

**Detailed abstracts of papers on 1.- The morphological relations of the nervous systems in the annulose and vertebrate types of organization. 2.- The morphological constitution of the skeleton of the vertebrate head. 3.- The morphological constitution of limbs : communicated to the Cheltenham meeting of the British Association, August 1856 / by Professor Goodsir.**

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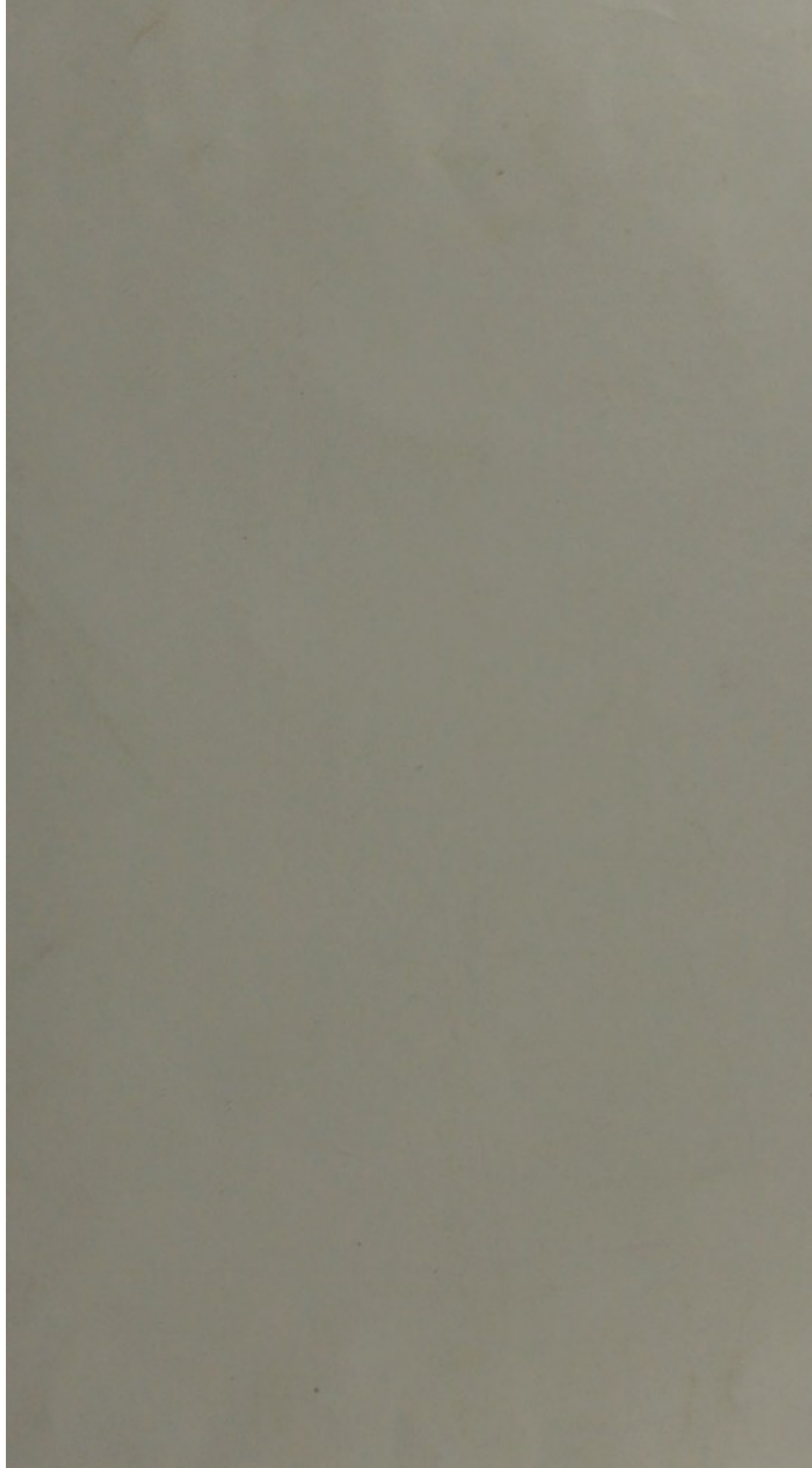
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## ERRATA.

Page 122, line 14, *for* Entomasome *read* Entomosome

... 125, line 28, *for* lamina *read* laminæ

... — line 29, *delete* " the " before the word superadded

... 127, line 16, *for* a principle *read* the principle

... 129, line 22, *delete* " at " before the word present

... 164, line 6 from bottom, *for* fossa, *read* fossæ,

... 165, line 18 from bottom, *for* their *read* these

... 166, line 11 from bottom, *read* Edentata, among the Mammalia. The  
great

... — line 4 from bottom, *read* extruded from the walls

... 178, lines 22 and 21 from bottom, *for* neuractinopophyses *read* neur-  
actinapophyses

... 181, lines 15 and 17, *for* element *read* segment



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*with the author's.  
Kind regards*

(27)

## DETAILED ABSTRACTS OF PAPERS

ON

- 1.—THE MORPHOLOGICAL RELATIONS OF THE NERVOUS SYSTEMS  
IN THE ANNULOSE AND VERTEBRATE TYPES OF ORGANIZA-  
TION.
- 2.—THE MORPHOLOGICAL CONSTITUTION OF THE SKELETON OF  
THE VERTEBRATE HEAD.
- 3.—THE MORPHOLOGICAL CONSTITUTION OF LIMBS.

COMMUNICATED TO THE

CHELTENHAM MEETING OF THE BRITISH ASSOCIATION,  
AUGUST 1856.

BY

PROFESSOR GOODSIR.

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*From the Edinburgh New Philosophical Journal, New Series, vol. v., Jan. 1857.*

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## PROCEEDINGS OF SOCIETIES.

*British Association for the Advancement of Science,  
Cheltenham, August 5-12, 1856.*

The following detailed abstracts of the papers submitted by Professor Goodsir to Section D. at the Cheltenham Meeting of the British Association in August last, were prepared by the author for our last number :—

1. On the Morphological relations of the nervous systems in the Annulose and Vertebrate types of organization.
2. On the Morphological constitution of the skeleton of the Vertebrate Head.
3. On the Morphological constitution of Limbs.

1. *On the Morphological relations of the Nervous System in the Annulose and Vertebrate types of Organization.*

The object of this communication is to indicate the morphological character of the apparently different anatomical relations of the central portions of the Annulose and Vertebrate nervous systems.

The term Annulose is employed provisionally, and in a morphological sense, as including all animals possessing a ganglionic nervous collar and axis, and presenting, at the same time, more or less distinct indications of a segmented structure of body.

Physiologists appear generally inclined to consider the central portions of the Annulose and Vertebrate nervous systems as modified forms of the same arrangement. These forms are held to possess a general similarity of structure, and correspondence in function; and the ganglionic collar and axis of the Annulose are assumed to be homologous either with the cerebro-spinal axis, or with the series of ganglions on the posterior roots of the spinal nerves, or with the system of sympathetic ganglions of the Vertebrate animal.

In my own examination of this subject I have been strongly impressed with the necessity of determining the morphological character of the œsophageal collar, and the opposite positions of the so-called brain and abdominal ganglionic cord, before any satisfactory advance could be made in ascertaining the relations of the two forms of nervous system. The apparent morphological difference between them does not appear, in the estimation of physiologists generally, to present that obstacle to a satisfactory comparison which its essentially fundamental character would lead us to expect. The difficulty has, however, been clearly stated by Professor Owen, who, in discussing the relations of the endo- and exoskeletons in his Lectures on Fishes, page 21, says,—“Geoffroy St Hilaire thought it needed but to reverse the position of the Crustacean—to turn what had been wrongly deemed the belly upwards—in order to demonstrate the unity of organization between the Articulate and Vertebrate animal. But the position of the brain is thereby reversed, and the ali-



mentary canal still intervenes in the Invertebrate between the aortic trunk and the neural canal."

I must here premise, that while I hold the general morphological relations of the Annulose and Vertebrate nervous systems to be identical, I do not consider these two types of organization to be mutually reducible. On the contrary, they are fundamentally distinct, presenting differences which demand careful consideration. It is, nevertheless, incumbent on the morphologist to ascertain in what respects they correspond, so as to determine their distinctive limits.

My earlier conception of the morphology of the Annulose nervous system was based on that of Carus. I conceived that each segment of the Annulose animal contains potentially an annular nervous arrangement, set in a plane at right angles to the axis of the segment, or longitudinal axis of the animal; that the only complete nervous ring is that one through which the œsophagus passes; that the ganglions on this ring are arranged in the various forms of superior, lateral, and inferior œsophageal masses; that the nervous rings in the post-cephalic segments are all incomplete above, and have their ganglions united into a single or double mass below; and that all the rings are united by a series of longitudinal abdominal commissures. According to this view, the œsophageal collar, with its superior, lateral, and inferior ganglions, is homologous with each pair of segmental nerves, and the corresponding abdominal ganglionic centre; the œsophageal collar being in a plane parallel to those in which the post-cephalic ganglions and their pairs of nerves are situated, but at right angles to the line of the series of abdominal ganglions.

I first recognised what I believe to be the real morphological relations of the Annulose nervous system during the delivery of a course of lectures on Invertebrate Anatomy in 1849; but more fully and completely during courses on the Anatomy of the Mollusca in 1850, and on the Anatomy of the Crustacea in 1851.

I now perceived that the fundamental difference between the morphological relations of the Annulose and Vertebrate nervous systems, consists in the position of the mouth.

I saw that the entire axis or central portion of the nervous system extends along the neural aspect of the body in both types of organization; but that while, as is well known—although its morphological importance does not appear to have been perceived—the Vertebrate mouth opens into the hæmal, the Annulose mouth passes through the neural aspect of the body.

In the Annulose animal, therefore, the buccal entrance interferes with the nervous axis—passing up between the two lateral halves of one of its longitudinal commissural or inter-ganglionic cords, so as morphologically to divide the continuous axis into a *pre-stomal* and a *post-stomal* portion.

These relations are most satisfactorily seen in the Crustacea, in which the so-called brain, or supra-œsophageal ganglion or nervous mass is actually in front of the mouth, and not above it.

In Insects, Annelids, and Mollusca, the bulk of the buccal mass, and other necessary modifications of the oral apparatus, elevate the so-called brain, curving upwards the morphological axis of the body of the animal.

By comparing the indications of segments in front of the mouth, and their corresponding diverging appendages, with the arrangement and distribution of the nerves given off from the so-called brain, it appears very evident that this brain is the aggregate of the segmental nervous centres in front of the mouth.

In like manner indications afforded by the segments, and their appendages immediately behind the mouth, enable us to determine whether the



so-called sub-œsophageal ganglionic mass is a single segmental ganglion, or an aggregate of antero-posteriorly united segmental ganglions.

In this way I was enabled to perceive that the axis of the nervous system of the Annulose animal does not consist of a supra-œsophageal mass, of an œsophageal collar, of a sub-œsophageal mass, and a continuous sub-intestinal ganglionic chain; but of a continuous line of connected and serially homologous ganglions situated in the mesial line of the neural aspect of the body.

