pressure and tension allowed by the presence or absence of teeth, and the mode in which the jaws are used.

If an ossified brain-case is examined, it will be seen to be more or less easily divisible into three segments, as, indeed, is generally admitted. The first of these, following Professor Huxley, I take to consist of the basioccipital, the exoccipitals, and the supraoccipital; the second consists of basisphenoid, the alisphenoids, and the parietals; while the third is made up of the presphenoid, orbitosphenoids, and frontals.

As compared with vertebræ, it will be seen, as is remarked by Mr. Robertson and others, that these segments differ in being roofed in by bones (the supraoccipital, parietals, and frontals) to which there is obviously nothing corresponding in the covering of the spinal cord; and they also differ from most vertebræ in the arches touching each other at every point.

Thus, remembering that the brain was originally but the anterior end of the spinal cord, and so far, as evidenced by the law of pressure and tension which has been considered, must have been roofed in by similar structures, we find that when the brain expands in height and size above the proportions of the spinal cord, it becomes roofed in by additional bones, just as the thorax was when it expanded in depth below the limits of the small neck. So that the alisphenoids are epiphyses of the basisphenoid, just as the neurapophyses are epiphyses of an ordinary centrum, and the parietals are epiphyses of the alisphenoids, just as the sternal ribs or sternum in birds, for instance, are epiphyses of the ordinary ribs; and it will hardly be maintained that the inferior arch of a cervical vertebra of a bird differs less from the inferior arch of a dorsal vertebra than does the ordinary upper arch of a vertebra from the upper arch of a segment of the skull. In the thoracic region the growth and development of viscera is chiefly in depth, as is the weight of the lungs; and in *Amphioxus lanceolatus* the notochord extends anterior to the neural cord, whereas in mammals, even in a very early embryonic state, the neural rudiment which becomes the brain is prolonged far in front of the notochord; and thus it is seen that with its development in height the brain undergoes a development in length, which the thorax did not. And nothing can be more evident than that, restrained by the structures in front and by the vertebræ behind, the growth in length must exercise a pressure and tension in that direction exactly corresponding to the forces which gave rise to the epiphysial bones which roof in the brain as it developes in height. And therefore, since by the influence of such enormous and equable pressure and tension epiphyses are developed in height, exactly the same forces exerted in length cannot but have produced epiphyses at each end; and so, remembering how, up to a certain point, the plan of the brain and the spinal cord must have been the same, it is curious to observe that while the basisphenoid developes the basioccipital and presphenoid for its epiphyses much after the plan of an ordinary centrum, the bones of the neural arch also develope epiphyses in length just as they do in height, as we saw was the case with some fishes—the entire occipital segment answering to the posterior epiphysis, and the entire frontal segment being the anterior epiphysis of the parietal segment of the skull. And accordingly it is found that the elementary bones of these epiphyses converge and close in the brain at both ends, thus demonstrating that they owe their growth to its growth, and extend no further than they are forced by its pressure; and therefore, though the skull will obviously develope quite regardless of the degree of growth in the several parts of the brain, by the simple law of inheritance, yet in many cases the relative size of several bones will be found to vary with the size of the division of the brain which is underneath them. Thus Mr. Robertson remarks that fishes may be divided into a sluggish group, typified by *Lophius*, in which the cerebellum is small, and an active group, in which the cerebellum is large, typified by the *Tunny*; and finds that in skulls of equal length, the occipital segment of the skull measures $4\frac{1}{2}$ inches long in the Tunny, while in *Lophius* it only measures 2 inches: and, ascending in organization, it is seen that as the brain rapidly expands, bones which before, in the lower forms, were quite exterior to the skull become gradually introduced to form part of the cranial walls.

Thus, excluding the sense-bones and dermal bones, I would interpret the neural part of the skull as having been originally developed from a single vertebral centrum and neural arch, following in its development, only in a more perfect way, exactly the same laws as govern the formation of ordinary vertebral arches. That it is a vertebra is not affirmed, because it presents modifications of structure which are nowhere seen in vertebræ; but these, which are the development of epiphyses by a neural arch, are of a kind quite consistent with the vertebrate plan, and certainly to have been expected under the influence of pressure. Indeed it is not too much to say that, under the influence of the requisite pressure, any other neural arch could have similarly been developed into a cranial cavity; and therefore a definition by Professor Huxley, "that the skull no more consists of a chain of vertebræ than the vertebral column consists of a chain of skulls," more faithfully expresses the kind of relation between the neural regions of the two structures than any statement that I have yet met with. And if the neural part of the skull is considered to be a vertebra at all, it can only be an ideal typical vertebra, where every possible part is present, and to which, therefore, the ordinary uniformity of imperfect development of most vertebral arches offers no near parallel. On the whole, the differences and affinities are perhaps so well marked as nearly equally to justify those who would call it part of a skull and those who prefer naming it a transformed and thoughtful vertebra, both of which statements would be equally true.

If the cranium of a full-grown *Gallus domesticus* be boiled, from the great intensity of ossification in the animal, it readily separates into two portions—an anterior part, which is made up of the bones of the face and jaws, and a posterior part, namely the brain-case. And here it is seen that the interorbital septum, which is formed from the trabeculæ, is embraced by the presphenoids and frontals reaching the orbitosphenoids so as to close up the brain as in Mammals; so that the ethmoid presents the relations of a cranial bone, and might be regarded as an ossification produced by the olfactory ganglia—a sort of special epiphysis. The bones which have been considered, it will be remembered, only correspond to the neural arch of a vertebra. Of the inferior arch, or that which corresponds to the ribs, it is at first hard to see any indication. There are under the basisphenoid of most animals two ossifications which Mr. Parker has named basitemporals, which are clearly epiphyses of the basisphenoid. In the subclass of birds called Pterodactyles, these bones are anchylosed to the anterior margin of the basioccipital, and in *Plesiosaurus* they appear to form the inferior surface of that bone, and to enter into the condyle. But they differ from the inferior epiphyses of vertebræ in being united and never surrounding any vessels; and therefore, perhaps, they are rather to be regarded as distinct ossifications peculiar to the skull.

As we have already remarked, the mouth is the prehensile end of the digestive canal, and in *Amphioxus* it is surrounded by jointed rings of cartilage. And, ascending in organization, it were easy to trace, by way of the lampreys and sharks, the gradual union between the jaws and the skull; and therefore we have to discover the origin and the law which governs the uniformity of development of these bones of the face.

And here I seek the aid of embryology to resolve the bones into their natural groups, though somewhat reluctantly, because the results from one tribe of animals cannot hold quite true for another tribe where the organization differs; but it is so conclusive on the significance of the jaws, that I will give, in a translation of Professor Rathke's own words, his remarks on their origin. He says, "That part of the investing mass of the notochord in which the basisphenoid is developed in many animals, sends out a 'ray' or band downwards on each side, which presents a remarkable similarity to a rib, not only in its mode of origin, but in its original position and form." These, then, it will be seen, are the true epiphyses which correspond to ribs, and, as was to be expected, they grow out of the basisphenoid, which was the original centrum of the skull; and as the true ribs grow down to enclose the posterior part of the digestive organ, so we shall see these ribs grow down to embrace its anterior end, and become modified into prehensile organs. Professor Rathke goes on to say, "But very early there grows out from near the upper end of the ray a long thin process, which passes off at an obtuse angle to it and applies itself to the inferior wall of the future brain-case." Thus the ribs, growing down on the digestive canal, appear to become split, and the upper parts run along the top of it and the lower parts run down the sides, thus eventually coming to embrace the mouth without bringing it in contact with the centrum; but it ought to be remembered that, in the adults of all the animals in which this is observed, union has already taken place between the face and the brain-case.

That the ribs really become split as they apparently do, I do not see any reason for believing, and should rather regard the upper portions of the forks as connate growths produced by causes presently to be considered. The proximal end of the cranial representative of a rib ossifies and becomes the quadrate bone or incus; an intermediate part becomes the os articulare; while the distal end remains unossified, but developes bones on its surface which become the lower jaw.