The Annulose, like the Vertebrate animal, is developed with its nervous axis turned away from, and its hæmal axis applied against, the vitellary mass.\*

But, in the course of development, the mouth of the Vertebrate opens through the surface applied against the vitellary mass, whilst that of the Annulose animal passes through the aspect turned away from it. The Vertebrate mouth is hæmal, the Annulose mouth neural.

Rathke formerly described the pituitary body as originating in a diverticulum passing up from the pharyngeal mucous membrane through the basis of the embryo skull. I at one time conceived it to be probable that the pituitary body, and the mucous tube, in which, according to Rathke, it originates, might be indications in the Vertebrate of a structure which, in the Annulose animal, is converted into the mouth. This presumed neural alimentary passage may be conceived as passing up between the bodies of the anterior and posterior sphenoid bones into the sella turcica, along the course of the infundibulum to the third ventricle of the brain, and through the cavity of that organ to its upper surface behind the cerebellum, thus leaving the origins of the nerves of smell and vision in the pre-stomal portion of the organ, while the origin of the nerve of hearing would remain in the medulla oblongata or post-stomal portion of the cephalic nervous mass. The arterial circle of Willis, and other peculiar arrangements at the base of the skull and brain, appeared to support the view taken. I shall not, however, pursue this hypothesis further, because, from the observations of Reichart, we know that the base of the cranium is not perforated in the embryo, and that the supposed canal or diverticulum was an incorrect interpretation of the peculiar appearances produced by the curvature downwards of the early Mammalian head.†

If I have determined aright the morphological relations of these two forms of nervous system, we shall have advanced a step in our conceptions of the anatomico-physiological relations of the Annulose and Vertebrate animals, and this without losing sight of the fundamental differences,

\* From the passage in his Lectures already quoted, Professor Owen would appear to consider the dorsal heart, with its anterior and posterior arterial trunks in the decapod Crustacean, and consequently the dorsal vessel in the Insect, Arachnid, and Annelid, as corresponding to the thoracic, abdominal, and caudal aortic trunk of the Vertebrate animal. On this supposition only can we understand his assertion, that when the so-called belly of the Crustacean is turned upwards, its alimentary canal is still interposed between the aortic trunk and the neural canal. Embryology, Comparative Anatomy, and Physiology, appear to me, however, to afford ample proof that the cardiac-arterial dorsal trunk of the Annelid, Crustacean, Insect, or Arachnid, is homologous not with the sub-spinal aorta of the Vertebrate, but with the primordial cardiac-arterial tube in all the forms of the embryo Vertebrate, and, consequently, with the heart and trunk of the branchial artery of the Fish. If this, then, is the real homology of the "aortic trunk" of the Crustacean, and if its "brain" is in fact only a *pre-stomal* portion of its nervous axis, the French anatomist was quite correct in his general morphological statement, although he was not legitimately entitled at the time to employ the illustration.

† I have introduced the hypothesis of a Vertebrate neural mouth (cast aside in the course of my examination of the subject), because I believe it will be found to involve relations of importance in the anatomico-physiological investigation of the pre-stomal and post-stomal portions of the Vertebrate and Annulose cephalic nervous masses.



developmental and structural, between them. The researches of Milne-Edwards, and of Newport and others, on the Annulose nervous axis may thus be physiologically associated with those of Wagner, Schroeder Van der Kolk, Owsjannikow, Jacobowitsch, and Kupffer, on the cerebro-spinal axis; and we may now legitimately employ the Annulose animal in the morphological investigation of the Vertebrate skeleton.

Omitting, for the present, the consideration of the mode in which the nervous systems in the Tunicata, Rotifera, and Entozoa, are reducible to the typical Annulose form, I proceed to make some general morphological statements, based to a certain extent on the principle indicated in this, and introductory to the two following communications:—

1. The morphology of any one organic system in the Annulose or Vertebrate animal, cannot be safely or satisfactorily investigated, without constant reference to the others. That it must be so is evident from the fact, that all the organic systems are dependent on one another, in the constitution of the organism.

2. All sound morphological inquiry demands constant reference to the series of embryo, as well as of adult forms.

3. As morphology deals with forms and relations of position, it demands a careful selection of terms, and a methodized nomenclature. All terms involving more or less than their morphological application demands, must be avoided. Terms derived from other departments of the science, and having therefore an established technical meaning, have invariably produced misconception, when transferred for morphological purposes.

Influenced by these considerations, and satisfied that the Annulose and Vertebrate types of organization, although fundamentally distinct, present parallel forms of structure, and must consequently be closely linked together in morphological inquiry, I have to suggest a more extended and precise system of nomenclature for this department of the science.

In the Annulose and Vertebrate types of organization, the body of the animal consists of a linear series of segments. To the constituent segment, with its diverging appendages, I apply the term *Somatome* (σωμα. τεμνω).

For the purpose of avoiding circumlocution, and of supplying a term for a generalized conception, and thereby facilitating morphological description, without encroaching on zoological nomenclature, I denominate a segmented animal, whether Annulose or Vertebrate, an *Entomosome*—an entomosomatous animal (εντομος. σωμα).

As the constituent somatomes are invariably arranged in groups, in each of which they are more or less modified in form, or fused together, I find *syssomatome* (συν. σωμα. τεμνω) a convenient designation for such a group. A typical Crustacean presents a cephalic, a thoracic, and a caudal syssomatome, in each of which there are seven somatomes—twenty-one in all.

The constituent somatomes lie in planes at right angles to the *morphological axis* of the body, and are symmetrical in the transverse, but unsymmetrical in the perpendicular direction. They are, however, not only unsymmetrical in their upper and under surfaces, but the surfaces so named in the Annulose are morphologically distinct from those similarly designated in the Vertebrate animal. The Annulose animal moves on the surface which was turned away from the vitellary mass during development; the Vertebrate animal moves on the surface which was applied to it during development. As the axis of the nervous system is formed at the surface turned away from the vitellary mass, and the axis of the vascular system is formed at the surface applied to it in both types of organization, I employ, as morphological designations, the term *Neuropod* (νευρον.



πους) for an Annulose, and Hæmapod (ἄμα. πους) for a Vertebrate animal.

The mouth of the entomosomatous animal is invariably situated between two somatomes, and so that a certain number of somatomes are interposed between it and the anterior termination of the body. As the mouth is only one of a number of openings situated between somatomes, I find such openings conveniently distinguished as *metasomatic*.

The mouth of the Neuropod is a neural, that of the Hæmapod a hæmal metasomatic opening.

As the somatome exhibits in its structure corresponding segments of certain or of all the organic systems, I have found the following morphological terms extremely convenient in referring from the segment of one organic system, to the corresponding segments of the others.

For the entire framework of an Entomasome, whether this framework be developed in its integument or in its interior, whether it be fibrous, cartilaginous or osseous, I employ the term *Sclerome* (σκληρος, with the termination of completeness). To a segment of the sclerome I apply the designation *Sclerotome* (σκληρος. τεμνω). An aggregate of more or less modified sclerotomes, I name a *Syssclerotome* (συν). Making use of my former illustration, the sclerome of a typical Crustacean consists of twenty-one sclerotomes grouped in three syssclerotomes. Again, the sclerome of a Mammal consists of a number of sclerotomes, grouped into the cephalic, cervical, thoracic, lumbar, sacral, and caudal syssclerotomes.

For the muscular system I employ the terms *Myome*, *Myotome*, *Synmyotome*; for the nervous system, *Neurome*, *Neurotome*, *Synneurotome*; for the vascular system, *Hæmome*, *Hæmatome*, *Synæmatome*; for the morphologically as well as physiologically important digestive system, with its segments, and groups of segments, *Peptome*, *Peptatome*, and *Synpeptatome*, &c.

Till very lately, I had not met with any indication of the actual morphological character of the so-called supra-oesophageal ganglion in the works of British or Foreign Physiologists. I have now found, in an obscure corner of Von Baer's works, sufficient evidence that he had recognized its pre-stomal character. His statements are contained in a single paragraph, which forms an episode in the middle of the second corollary of the fifth scholium of his work on the Development of the Chick *in ovo*. Von Baer holds, with E. H. Weber and Treviranus, that the nervous axis of the Neuropod is homologous with the series of ganglions on the posterior roots of the spinal nerves of the Hæmapod; and he considers the "supra-oesophageal" ganglion to be the homologue of the Gasserian ganglion; but he adds, "peculiar stress is laid on this, that it (the supra-oesophageal ganglion) lies above the mouth (über). This appears to me to be a false view of the matter; it lies, in fact, in front of (vor) the mouth." He gives a diagram of the arrangement, and proceeds: "The following sketch will make it evident that the so-called brain of the Insect has the same signification as the posterior ganglions; and the oesophageal ring is only a secondary formation, dependent on the breaking through of the mouth, permitted by the symmetry of the structure, and the necessary connection of the ganglions."

It is somewhat remarkable that no one, even of Von Baer's own countrymen, has, so far as I know, made any allusion to this passage. Indeed, he does not appear to have been himself aware of the value of the observation, as he adduces it merely in the form of an argument in illustration of another subject, and does not again recur to it. For my own part, having ascertained, on independent grounds, and publicly taught and illustrated, for some years the principle stated in this communication, I



feel gratified in having this opportunity of rescuing from temporary oblivion, and of adducing in support of my own statement of the principle the original announcement of it, made twenty-eight years ago, by one of the most philosophic of modern Anatomists.\*

## 2. *On the Morphological Constitution of the Skeleton of the Vertebrate Head.*

In an abstract which professes to give only the general results of my own investigations, I cannot enter into such critico-historical details as would be necessary were the corresponding or opposite results obtained by other inquirers to be in every instance brought forward. I am therefore obliged at present to state, in a somewhat dogmatic form, the results which I conceive I have obtained, and the views I have been induced to take of a subject in itself extensive and difficult, and one to which so many distinguished anatomists have devoted themselves.

*Nature of the subject.*—The framework of the Vertebrate head is a syssclerotome—that is, a group of sclerotomes variously modified, and more or less connected, so as to form a distinct whole. The points to be determined are the number and modifications of the sclerotomes in the various forms of Vertebrate head. There are, however, some preliminary questions which must be briefly examined.

*The source and mode of origin of the Sclerome in the Vertebrate Embryo.*—The knowledge we at present possess of the source and mode of origin of the Vertebrate sclerome is the result of the successive researches more particularly of Pander, Von Baer, Rathke, Reichart, and Remak, on the development of the blastoderma.

Von Baer, while he adopted the doctrine of Pander regarding the so-called “serous” and “mucous layers,” took a somewhat modified view of the “vascular layer,” and directed attention more particularly to the “dorsal” and “ventral folds” of the blastoderma, in connection with the “corda dorsalis,” as fundamental embryological characteristics of the Vertebrate type of organization.

Among the numerous results of the researches made by Rathke in every department of Embryology, there are two which bear particularly on the present subject. These are his early discovery of the so-called branchial clefts; and his later recognition of the fact that the series of quadrilateral bodies on each side of the “corda dorsalis,” instead of being the rudiments of vertebræ, contain potentially the germs not only of these bones, but of the dorsal muscles, and “probably” of spinal nerves.

Reichart supplemented the previous observations of Rathke on the development of the “branchial” or “visceral laminæ,” and of the nasal and maxillary portions of the face.

Finally, Remak has ascertained, on independent grounds, that each pair of the dorsal quadrilateral bodies, usually considered as the rudiments of vertebræ, becomes developed superiorly into a right and left muscular plate, and inferiorly into a pair of spinal nerves, with their ganglions, along with the rudiments of a vertebra and pair of ribs, the nerves being in front of the sclerous elements. In the course of development a change takes place in this “primordial vertebral system.” The rudiments of the vertebral arch and ribs move backwards, from their original site under the posterior margins of the overlying muscular plates, to the anterior margins of the pair of muscular plates immediately behind, and become united to both pairs. A transverse division takes place at the same time

\* I accidentally discovered, a few weeks ago, that Professor Huxley had published translations of portions of Von Baer's works in the Scientific Memoirs for 1853. This judicious selection contains the passage referred to in my paper. (Dec. 4, 1856.)



in the rudimentary central masses of each of the primordial vertebræ. These changes constitute a new order of parts—the order or arrangement of the “permanent vertebral system.” Thus, the products of the development of a single primordial vertebra are—1. A pair of spinal nerves, with their ganglions; 2. The vertebral arch and pair of ribs immediately behind this pair of nerves; 3. The anterior part of the body of the vertebra to which this arch and ribs are attached; 4. The intervertebral disk in front of it; 5. The posterior part of the body of the vertebra in front; and, 6. The group of spinal muscles between these two vertebræ. The bones, muscles, and nerves of the abdominal and thoracic wall are formed by an extension downwards, and adhesion of the lower or costal portion of the “primordial vertebral system” to the inner surface of the external of the two layers into which the “primary abdominal wall” divides. This outer or adherent layer of the “primary abdominal wall” becomes the areolar layer of the integument, and enters into the formation of the limbs. The inner layer, separated from the outer by the pleuro-peritoneal space, forms, with its fellow of the opposite side, the Wolffian bodies, reproductive glands, spleen, permanent aorta, mesentery, and the muscular and serous covering of the alimentary tube.

From these remarkable observations of Remak, it would appear that the sclerome of the Hæmapod, from the anterior part of the neck backwards, originates as a series of independent sclerotomes, and that, contemporaneously with each sclerotome, a corresponding myotome and neurotome take their rise in a common primordial segment of blastema.

The cephalic portion of the early Vertebrate embryo is peculiar, more particularly, according to Remak, in the nonappearance of distinct “primordial vertebræ,” and of the subsequent changes which result from their development. The great divisions of the brain and of the cerebral nerves indicate, indeed, the segmented character of the entire structure, but I am inclined to believe that, in the present state of the subject, these indications are not to be depended on for the determination of the segments of the embryo or adult head. It appears to me that the segmented structure of the brain is to be looked for, not in its greater masses,—those developments on its upper surface in which it differs from the spinal cord, and by the possession of which it becomes a brain,—but in the series of groups of ganglion cells, the nervous centres of the cerebral nerves, whatever the typical number of these may be, arranged along its base, and strictly homologous with the groups of ganglion cells which undoubtedly constitute the morphological segments of the spinal cord.

The “visceral,” or “branchial laminae” afford, in the present state of the subject, a more secure embryological basis for the determination of the segments of the head. The so-called “first visceral lamina,” the one in which the mandibular arch is developed, and the two succeeding “visceral laminae,” those in which the anterior and posterior segments of the hyoid of Mammals and Birds are formed, must be looked upon as embryological indications of three cephalic segments.

On the under surface of the forepart of the embryo head, in front of the so-called “first visceral lamina,” there are five processes, in which are developed the palate and pterygoid, the maxillary, malar, and lachrymal, the intermaxillary and nasal bones. The first of these processes on each side extends obliquely forwards from the “first visceral lamina” towards and under the eye. It is the so-called “superior maxillary lobe.” The second process on each side—the “lateral frontal process” of Reichart—passes down in front of the eye, the eye being situated in the cleft between it and the former process. The fifth process is situated in front, and in the median line. It is the “anterior frontal process” of Reichart. The clefts or notches between this process and



the "lateral frontal process" are considered by Rathke and Reichart to be the external nostrils.

Now, in regard to the so-called "superior maxillary lobes," it is clearly established that the palate and pterygoid Bones are formed in them, but there is no sufficient evidence that they contain the germs of the superior maxillary bones. No traces of the superior maxillary bones appear until these so-called "superior maxillary lobes" have extended forwards, and united with the "lateral frontal processes" and the "nasal process," and until the maxillary margin has become considerably extended. I am, therefore, of opinion that the "lateral frontal processes" of Reichart are, in fact, the real maxillary lobes, and contain not only the germs of the lachrymal, but those also of the maxillary and malar bones. This view of the place of origin of the superior maxillary is in accordance with the adult relations of these bones. The position of the superior maxillary is in front of the eye; the orbit being, in fact, an expanded cleft between it and the palate bone.

Again, the nasal bones of the Mammal are formed in the upper part, and the intermaxillary bones in the lateral angles and palatal lobes of the "anterior frontal process." The notch or cleft on each side of this process cannot therefore become the external nostrils, for these are not situated in the Mammal behind the intermaxillary bones, but in front of them. From these circumstances, I am inclined to consider the external nostrils of the Mammal to be formed by the transverse union of the palatal lobes of the "anterior frontal process," and by the formation of the cartilages of the external nose in the mesial portion of the free margin of that process.

Embryologists generally consider the so-called superior maxillary lobes to be the upper portions of the "first visceral lamina" bent forward, and the "lateral" and "anterior frontal processes" to be the super-added structures in no way related to the "visceral" or "branchial laminae." It appears to me, however, that the general aspect, the relations, and the changes undergone by them in development prove these parts to be serially homologous with the "visceral laminae," and to be, like them, indications of the segmented structure of the head in front of the so-called first visceral arch. The so-called superior maxillary lobes indicate a segment of which the palate and pterygoid bones are elements. The "lateral frontal" indicate a second segment containing the maxillary, malar, and lachrymal bones. The external margins and angles of the "anterior or frontal processes" indicate an intermaxillary segment; and the development of the mesial part of the same process into the cartilages of the nose indicates a segment probably only fully developed in the Mammalian head.

In addition, therefore, to the "visceral laminae" behind that one in which the mandibular arch is formed, there would appear to be a series of less developed "visceral laminae" in front of it, all of which, in addition to other structures, give rise to hæmal arches of the sclerome, and indicate a number of corresponding sclerotomes.

*Of the Primary or Fibrous Sclerome.*—The bones and cartilages to which, from their palpable character, the attention of anatomists has been hitherto chiefly directed, are parts only of the Vertebrate sclerome. They are imbedded in a continuous fibrous matrix which, variously modified, binds them together, and co-operates in their general economy and functions. This matrix forms a more extensive, and, in some respects, a more important element of the sclerome in the lower than in the higher Vertebrata; and if viewed in the former in connection with



its early stages of development in the embryo, it will be found to be arranged on the plan of the "primordial vertebral system." It is most satisfactorily studied in the Fish, and particularly in those forms in which the bones and cartilages are feebly developed. The fibrous element of the sclerome forms the sheath of "corda dorsalis" in the Lancelet, and envelopes the column formed by the bodies of the vertebræ in other Fishes. It then bounds the neural and hæmal cavities, and from these cavities passes in the mesial plane above and below to the neural and hæmal margins of the body. Corresponding cartilaginous and osseous parts are imbedded in these fibrous neural and hæmal laminae. From the right and left sides of this deep or central system of fibrous laminae, other laminae extend outwards between the myotomes and are connected to the deep fibrous layer of the integument. The bones usually distinguished as "additional ribs," "upper ribs," "epipleural spines," "diverging appendages," are imbedded in these metamyotomic laminae; and as the class of radiating bones to which these so-called additional ribs belong may be conveniently distinguished as actinapophyses (*ακτιο-ίψος*), I apply the term actinal to the metamyotomic fibrous laminae of the sclerome. As those dermal bones or plates which, from their histological as well as their teleological characters, certainly constitute elements of the sclerome, are formed in the layer of the integument to which the actinal sclerous laminae are attached, this integumentary fibrous structure must be considered as constituting a dermal sclerous lamina, and so completing the fibrous portion of the sclerome.

The sclerome thus consists fundamentally of a fibrous structure, which surrounds the "corda dorsalis," bounds the neural and hæmal cavities, forms a mesial septum above and below, separates the myotomes from one another, and, under the integument, envelopes the deeper parts.

*The Development of Cartilaginous and Bony Elements in the Fibrous Sclerome.*—The immediate development of certain bones from or in a fibrous matrix, and of others in cartilage previously formed in it, has given rise, among other questions, to one, as to whether the former are to be included in the vertebrate system of bones. Now, while I admit the importance of the embryological and histological facts which the discussion of this question has afforded, I am inclined to think that a histological bias has influenced both the views which have been taken of it. Why certain bones originate in a fibrous matrix, why others originate in cartilage which has been previously formed in the same matrix, are questions of undoubted importance, but which at the same time cannot legitimately be put in opposition to the unity of the fully developed sclerome.

*Of the Cartilaginous and Bony Elements, and of the general Morphological Constitution of the Sclerotome.*—A sclerotome is, fundamentally, a segment of the fibrous sclerome, and the series of fibrous sclerotomes is indicated by the actinal laminae, each of which, for reasons to be afterwards stated, ought probably to be considered as potentially double, that is, as consisting of two layers, one belonging to the sclerotome behind, the other to the sclerotome in front.

The fully developed Hæmapod sclerotome is therefore a fibrous structure, in which all the cartilaginous and osseous parts are formed and embedded. With regard to these cartilaginous or osseous elements, I shall at present only direct attention to certain points which bear on the constitution of the sclerotomes of the Head. In doing so, I must bear testimony to the general applicability and convenience of the terms employed by Professor Owen to designate the elements of his typical vertebra, venturing to suggest modifications in their application only



where I am compelled to differ from him in regard to the relations of the elements themselves.

The term "centrum" is highly useful as a designation for the cartilaginous or osseous mass formed around the "corda dorsalis," whatever the constitution of that mass may be.

The neurapophyses or hard parts developed in the lateral neural laminae are "typically" two at least on each side. Not only are there two on each side in the trunk sclerotomes of certain cartilaginous and probably osseous Fishes; but there are two on each side in certain cephalic sclerotomes in at least Fishes and Reptiles. Professor Owen admits one neurapophysis only on each side of his typical vertebra. He accounts for the additional pair in the spine of the sturgeon on the principle of "vegetative repetition;" while the additional elements in the neural arches of certain cephalic vertebræ he at one time considered as parapophyseal, and latterly as diapophyseal elements. But it appears to me that a principle of "vegetative repetition" is out of place in a morphological question; and a parapophysis cannot, according to Professor Owen's archetype, be intercalated between a neurapophysis and a neural spine; nor can a diapophysis become an independent element.

The superior or posterior spinous process, "neural spine," or (as a more convenient general designation) metaneurapophysis, is developed in the mesial neural fibrous lamina. As this element is situated in the mesial plane, it is potentially double, and its right and left halves become depressed and more or less flattened out in the cephalic sclerotomes. With the neurapophysis it completes the neural arch.