So far, then, in its general plan the skull follows the vertebral type. But by the narrowing down of the bronchial tube, and the resistance of the surrounding organs, the mouth below and the brain-case behind, a powerful ossifying force, of which we have already seen evidence in the trachea, comes into play, different to that of the chest; for there the digestive canal is *enclosed* by the breathing-apparatus, while here the breathing-canal is small, and nearly shut in by the digestive canal below and by the resisting vertebral centrum above. So that, seeing what the result of the thoracic action was in the development of ribs and in the development of the trachea, it must be anticipated that ossifications will likewise take place in the skull from the same cause in the direction of greatest resistance, *i.e.* above and below the termination of the trachea in the skull; and accordingly we find a triple series of bones above and in front, and another triple series below and behind. The first series consists of the nasal bones, the ethmoid, and the vomer, the nasal bones and vomer being in the position of epiphyses of the ethmoid; and below these are the pterygoid and palatine bones, and an unossified blastemous extension of the latter anteriorly, on which the maxillary and premaxillary bones are developed, just as the prehensile bones of the lower jaw were developed on a cartilaginous extension. This, then, is clearly a distinct region of the skull, to which there is obviously nothing even analogous in a vertebra; and in reviewing its comparative osteology, I find no reason for considering it less a fundamental essential of a developed skull than the neural region itself. And just as the brain-case is known as the neural region, so this part may well be called the bronchial region; for just as the former is a modified neural arch and its centrum, so the latter is a modified termination of the trachea: and thus, although the skull appears in this matter to deviate from our conception of a vertebra as merely an ossified structure, yet it conforms even in that deviation to the plan of a segment of the body, and so brings the skeleton into a closer and more natural unity.

The lower jaw and its upper appendages being a modified rib, we thus exhaust all the vertebral elements without accounting for the maxillary or premaxillary, or the distal elements of the lower jaw exterior to Meckel's cartilage. The maxillaries, by development no less than by function, are the anterior epiphyses of the palatines; while the premaxillaries appear to be the lateral epiphyses of the ethmoid. Such is the circumstance of their origin, though no doubt their development is due to the same pressure by which we have seen that all bones are formed. Thus in the elephant, where the premaxillaries have to support the enormous tusks, they attain an enormous development, covering the face, extending over the maxillaries, but entering, as in birds and Ichthyosaurs and most animals, into the anterior nares. In ruminants and pachyderms, where the pressure from the teeth is more uniform than in some animals, it is seen that the maxillaries are deep and their upper and lower margins subparallel; and, as though illustrating the community of origin, in some animals the palatines and pterygoids both bear teeth. The bones forming the elements of the oviparous lower jaw I believe to have been developed as epiphyses of Meckel's cartilage by pressure; the dentary element presents the aspect of a terminal epiphysis, and the four other bones a superior and inferior and two lateral epiphyses, which functionally are a diapophysis. And now, of the important elements of the skull, there only remain the eyes and the ears, which correspond, in their relations to the alisphenoid, with the intervertebral nerves. The growth of the eye is a sufficiently evident cause of pressure to account for sclerotic, superorbital, and lachrymal bones; but the periotic bones, which have been so laboriously elaborated by Professor Huxley, appear to me to be nothing but ossifications around the auditory canals which have afterwards grown by contact with other ossifications. The quadrate bone is large when placed between the jaw and the skull, but dwindles to the incus when the pressure is removed; and so the mastoid, squamosal, and petrosal obviously owe their development to their relations with the jaw. They are clearly sense-bones, and therefore, forming no part of the skull except as such, may be here passed over without further notice.

Such, then, is an outline of the mechanical theory of the skull; and such are some of the chief points which I hope to illustrate and demonstrate in the collections of fossil vertebrata which are among the best treasures of the Woodwardian Museum. This theory differs from others in the subordination of structure to function, and the belief that, except for the variation in organization, similar functions will always develope similar structures. It differs from other theories in giving a mechanical reason for the presence of every bone. Its final conclusion is, that the skull is the terminal segment of the body, and that, just as the adjacent segments consist of the pharynx, the larynx, and a vertebra enclosing part of the neural column, so also the skull, which is the termination of these three organs, and where their outlets are visible, must consist of them also; that the brain-case, therefore (the termination of the neural system), is a modified vertebra, that the bronchial circle of nasal and palatine bones is a modification of the trachea, and that the lower jaw is a modified rib developed by the mouth. The respiratory circle of bones is the key to the skull.