The cartilaginous or osseous elements developed in the lateral and mesial hæmal laminae of the fibrous sclerotome constitute the hæmal arch. The fundamental character of the inferior or hæmal arch, as I understand it, consists in this that its constituent elements take their rise at or close to the inner surface of those "ventral laminae" or "folds" in the embryo, which form the lateral and inferior walls of the visceral chamber. Every hæmal arch, therefore, within the antero-posterior range of the alimentary tube must, according as it is more or less developed, necessarily inclose that tube more or less completely. Accordingly no arch within the range of that tube, if it excludes the tube, can be considered as a hæmal arch, merely because it incloses great bloodvessels. Again, before any arch beyond the range of the alimentary tube can be considered as a proper hæmal arch, its development must have been ascertained; or its relations to those muscular, vascular, but more particularly nervous elements, which constitute in their respective systems the arrangements corresponding to the hæmal arch in the sclerotome, must have been determined.

I must confess therefore my inability to discover the precise view of the hæmal arch taken by Professor Owen. Judging from his diagram of the "ideal typical vertebra," and from his general treatment of the subject, a chevron bone in the Reptile or Mammal, or that portion of the cervical vertebra in certain Birds which completes the canal beneath the centrum, represents the primary typical form of this arch. It would also appear to follow from his doctrine, that the expanded form of hæmal arch, provided for the lodgment of the central organ of circulation, and presented by the thoracic segments, is a secondary formation—the result of the removal of the primary hæmal arch from its "typical" position under the centrum, and its intercalation between the elongated pleurapophyses. But this doctrine appears to me to involve embryological contradictions. The relations of these primary and secondary forms of hæmal arch in the neck and throat respectively are not explained by it. The so-called



hæmal arch under the cervical vertebra of the pelican is undoubtedly hæmal in function; but as it excludes the œsophagus and trachea, it cannot be the real or morphological hæmal arch. In other words, this so-called hæmal arch cannot have been formed in the "ventral folds" of the embryo neck.

Again, it is difficult to conceive how the pleurapophyses and hæmal arch of Professor Owen's "ideal typical vertebra" can be developed together in the "ventral folds" of the embryo. For, according to the doctrine of Professor Owen, a pleurapophysis may, in different instances, present two sets of relations. In the thorax it is attached by opposite ends to adjoining sclerous elements, and lies in the wall of the hæmal chamber. In the neck and tail it is connected to its own vertebra at one end only, and does not lie in the wall of the hæmal chamber. The mode in which the continuously arranged elements of the costal arch of a Bird—the "pleurapophyses," "hæmapophyses," and "hæmal spine"—are developed in the embryo is known. But it is difficult to conceive how the detached and peculiarly arranged "pleurapophyses" and "hæmal arch" as represented in the "ideal typical vertebra," or exemplified in a proximal caudal vertebra of a Reptile or perenni-branchiate Amphibian, have assumed the positions they occupy, if they belong to the same group of elements—that is, if they all spring from or originate in the wall of the visceral chamber.

Is the pleurapophysis a fundamental or primary element of the hæmal arch? In other words, is it originally developed in the wall of the visceral cavity, and in certain instances afterwards extruded from it? or is it merely a secondary element in the hæmal arch, that is, formed externally to, or away from it, and only intercalated into it in certain vertebrae?

As a rib, so far as its development has been traced in the series, appears to be formed in the inner layer of the "ventral fold;" and as it is previously connected or continuous with the diapophyseal portion of the neurapophyses, its head and neck being secondary formations, I am inclined to consider the caudal transverse processes in the Mammal, Lizard, and Amphibian, as lying in the position of the original "ventral folds;" and that, therefore, the feebly developed "pleurapophyses" of this region are the only representatives of its hæmal arches; while the chevron bones have no title to this morphological distinction.\*

\* 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 embedded 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 meta-myotomic 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.

This arrangement appeared to me to indicate that the transverse processes, 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.



The processes which complete the canal under the posterior cranial and anterior trunk centrums in certain Fishes, and of the cervical centrums in certain Birds, are probably of the same nature as the chevron bones, which, according to Joh. Müller, appear to be developments of the inferior pair of constituent pieces of the centrum.

We are entitled, then, to require that every part to which the pleurapophyseal or hæmapophyseal character is attributed, should have been proved by direct observation, or otherwise, to have been developed in the "ventral folds."

It appears to me very doubtful whether there are sufficient grounds for limiting the number of morphological elements in the hæmal arch to one pair of "hæmapophyses" and a "hæmal spine;" or to a pair of "pleurapophyses," a pair of "hæmapophyses," and a "hæmal spine;" while an increase in the number of sclerous pieces is accounted for by the principle of "vegetative repetition," or "teleologically." While I admit the grouping of the elements of the more complex hæmal arches into an upper and a lower series, I am compelled on philosophical grounds to deny that the subdivision of a "pleurapophysis" or of a "hæmapophysis," is beyond the range of morphological law; or that morphology and teleology are distinct in the sense that the latter principle provides for what the former is insufficient. Morphology and teleology are merely opposite, because, in the at present phase of science, necessary anthropomorphic aspects of the same Divine principle evinced in the laws of organization.

Until then we know more than we do at present of the laws which regulate the number of "centres of chondrification and ossification;" and, until the constitution of the inferior vertebral arches in the embryo and adult series has been more fully analysed, I cannot give my assent to the expression for a hæmal arch involved in Professor Owen's osteological doctrine.

I must here allude to a point which does not appear to have attracted that attention which it deserves. None of the hæmal arches of the head inclose the hæmal axis. If we are to consider the so-called median and lateral frontal with the superior maxillary lobes as visceral laminae, then, as such, they have no primordial relation with the hæmal axis, which, under the form of the cardiac-branchial tube, extends forward as far only as the so-called "first visceral lamina." After the hæmal arches have been formed in "the first and other visceral laminae," usually so called, of the head, the hæmal axis is found to be excluded from them. It is in consequence of this remarkable developmental arrangement, that the heart, branchial artery, and its branches, in the Fish and Amphibia, are situated below and external to the skeleton of the branchial apparatus.

Before pointing out what appear to me to constitute certain of the developmental conditions on which this peculiar relation of the hæmal arches of the head to the hæmal axis is dependent, I must direct attention to another relation, in which the cephalic hæmal arches are peculiar. The hæmal arches of the head are in immediate contact with the alimentary tube; they are lined by the mucous membrane, which is also in contact with their centrums. There is, in fact, no extension of the peritoneo-pleuro-pericardiac space into the head. The cephalic portion of the primary abdominal wall (Kopfseitenplatte of Remak) becomes from the first united to the corresponding portion of the cephalic primordial vertebral system (Kopfurwirbelplatte); and the former, instead of dividing into two layers, one for the wall of the alimentary tube, and another for the wall of the visceral cavity, with a serous space between them as in the trunk, becomes, in conjunction with the latter, perforated by the branchial clefts.

The hæmal portion of the head, therefore, is distinguished from the cor-



responding portion of the trunk, in presenting meta-somatic clefts, in having no serous cavity, and in having the hæmal axis external to the hæmal arches of its sclerotomes. We are not yet in possession of sufficient data to explain these various peculiarities of the head in the Hæmapod. I must direct attention, however, to the following facts, which bear upon the cephalic exclusion of the hæmal axis. The anterior portion of the primordial alimentary tube, from the cul-de-sac in which it terminates in front, back to its vitellary margin, consists essentially of two parts; a cephalic portion, terminated by the cul-de-sac, is bounded laterally by the "visceral laminae," from the so-called first pair of laminae backwards, and becomes developed into the pharynx; and a cervico-thoraco-abdominal portion, bounded laterally by the anterior portion of the primordial vertebral system of the trunk and the corresponding portions of the primary ventral wall. The primordial hæmal axis (heart and branchial artery) is formed within the pericardiac space, on the inferior aspect of the posterior or trunk portion of the tube from which are afterwards developed the œsophagus, stomach, duodenum, liver, pancreas, and lungs. The heart and pericardium are at first comparatively large, project downwards, and only pass backwards at a comparatively late period into the interior of the hæmal arches of the thoracic sclerotomes in Reptiles, Birds, and Mammals. The cephalic portion, or pharyngeal cul-de-sac, on the other hand, does not present originally any traces of the development of the hæmome. This may be to a certain extent explained by the great comparative development of the cephalic portion of what would have been formerly considered the "serous layer" of the blastoderma. The extremities of the so-called "first visceral laminae" have in fact approached one another below, before the apex of the cardiac tube has advanced so far forwards as to communicate with them. The precise conditions, however, which determine the formation of the sclerous elements of the mandibular, hyoidean and branchial arches on the inside of the corresponding vascular arches, remain to be ascertained by future inquiry. At present I can only conceive of these conditions as in some way dependent upon the developmental relations to which I have alluded.

These relations of the hæmal arches of the head must be taken into consideration in determining the signification of the branchial arches of the Amphibian and Fish. The division of the sclerous system, into dermo, neuro, and splanchno skeleton was first systematically carried out by Carus. I was early brought, by the study of the works of the philosophical and ingenious Dresden Anatomist, to adopt this three-fold division of the skeleton. I have latterly, however, been induced to reject as untenable the doctrine of a splanchno-skeleton. I believe it may be confidently asserted that no structure referable in any way to the skeleton is developed in or around any portion of the mucous layer of the vertebrate alimentary tube beyond that part of it which belongs to the head; in other words, beyond the pharynx, or part perforated by the branchial clefts. The mandibular, hyoidean, branchial, and pharyngeal arches, the cartilages of the larynx, trachea, bronchial tubes, and lungs, are all primarily developed in immediate relation to the cephalic portion of the alimentary tube.

It is remarkable 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. On this ground, however, the hyoidean, and, I believe, the mandibular arch also, as internal to the first, or to the first and second aortic arches, would be also thrown into the system of the splanchno-skeleton. Carus has accordingly done so in the case of the hyoidean arch; but Professor Owen,



overlooking the fundamental embryological relations which indissolubly connect all these arches as serially homologous, holds the hyoidean to be a "strong, bony, persistent arch of the true endo-skeleton;" while, on grounds which appear to me altogether secondary, he refers the branchial and pharyngeal to the splanchno-skeleton, and thus relieves himself of the onus of determining their "homologies." From the view I have been led to take of this subject, I am under the necessity of considering these arches as true hæmal arches, and as certainly referable to the endo-skeleton as the mandibular arch itself. I also, for the same reason, conceive that the complete morphology of the skeleton of the head includes the homologies of the cartilages of the larynx, trachea, and lungs.

The cartilages and bones developed in the actinal fibrous laminae are most important elements in the sclerome. In the head they are variously modified and arranged, not only for the protection of organs, but also as a system of props to afford additional security to the fundamental parts of the skeleton. In the trunk they are chiefly subservient to the myome. They thus exhibit their highest development in the framework of the limbs, for the entire constitution of which they alone, I believe, supply the elements.

The bony rays developed in the meta-myotomic laminae of Fishes exhibit the most elementary forms of actinapophyses. Here, again, I must differ from Professor Owen, who limits the number of these "diverging appendages" to one—generally attached to the pleurapophysis—on each side of the vertebra. This "epipleural element" he considers to be a part of the endo-skeleton, while the additional radiating bony filaments he refers to the exo-skeleton, and recognises in them a manifestation of the principle of "vegetative repetition." While I admit that the so-called "epipleural spines" are the most constant of these bones, yet as the others are developed in the same fibrous membrane, which has, moreover, no primary relation to the dermal system, I cannot see on what grounds they can be excluded from the endo-skeleton. As, again, I cannot avail myself of the principle of "vegetative repetition" in a morphological inquiry, and as I find all of these "additional ribs" connected with important modifications of the myome, I account for their presence teleologically, and hold, therefore, that they must also be explicable morphologically.

The question as to the typical number of actinapophyses in a sclerome cannot, it appears to me, be determined in the present state of the science. Their existence and general morphological relations having been ascertained, the conditions which determine their position and number must remain for future inquiry.

On these grounds I cannot, with Professor Owen, regard the branchiostegal rays on each side collectively as a single "diverging appendage." I not only recognise on each side of the hyoidean arch of the osseous fish one series, but a double series of actinapophyses. This double arrangement of the branchiostegal rays has not, so far as I know, been recorded. One series of these rays are attached along the outer, and therefore morphologically anterior surface, and the other along the inner, and therefore posterior surface of the cerato-hyal; but as the two series are attached, the one to the upper, the other to the lower part of the bone, they form together a single range for the support of the branchiostegal fold.

I recognise a similar but more developed form of this double arrangement of actinapophyses in the variously modified cartilaginous or semi-osseous double styles or plates which are attached to the convexities of the branchial arches for the support of the respiratory membrane of



osseous Fishes. These branchial actinapophyses also exhibit that jointed or multiarticulate structure so generally presented by the rays of the mesial and bilateral fins.

This leads me to observe, that I have not been able to satisfy myself of the truth of the doctrine at present generally held, that the inter-spinous bones and rays of the mesial fins belong to the dermo-skeleton. I admit that, in certain instances, these fins present more or less dermal bone in their composition; but I cannot see how fin-rays, from which the skin and sub-cutaneous texture may be stripped, can be considered as portions of the dermo-skeleton. These rays can scarcely, I conceive, be referred to the dermo-skeleton in the cartilaginous Fishes; and as the rays of the bilateral fins resemble those of the mesial in their histological as well as in their general relations, they ought to be placed in the same category. The rays of the mesial, as well as of the bilateral fins cannot, therefore, in my opinion, be consistently excluded from that portion of the sclerome usually denominated neuro- or endo-skeleton; but like other elements of the endo-skeleton which approach the dermal sclerous fibrous lamina, they may coalesce with dermal bone.

I have been led to consider the inter-spinous bones and mesial fin-rays as actinapophyseal elements. With reference to the mesial position and characters of these bones, I would remark, that it appears to me to be quite permissible, on morphological grounds, to look upon each inter-spinous bone, with its corresponding fin-ray, as consisting of a right and left actinapophysis mesially united,—that is, to consider the right and left halves of which they consist in the young fish as fundamental elements of opposite sides of the body. This view of the actinapophyseal character of the bones of the mesial fins appears to be supported by the occurrence of double anal and caudal fins in monstrous fishes, and also by the so-called urohyal bone. The relations of this bone appear to me to indicate that it is not referable to the basohyal elements of the arch, but to the actinapophyseal. I recognise it as consisting of two of these elements fused together at the mesial plane.

I am further supported in the view which I take of the actinapophyseal character of the inter-spinous bones and mesial fin-rays, by the well-known and hitherto unexplained antero-posterior duplicity which they exhibit in certain fishes. In the *Pleuronectidæ*, for instance, the inter-spinous bones are attached in pairs, one bone in front and another behind each spinous process. In these instances I conceive we have examples of mesial anterior and posterior actinapophyses in each sclerotome. The corresponding fin-rays are, it is true, alternate, but this does not affect the general principle, when we keep in view the remarkable antero-posterior movements of certain elements of the sclerome discovered by Remak in the embryo, and the highly important observations of Professor Owen with reference to the alternations of some of the elements of the spine in certain Reptiles and Birds,—alternations undoubtedly referable to movements of the kind discovered by Remak.

In the head actinapophyseal elements are generally bar-like, or more or less flattened from without inwards. From the peculiar forms assumed by these elements in the head, an anterior actinapophysis of one sclerotome may meet a posterior one from the sclerotome in front, so as to form together a bar-like or flattened bridge, or buttress, between the two. These bridge-like connections of neighbouring sclerotomes are not unfrequently completed by the fibrous basis of the sclerome. In Birds, and the typical Lacertians, indeed, in which the actinapophyseal elements exhibit remarkable adaptations, the fibrous matrix in which they are imbedded, and by which they are connected, forms an essential feature of their arrangement.



The actinapophyseal elements of a sclerotome are to be distinguished as hæmal and neural—those attached to the hæmal and those connected with the neural arches. The hæmactinapophyses are the most usual and numerous, and have hitherto been alone recognised as such by anatomists. I shall therefore at present only remark, in reference to the neuractinapophyses, that I consider as such the neural range of “additional ribs,” the interspinous bones and rays of the dorsal fins, and of the neural half of the caudal fin in cartilaginous fishes, and also the inter-neural cartilages, to which attention was first directed by Joh. Müller. In the cephalic sclerotomes, the neuractinapophyses constitute the so-called “sense capsules” and the system of “muco-dermal bones.” The so-called “muco-dermal bones” have been latterly referred by the continental anatomists to the dermo-skeleton. I am, nevertheless, inclined to believe, that when the general morphological relations of these bones, and their existence in at least Reptiles and Birds, are taken into consideration, they will be admitted as elements of the endo-skeleton. They are not the only bones in the head of the osseous Fish which are traversed by mucous tubes; but from their superficial position they generally are so, and from the same circumstance are frequently overlaid by dermal bone. Professor Owen has adopted the doctrine of the muco-dermal character of these bones, and includes the lachrymal among them. Believing the lachrymal to be a cephalic neuractinapophysis, I cannot assent to the rejection of this bone from the endo-skeleton, and more particularly to referring the perforation which generally characterises it to the system of dermal mucous canals. The lachrymal canal is a metasomatic opening. It is the remaining portion of the cleft between the maxillary and palatine visceral laminae. The lachrymal bone is situated at the upper end of this cleft, at the extremity of that metasomatic space in which the eyeball is situated—viz., the orbit. The lachrymal bone is therefore grooved or perforated by an integumentary canal which, as a portion of one of the original clefts in the wall of the face, is retained in the adult as a passage for the secretion of the lachrymal gland.

The most important cephalic neuractinapophyses are those fibrous, cartilaginous, or osseous structures which support and protect the nose, eye, and ear. They exhibit their fundamental character most distinctly in the Cyclostomatous and Plagiostomatous Fishes, in which they consist of sessile or pedunculated cartilaginous cups or capsules attached to the outer margins of the cranium. In the other Vertebrata these “sense capsules,” variously modified in form and texture, become more or less involved in the wall of the cranium. In their fundamental form they must be considered as parts of the endo-skeleton, homologous in the Hæmapod with those parts of the dermo-skeleton of certain Neuropods, such as the Crustacean, which carry the organs of sense, and are serially homologous with its masticatory and ambulatory limbs.

Professor Owen refers the “sense capsules” to the splanchno-skeleton. But the organs of hearing, vision, and smell, are developed not from or in connection with the mucous layer of the blastoderma, but from the so-called “serous layer”—that is, from that superficial layer which produces the skin, its appendages, the cerebro-spinal axis, and the primordial vertebral system. It appears to me that it would have been more natural to refer the sense capsules, as De Blainville did, to the dermal system; but their histological, embryological, and general relations, indicate, I believe, their real nature as parts of the neuro-skeleton.

The most complex and important development of the actinapophyseal



elements of the sclerome are those arrangements which constitute the framework of the limbs. As, however, I find myself compelled to dissent from Professor Owen's determination of the anterior pair of limbs as the hæmal arch and "divergent appendages" of the occipital vertebra; and as I also dissent from his general doctrine of limbs, I shall reserve my observations on the subject for a separate communication.

The osseous formations in connection with the subintegumentary fibrous lamina constitute collectively the dermal portion of the sclerome. As the constitution of the exo-skeleton does not immediately bear on the object I have in view, I shall merely observe, in reference to it, that a more extended and systematic investigation of its structure and morphology is at present very much to be desired.

From the statements already made, it will be observed that I consider that the most general conception we can at present reach of a vertebra or sclerotome, is a somewhat expanded or detailed form of Von Baer's ideal transverse section of the Vertebrate Animal, which is based on the original neural and hæmal foldings of the blastoderma from the sides of the corda dorsalis. With reference to the further development of the idea, I venture to express my decided opinion, that formally to announce the archetypal number of elements in a segment of the skeleton is a premature attempt at generalisation, and that a dogmatic statement on a subject of this kind must have a greater tendency to check legitimate induction the higher the authority from which it emanates.

*The modifications which occur in the Sclerotomes towards or at the front of the Head.*—It is generally admitted, that in tracing backwards the series of sclerotomes in a vertebrate animal, they become modified in form in proportion to the withdrawal of the other organic systems, until at last the sclerotome may become a mere nodule or filament. Although it is also generally admitted that a certain amount of deterioration takes place in the sclerotome towards the anterior part of the cranium, the nature and extent of the change has not hitherto been precisely determined. I find that it presents, according as the nasal fossæ are or are not present, two forms.

*First general form of deterioration.*—The deterioration is much less in the first form than in the second. The first form may be best observed in the Mammal, in which alone the nasal cavities are complete. The nasal fossæ of the Mammal are bounded below by a series of at least four hæmal arches, the palatine, maxillary, intermaxillary, and ali-nasal, which, along with the soft parts, form collectively the palatal vault of the mouth, with the upper lip and under surface of the external nose; these three continuous surfaces forming in fact the anterior part of the sternal or hæmal aspect of the head, the palatal portion being inclosed within the mouth in consequence of the elongation of the lower jaw. If now the sclerotome, of which the intermaxillary bones constitute the hæmal arch, be examined, it will be found to present superiorly the two nasal bones, as its neural elements; but which, instead of bounding along with their corresponding centrum, a neural space, assist the intermaxillary bones in forming two spaces, which are completed, and at the same time separated from one another by the centrum, which no longer separating a neural from a hæmal space, separates a pair of lateral neuro-hæmal spaces, or nostrils, from one another. This modification of the sclerotome depends, primarily, on its not being required to enclose a segment of the neural axis; and, secondarily, on its co-operating in the formation of the nostrils. This form of sclerotome, in which the centrum passes from above downwards, I denominate *catacentric*, to distinguish it from the ordinary form in which the centrum passes across, which, there-



fore, I also occasionally find it convenient to indicate as the diacentric form of sclerotome. The passage from the diacentric to the catacentric form is exemplified in the ethmoidal sclerotome, the hæmal arch of which, consisting of the pair of maxillary bones, enters into the formation of the nasal passages. The centrum of this sclerotome has assumed the form of a more or less compressed plate, which, while it retains its lateral connections with the neurapophyses, extends at the same time more or less upwards into the neural space, and downwards between the nostrils, which, under this sclerotome and the one behind, consist of a mesially bisected hæmal cavity.

The anterior terminal sclerotome in the non-proboscidian Mammals is cartilaginous and catacentric. Its neuro-hæmal chambers are closed in front by the junction of the anterior margins of its neural and hæmal elements. In consequence, too, of the position of the external nostrils, which, as metasomatic openings, are situated between the hæmal elements of this sclerotome and those of the sclerotome immediately behind, its hæmal elements are tilted forwards, so that towards their junction with the neural elements, their sternal margins are continuous with the dorsal line of the nose. In the more developed forms of this sclerotome, from one to three hæmactinapophyses on each side enter largely into its arrangements.

In the proboscidian Mammals, instead of being greatly developed, as might naturally be expected, this sclerotome is, on the contrary, much simplified. In the Tapir the hæmapophyses have disappeared, while in the Elephant, the neurapophyses alone exist in a comparatively undeveloped form. I believe, however, that it will ultimately be admitted, that the proboscis is not a mere elongation or development of the external nose, like the pseudo-proboscis of the Bear, Racoon, and Coati, but a syssomatome.

*Second general form of deterioration of the Sclerotome at the front of the Head.* The character of this form of deterioration may be best observed in the intermaxillary or vomerine sclerotome of the osseous Fish. Instead of being reserved for the purpose of forming portions of nostrils, the neural space no longer required for the lodgment of a segment of the neural axis disappears entirely, the neurapophyses being at the same time generally absent. The centrum may also disappear, or may exist in the form of a cartilaginous nodule; a pair of neurapophyses may therefore form the entire sclerotome. These hæmapophyses generally extend outwards and downwards from one another, or from the centrum if it exists at the mesial plane. They form together, therefore, an arch suspended at its centre, with its piers unsupported. The hæmapophyses of the two sclerotomes immediately behind, form respectively two arches, the maxillary and palatal, suspended by their centres from the base of the skull. The centres of these three arches are, however, morphologically their approximated piers, the actual centres, their sternal or hæmal conjunctions are not completed in the osseous Fish, in consequence of the nonformation of the nasal fossæ. These three incomplete hæmal arches retain their embryonic form of imperfect visceral laminae. They do not bridge across to form a palate, and therefore the first complete hæmal arch in the osseous Fish is the mandibular. The palate in it is, therefore, like that of the Mammal, morphologically a portion of the external surface of the animal. But they differ from one another in this respect, that the palate of the Fish is a primary, that of the Mammal a secondary surface.

*Number of Sclerotomes in the Vertebrate Head.*—It has tended not a little to throw discredit on the vertebral theory of the skull, that its ad-



vocates have differed much as to the number of its constituent vertebræ. I am inclined to think, that these discordant views are the result of a tendency in later inquirers to be influenced by that *à priori*, or "transcendental" method, characteristic of those German and French anatomists with whom the subject originated. For my own part, so far from coinciding in the received opinion, that the number of segments in the vertebrate head is the same in all its forms, I believe that it varies. I shall state in the sequel the grounds on which I hold the number of sclerotomes to vary slightly in the heads of the ordinary forms of vertebrata. I am, however, inclined to believe, that there are indications afforded by embryology and comparative anatomy, of the existence in certain forms of vertebrate head of a considerably greater number of sclerotomes than has been generally supposed. I base this conjecture, first, on the system of cartilaginous nasal segments in the Cyclostomes; and, secondly, that if the head is to be distinguished embryologically from the trunk, by the presence of "visceral laminæ" separated by clefts, then not only the Cyclostomes, but the still more remarkable Branchiostoma indicate a number of cephalic segments, and a form of vertebrate structure, of which, in the present state of the science, it can only be said, that such a form is deducible from the vertebrate type.

I recognise in the head of the Fish, exclusive of the Cyclostomes, six sclerotomes; in that of the Amphibian and Reptile also six; with the exception of the Crocodiles, in which the seventh is feebly developed; in that of Birds, six; and in that of Mammals, exclusive of the Proboscidi-ans, seven.

I find it more convenient to examine these sclerotomes from before backwards; and I distinguish them provisionally by the following designations—

- |                    |                     |
|--------------------|---------------------|
| 1. RHINAL.         | 5. POST-SPHENOIDAL. |
| 2. VOMERINE.       | 6. TEMPORAL.        |
| 3. ETHMOIDAL.      | 7. OCCIPITAL.       |
| 4. PRE-SPHENOIDAL. |                     |

Keeping out of view, therefore, the Cyclostomatous Fishes and the Proboscidian Mammals, which present indications of a greater number, the Vertebrata generally possess all the sclerotomes enumerated above, except the Rhinal, which exists only in Mammals and Crocodiles.

*On a fundamental difference between the cranium of the Mammal, and that of the Bird, Reptile, Amphibian, and osseous Fish.*—In my earlier attempts to unravel the intricacies of this subject, I found myself opposed by difficulties in passing from the Mammalian to the lower form of cranium, and *vice versa*. I afterwards discovered, that this mainly depended on the reciprocal development and atrophy of the meta-neurapophyseal elements of four sclerotomes in the two forms. In consequence of this, we had been hitherto confounding the frontal bone, or meta-neurapophysis of the ethmoidal sclerotome of the Mammal, with the so-called "proper frontal bone," which is in fact the meta-neurapophysis of the pre-sphenoidal sclerotome of the Bird, Reptile, Amphibian, and osseous Fish, an element of which there are, and this only in rare instances, faint or doubtful traces in the former; and *pari passu*, we had been confounding the parietal bones, the double meta-neurapophysis of the post-sphenoidal sclerotome of the Mammal, with the so-called parietals, the largely developed meta-neurapophyses of the temporal sclerotome of the Bird, Reptile, Amphibian, and osseous Fish, elements which



are much reduced in size, and masked in the former. Among other important organic relations indicated in the existence of these two forms of cranium, I would here more particularly note their bearing on the encephalon. Of the two forms, that of the Fish, Reptile, and Bird, while it adheres to the common type, is modified mainly in relation to the organs of smell, sight, and hearing. That of the Mammal, also adhering to the common type, is modified in relation to the cerebrum proper—to that nervous structure superimposed upon the series of ganglionic masses at the base of the brain which are serially homologous with the spinal cord.

**RHINAL SCLEROTOME—In Mammals.**—The principal parts of the cranium which remain unossified in the Mammal are the nasal septum and the cartilages of the nose. Of these, the unossified portion of the nasal septum is the anterior prolongation of the basal portion of the so-called “primordial cranium.” It is consequently a continuous mass of cartilage, but is nevertheless referable to three sclerotomes; its superior portion completing the centrum of the ethmoidal; its lower portion, the centrum of the vomerine; and its anterior, that of the rhinal sclerotome.

The rhinal sclerotome in the Mammal is fibrous, cartilaginous, and catenarcentric. Its centrum, formed by the anterior portion of the nasal septum, extends from its neural to its hæmal margin. Its right and left neural elements are the so-called superior or triangular cartilages of the nose. They may be continuous with or merely attached to the neural edge of their centrum. The anterior margins, or angles of these cartilages, and the corresponding point of the septum or centrum is the absolute anterior termination of the animal, or more precisely of its morphological axis. The ridge of the nose downwards and forwards to that point is neural or dorsal; beyond it, although continued in the same line, the ridge is hæmal or sterual.

The two alar cartilages are the hæmapophyses of this sclerotome. Variously modified in form, they are more or less firmly attached to the lower margins of the upper cartilages. In front they are attached to the septum, to which also they are more loosely connected round the tip of the nose, being frequently folded in on the ridges of the septum. In the fibrous membrane occupying the sides of the space between the posterior margins of the alar cartilages which together constitute the hæmal arch of their sclerotome, and the anterior margins of the intermaxillary bones which form the hæmal arch of the succeeding sclerotome, there are generally a number of variously modified cartilaginous pieces. These pieces are teleologically highly important elements of the rhinal sclerotome. Morphologically they are actinapophyses. When fully developed, they are three on each side attached to the alar cartilage. In the Ox and other Ruminants, the superior actinapophyses is an irregular lamina, which, imbedded in the fibrous membrane, assists in supporting the wall of the nostril. The second is a thick, short bar, articulated to the alar cartilage in front, and jointed behind to the corresponding element of the vomerine sclerotome, by which arrangement it is immediately connected with the inferior turbinal bone, which is an actinapophyseal element of the ethmoidal sclerotome. The third or inferior rhinal actinapophysis is a crutch-like cartilage, articulated to the alar element by its stem, which is bent inwards, then downwards, and outwards to the margin of the nostril, which it supports by its curved transverse portion. In the Bear, Raccoon, and Coati, the two superior actinapophyses are much developed, and, along with the neurapophyseal, form the cartilaginous wall of the trunk-like nose, or pseudo-proboscis. In the Phacochoer the acuminate nasal bones curve down toward the intermaxillary,



so as to separate the neural elements of the rhinal sclerotome from one another. The rhinal centrum is therefore much diminished in extent; but is, at the same time, strengthened for the support of the nasal buckler by a deposit of bone. The hæmapophyseal and actinapophyseal elements are thus pushed outwards, along with the nostril, so as to produce that breadth for which the snout of this Pig is remarkable. In Man the rhinal actinapophyses are reduced to the sesamoid cartilages. In the Solipeds they disappear altogether. The so-called semilunar cartilage of the Horse is, in fact, the alar cartilage itself, the internal inferior angle of which, much elongated, supports the inner margin of the nostril, as the transverse limb of the crutch-like inferior actinapophysis of the Ruminant, supports the outer margin of the orifice.

*The rudimentary Rhinal Sclerotome in the Crocodiles.*—In the Crocodiles, as in the Mammalia, the vomerine sclerotome is traversed by the nasal fossæ, which open therefore in front, instead of behind it, as in the other Reptiles and in Birds. It is evident, therefore, that if the Crocodiles do not possess, like the Mammalia, a rhinal sclerotome, their external nostrils must present an exceptional arrangement; for, instead of being metasomatic, they must be terminal. I find, however, that in the Alligator, the hoods which extend from the anterior inner margins and septum of the osseous external nostrils consist of dense fibrous tissue, covered by the muscles which act upon them. This double fibro-muscular hood is so arranged on each side as to have the oblique slit-like nostrils situated between their outer margins and the intermaxillary edges. If a plate of cartilage were developed in the margin of each hood, the whole arrangement would occupy the position, and exhibit the relations of an ali-nasal cartilage—a rhinal hæmapophysis, or neurapophysis, as in the Elephant.

*VOMERINE SCLEROTOME—In Mammals.*—In the Mammal the vomerine is a perfect catacentric sclerotome. The nasal bones are its neural elements, as they occasionally run together, and are evidently, as has been generally admitted, serially homologous with the frontals and parietals; they must be viewed as meta-neurapophyses, the neurapophyses being absent in the absence of a nervous centre. The intermaxillaries meeting below form the hæmal arch, and the centrum consists of the vomer, with a corresponding portion of the cartilaginous nasal septum.

The vomer is a bone peculiarly Mammalian. It may be said to make its appearance as a developed element, along with the completed nasal fossæ. But its development in the Mammalian series is not only dependent on the nasal fossæ, but on the intermaxillaries, with which, as will be shown in the sequel, it is invariably connected. Its passage backwards under the centrum of the ethmoidal sclerotome to abut against that of the pre-sphenoidal, is, as will also appear, a Mammalian peculiarity, and an instance of that antero-posterior elongation and of that overlapping arrangement so frequent in the adaptation of the cephalic centums to one another.

When the inferior turbinal bone, an actinapophysis of the ethmoidal sclerotome, is highly developed, as in the Ruminants, a strong flattened bar of fibro-cartilage is attached to the inner aspect of the ascending process of the intermaxillary, and widening out into a soft curved cartilaginous plate, completes the fore part of the inferior turbinal connecting it at the same time to the second actinapophysis or turbinal process of the ali-nasal cartilage. I look upon this appendage as a hæmactinapophysis of the vomerine sclerotome; and serially homologous with the second or turbinal hæmactinapophysis of the rhinal, and with the turbinal hæmactinapophysis of the ethmoidal sclerotomes.



These hæmactinapophyses have all of them been enclosed within the nasal chamber during development; having passed in through the metasclerotomic clefts, instead of forming parts of the nasal wall, or projecting from its outer aspect.

*Vomerine Sclerotome in the Crocodiles.*—It is remarkable that the familiar fact of the peculiar position of the external nostrils of the Crocodiles should not hitherto have attracted attention. They open in front of the intermaxillaries as in the Mammals; whereas, in the typical Lacertians, and in the extinct Plesiosaurs, Ichthyosaurs, and Pterodactyles, in the Ophidians, Amphibians, and Birds, they open behind these bones. On this peculiarity in the Crocodiles depends the very perfect development of the anterior part of the nasal septum. Along with the complete and pervious intermaxillary arch, we find a complete although cartilaginous vomer. Of that part of the extended nasal septum of the Crocodiles, corresponding to the Mammalian nasal septum, the only ossified portion is an elongated single or double slip along the lower edge of its ethmoidal region, and continuous with the elongated presphenoidal centrum. Professor Owen considers this slip of bone as the vomer. I will only observe at present, that holding the vomer to be invariably in relation to the intermaxillaries, I can only conceive, as the vomer in the Crocodile, that elongated cartilaginous portion of the nasal septum which extends beneath the elongated nasal bones to the intermaxillary suture.

*Vomerine Sclerotome in Typical Lacertians.*—In the proper Lizards this sclerotome is imperforate. The intermaxillaries not only close in at the palate, but in front also; the more or less elongated and combined ascending processes joining the united or distinct nasal bones. The centrum is represented by the anterior part of the cartilaginous septum. The two bones usually described as the double vomer of the Lizard belong, as I shall endeavour to show in the sequel, to the succeeding sclerotome—the ethmoidal.

*Vomerine Sclerotome in Birds.*—The vomerine sclerotome of the Bird consists principally of the intermaxillaries, but partly of the persistent anterior portion of the primordial cranium. The intermaxillaries speedily unite below and in front, so as to form the first and principal part of the beak. Their united ascending processes extend up to the so-called “principal frontal bone,” and separate completely the so-called nasal bones. In the sequel the evidence will be adduced on which I found my belief that the bone called in Birds the “frontal,” or “principal frontal,” is not the frontal of the Mammal; but that the two so-called nasal bones in the Bird are the two halves of that bone which in the Mammals is called frontal. If so, where are the nasal bones of the Bird? as the ascending processes of their intermaxillaries, which occupy the proper position of the nasals, have not been observed as separate centres of ossification; and as the greater number of Chelonian Reptiles want these bones, and resemble Birds in the general character and horny covering of their beaks, I am inclined to believe that the nasal bones are deficient as ossified elements in the Bird. In young birds, after boiling or maceration, the osseous elements of the beak may be removed, and the anterior part of the primordial cranium brought into view. In the forepart of its septum we again recognise the vomerine centrum, but more or less deficient in certain Birds from the septal perforation peculiar to them. The upper margin of the cartilaginous septum, where it is in contact with the ascending processes of the intermaxillaries, flattens out into a lamina, which partly roofs over the external nostril on each side. These marginal processes of the cartilaginous vomerine centrum extends down in front, so as to line the fore and under part of the nasal fossæ, projecting somewhat behind the intermaxillary margin of the external nostril.



The broad projecting upper portion of the cartilaginous septum occupies the position of the nasal bones, while the inferior portions project from behind the intermaxillaries, like opercular actinapophyses. In the Chick the part of the primordial cranium just described as belonging to the vomerine sclerotome, presents an opaque aspect and fibro-cartilaginous structure, contrasting with the hyaline cartilage posterior to it—a peculiarity pointed out by Reichart as characteristic of certain portions of the primordial cranium. It will be observed that I do not consider the bone or bones usually called “vomer” in the Bird as correctly designated. In the sequel I shall indicate the grounds on which I hold these bones to be the upper elements of the palatine arch.

*The Vomerine Sclerotome in Chelonian Reptiles.*—The intermaxillaries in the Chelonian, united below, complete the front of the palate alveolar margin, and floor of the nasal fossæ. The only trace of ascending processes which they present, is a compressed spine which projects upwards at their junction in the median line of the nasal opening of the cranium. The lateral margins of that opening are formed by the maxillaries alone; its upper margin by the so-called pre-frontals, except in *Hydromedusa* and certain fossil forms. The cartilaginous septum of the nasal fossæ extends up from the intermaxillary suture to that of the pre-frontals.

Is the Chelonian vomerine sclerotome modelled on that of the Crocodile, or of the Bird? The Chelonian presents the first stage in the remarkable development of the nasal passages exhibited by the Crocodiles. But the general deficiency of the nasal bones, the indications of ascending processes of the intermaxillaries in the mesial plane, the formation of the posterior margins of the external nostrils by the maxillaries, appear to me to show that in the construction of its vomerine sclerotome, the Chelonian differs from the Crocodiles, and resembles the typical Lacertians, the Ophidians, Amphibians, and the Birds. The cartilaginous lining of its nasal fossæ, a remnant of its primordial cranium, projects, in general, a little beyond the margins of the osseous nostrils, as in Birds; but in *Trionyx* and *Chelys*, the projecting margins run forward together in the form of a double cartilaginous proboscis.

*The Vomerine Sclerotome in the osseous Fishes.*—I have already described the general constitution of the vomerine sclerotome of the osseous Fish, as one form of deterioration of the forepart of the cranium. Its centrum, the vomer, when it is present, is merely a cartilaginous nodule in the longitudinal axis of the basis of the cranium, in front of the bone usually described as the “vomer,” but which I believe to be the centrum of the ethmoidal sclerotome,—the neural elements, and those scale-like bones, which Cuvier recognises, I believe correctly, as the nasals. Professor Owen considers these bones to be the turbinal divisions of the olfactory “sense capsules”; and, according to his doctrine of the sense capsules, elements of the splanchno-skeleton. If Professor Owen understands by the turbinal divisions of the olfactory sense capsules, bones homologous with the inferior turbinated, or even the so-called ethmoidal turbinated bones of the Mammal, it is difficult to understand, on embryological principles, how, as splanchnic bones, and as developed in connection with the maxillaries, they come to be situated under the integument of the upper surface of the head. It is, moreover, questionable, whether the sclerous capsule of this, or of any of the special sense organs, is ever divided, and its parts separated from one another, under such relations as those presented by the so-called “turbinals” and “ethmoidal” of the osseous Fish.

The intermaxillaries form the principal and more peculiar elements of this form of vomerine sclerotome. The nasal fossæ being entirely absent,



the merely fibrous olfactory sense capsule is subcutaneous, or partly under cover of the nasal bones (turbinals); the vomer is not developed as a septum, but merely to supply a fulcrum for the intermaxillaries, which may even constitute the entire sclerotome, but are never united below, so as to form a complete hæmal arch.

**THE ETHMOIDAL SCLEROTOME.**—The ethmoidal sclerotome, and the pre-sphenoidal immediately behind it, present, in the different forms of Vertebrata various remarkable modifications of their elements, partly dependent on the position of the olfactory lobes of the brain, partly on the position of the olfactory capsules themselves, partly on peculiar adjustments of the nasal fossæ, and on the arrangements subservient to mastication.

The withdrawal from behind forwards of the neural axis, in the course of development, from the posterior extremity of the neural canal is accompanied by well-known changes in the evacuated, but rapidly increasing posterior trunk sclerotomes. Corresponding, but much more remarkable changes, to which attention has not been hitherto sufficiently directed, accompany the withdrawal from before backwards of the anterior part of the brain from the ethmoidal and pre-sphenoidal sclerotomes. The neural portions of these sclerotomes assume more or less of the catacentric character—they become demicatacentric. The neural chamber of the ethmoidal sclerotome of the Mammal, in addition to a portion of the cerebrum proper, lodges its homologous segment of the neural axis. In the Bird the neural chamber of this sclerotome is completely evacuated by the neural axis, which not only leaves it, but withdraws in part also from the pre-sphenoidal. The absence of the anterior extremity of the neural axis from the neural chamber of the ethmoidal sclerotome, is accompanied by the division of that chamber into a right and left compartment by a mesially laminar centrum, the two compartments being occupied by the olfactory capsules. The olfactory lobes in the Bird are not only withdrawn from the ethmoidal sclerotome, but retreat to a certain distance backwards in the neural chamber of the pre-sphenoidal. To this extent the chamber becomes catacentric; but instead of its two resulting compartments being occupied by new structures, having only to transmit the olfactory nerves, their outer walls collapse upon the mesially laminar centrum, and very generally disappear almost altogether, so as to leave the nerves uncovered on the sides of the laminar centrum as they pass forward to the ethmoidal chambers. The neural chamber of the ethmoidal sclerotome of the Bird, containing only the olfactory capsules, is so connected with the bones of the face, and with the neural arch and centrum of the pre-sphenoidal, as to be more or less moveable along with the lower mandible. The ethmoidal in the Mammal is thus seen to be the anterior cerebral sclerotome, while in the Bird it becomes the posterior facial sclerotome.

In the Reptile both the ethmoidal and pre-sphenoidal sclerotomes are evacuated by the neural axis, the olfactory nerves alone passing along in the compressed tubular, partially-catacentric neural chamber of the latter—the olfactory capsules occupying the right and left chambers of the former. In Reptiles, however, the very varied forms assumed by the bones of the face, and more particularly by those of the palatine arch, in relation to the nostrils, and the arrangements for mastication, produce numerous remarkable modifications of these two sclerotomes.

In passing from the Reptile to the Fish, the ethmoidal sclerotome may be said to gather together its scattered elements, and to present a centrum and neural arch frequently as compact as the Human; but modified by the deficiency of nostrils, and by the withdrawal of the neural axis.

*Ethmoidal Centrum and Neural Arch in the Mammal.*—The human



cranium, as the most perfect in the higher of the two forms of skull, will not unfrequently be found to afford a clue to the signification of bones which, being only applied to their final purposes in it, are more or less masked in the other Mammalia, and apt to be misunderstood altogether in the Fish, Reptile, and Bird. If we examine in connection the two bony masses, which, in the current nomenclature of Human Anatomy, are distinguished as frontal and ethmoid, they will be seen to constitute a ring, the space within which is greatly dilated behind, in consequence of the vast expansion, more particularly of the upper and lateral portions of the frontal; while it is diminished to a tubular chink in front, and is so indistinct towards the nasal fossæ, that the older anatomists named it "foramen cæcum." The development of this bony ring shows it to consist of five pieces. These are, the mesial plate, including the crista-galli of the ethmoid, the lateral masses of the same bone, including the corresponding halves of the crebriform lamina, and the two halves of the frontal. We have here therefore a centrum, a pair of neurapophyses, and a divided meta-neurapophysis. The pair of olfactory nervous centres, which terminate in front the entire series of segments of the neural axis, are the segments of that axis, homologous with this neural arch and centrum. In the Mammalia only, is the upper part of this neural arch expanded and adapted for the protection of the more or less developed forepart of the cerebrum proper. In the central portion and lateral masses of the ethmoid, and in the frontal bones of the Mammal, I recognise the centrum and neural arch of a sclerotome, which I provisionally distinguish as the ethmoidal.

*Centrum and Neural Arch of the Ethmoidal Sclerotome in the osseous Fish.*—The more or less concurrent statements of Oken, Bojanus, Geoffroy, Cuvier, and Owen, as well as the relations of the bones themselves, leave no doubt as to the homology of the so-called pre-frontals of the Fish. They are neurapophyseal elements, the lateral ethmoidal masses of the Mammal in another form, and *minus* the ossified olfactory capsules. The median bone superimposed upon the "pre-frontals" of the Fish, and which has been very generally held to be the united nasals, and the spine of the olfactory vertebra, must be homologous with the frontal bone of the Mammal, if its relations to the "pre-frontals" and olfactory nerves of the former are compared with those of the ethmoid and frontal bones, and the olfactory nerves of the latter. Professor Owen, while he adopts the determination of the superior median bone, as the united nasals, also holds by the hitherto unanimous opinion of anatomists, that the median bone armed with teeth, situated below the pre-frontals of the Fish, is the vomer. Guided by the ethmoid of the Mammal, I cannot see in this bone aught else than the homologue of the central element of the Mammalian ethmoid. The vomer is a Mammalian bone; if it appears in the Fish at all, it is a cartilaginous or semiossified nodule between the intermaxillaries. That the centrum of the ethmoidal sclerotome in the Fish, considered as the homologue of the central plate or bar of the Mammalian ethmoid, should carry teeth in the Fish, is not more remarkable than that one of the centrams of the cervical vertebræ in that class of animals should be so armed.

*Hæmal Arch of the Ethmoidal Sclerotome in the Mammal and osseous Fish.*—I have commenced my account of the morphological constitution of this important sclerotome, by pointing out the typical arrangement which its neural arch and centrum present in the Mammal and Fish. As the arrangement of these parts of this sclerotome becomes much and variously modified in Birds, Reptiles, and Amphibia, in relation to the various forms presented by the organs of smell and the nostrils, it will be necessary, before proceeding farther, to examine the constitution



of its hæmal arch. Even in its most complex form, this hæmal arch, like those of the rhinal and vomerine sclerotomes, consists of two elements only, the right and left maxillary bones. In the osseous Fish they resemble the "lateral frontal processes" in the embryo; they form only an incipient arch like that formed by the vomerine hæmapophyses in front of them. They do not invariably carry teeth. They are variously connected to the hæmapophyses before and behind them; and superiorly to the lateral and forepart of the centrum, neurapophyses, and meta-neurapophyses of the neural arch of their own sclerotome.

The maxillaries of the Mammal, more or less extended from before backwards, and increased in breadth and depth to adapt them to their functions in mastication; meeting one another below, to form a great part of the vault of the palate, and to assist in the formation of the nasal passages; hollowed out to combine lightness with strength; and buttressed by numerous connections with neighbouring bones, nevertheless retain their connection with the neural portion of their own sclerotome, being attached superiorly to the lateral masses of the ethmoid, and to the frontal. They are not articulated, as in the Fish, to their centrum; but those connections to the neurapophyses and meta-neurapophyses, which in Fish are affected by ligaments, are sutures in the Mammal. In the sequel it will be shown, that of the two connections of the maxillary, that to the frontal, and that to the lateral ethmoid, the former is the most constant; presenting in my opinion the fundamental discriminative character of the remarkably modified frontal of the Bird, Reptile, and Amphibian.

*The Ethmoidal Sclerotome in the Bird.*—The ethmoidal sclerotome is remarkably modified in the Bird. It forms no part of the cranium proper, but assumes the position and structure of a facial sclerotome. The Bird, like the Mammal, has two proper facial sclerotomes. In the former, there are the vomerine and the ethmoidal; in the latter the rhinal and vomerine. In the majority of Birds, also, the ethmoidal sclerotome, along with the vomerine, moves more or less freely on the pre-sphenoidal. It is, moreover, peculiar in being chiefly devoted to the economy of the organs of smell; in having its meta-neurapophyseal elements separated from one another by the passage backwards of the conjoined ascending processes of the intermaxillaries; in the feeble development of its hæmapophyses; and in its cavities being altogether neural, its neurapophyseal elements forming more or less of its palatal aspect.

The meta-neurapophyses of the ethmoidal sclerotome of the Bird, are the so-called nasal bones. From their invariable connection with the maxillaries, I cannot see in these "nasal bones," aught else than the proper frontal bones—the frontals of the Mammal. They are separated from one another by the ascending processes of the intermaxillaries; a circumstance which does not militate against their being the right and left halves of a meta-neurapophyses. They are more or less elongated in the antero-posterior direction; and they bound the posterior margins of the external nostrils by the descending processes which connect them with the maxillaries. To distinguish them from the meta-neurapophyses of the pre-sphenoidal sclerotome, I designate them ethmoido-frontals.

The arrangement of the centrum and neurapophyses of this sclerotome in the Bird, appear to me to have been in a great measure overlooked, from having been examined in the macerated skull, in which these parts, as consisting principally of cartilage, are to a great extent absent.

The centrum consists of the posterior and greater part of the mesial cartilaginous lamina, the interior portion of which forms the vomerine centrum. The ethmoidal portion of this laminar mesial cartilage flattens out at its upper margin, in the same manner as the vomerine portion in front; and like the flattened upper edge of the so-called "ethmoid bone,"



—the centrum of the pre-sphenoidal sclerotome behind. In the same manner as the flattened upper margin of the vomerine portion extends outwards on each side, so as to form a hood over the upper and forepart of the external nostrils, the flattened upper margin of the ethmoidal portion of the septum passes outwards on each side, under cover of the ascending processes of the intermaxillary, and under the ethmoido-frontal, extending down more or less to the level of the palatal plate of the maxillary, and then turning in towards the mesial plane, approaches or meets the lower margin of the mesial lamina itself. Posteriorly, these curved cartilaginous plates close in upon the posterior margin of the septum; which is not continuous with the anterior margin of the laminar septum of the pre-sphenoid. They are each, however, perforated or notched for the transmission of the olfactory nerve; and they also leave on each side of the septum at their posterior inferior angles, a space for the posterior nasal orifice. The superior and middle turbinated folds of the nasal chamber on each side, are also supported by turbinated cartilaginous projections from the internal surfaces of their plates.

I have already stated that the anterior fibro-cartilaginous portion of the persistent part of the primordial cranium of the Bird enters into the structure of its vomerine sclerotome; it will now be observed that its posterior hyaline portion enters into the formation of the ethmoidal sclerotome. In the majority of Birds, the septal lamina continues cartilaginous, as well as the greater part of the curved lateral plates, with their internal turbinal projections. A more or less extended portion only of each curved plate becomes ossified when it extends inwards across the palate; and the ossified portion becomes ankylosed to the maxillary, or to the descending maxillary process of the ethmoido-frontal ("nasal"), and in many Birds to the anterior extremity of the palate bone.

I recognise, therefore, the posterior part of the nasal septum as the centrum; the so-called "nasals" as the meta-neurapophyses; and the more or less ossified lateral and inferior walls of the olfactory chambers as the neurapophyses of the ethmoidal sclerotome of the Bird. If it be objected to this determination, that the parts which I consider as neuropophyses, are only portions of the olfactory sense capsules, I would merely observe, that these sense capsules are in fact combined with the neurapophyseal portions of the ethmoidal sclerotome in the Bird, as in the primordial cranium of the Mammal, Reptile, and Amphibian, and as in cartilaginous Fishes; but that this circumstance in no way nullifies the existence of the neurapophyseal element itself, either in the sclerotome with which the olfactory capsules, or in those with which the ocular and auditory capsules, are connected. I would also observe, that I base my determination of the neurapophyseal character of these parts, not merely on their relations in the Bird, but on the varied relations exhibited by their corresponding parts in Reptiles.

The maxillaries or hæmapophyses of the ethmoidal sclerotome are feebly developed in the Bird. Connected above, chiefly to the descending processes of the ethmoido-frontals, and more or less prolonged in the antero-posterior direction, the maxillaries do not invariably complete the hæmal arch. Their region, therefore of the palate, is more or less completely occupied by the neurapophyseal plates of their own sclerotome.

*The Ethmoidal Sclerotome in the Chelonian.*—The connection of the maxillaries of the Tortoises and Turtles, by means of the ascending processes of these bones, with the so-called pre-frontals, appears to me to indicate that the latter are homologous with the ethmoido-frontals of the Bird, or the frontals of Mammalia. I recognise in them the meta-neurapophyses of the ethmoidal sclerotome. Each of these bones sends down from its posterior margin a lamina, concave in front, and forming



with the concave under surface of the bone itself, the posterior superior hollow of the nasal fossa. The inner margins of these two descending laminae give attachment to the anterior margins of the fibro-cartilaginous laminae, which bound laterally the compressed pre-sphenoidal neural space, and form the so-called interorbital septum. The inner margins of the two descending frontal laminae are, therefore, separated from one another above by the breadth of the forepart of the groove on the mesial part of the under surface of the combined so-called "frontals." If now the macerated skull of the Turtle be examined, it will be found that a complex bony piece, the so-called "vomer," connects by its pair of short divergent upper processes the inferior extremities of the inner margins of the descending frontal processes, converting the space between them into a triangular orifice. This so-called vomer, after sending a horizontal plate backwards between the palatines to form the mesial portion of the common orbital floor, and to support the cartilaginous bar-like centrum of the pre-sphenoid, passes down as the osseous septum of the posterior nares, and terminates in the form of a pentagonal plate in the palate, between the palatines and maxillaries, and in some species in a hexagonal form, between the palatines, the maxillaries, and inter-maxillaries. The relations of the ethmoidal neurapophyses to their meta-neurapophyses in the Bird, and the presence of the former in the maxillary region of the palate, led me to suspect that the so-called "vomer" of the Turtle is the combined neurapophyses of its ethmoidal sclerotome. But its posterior horizontal laminar process, which supports the cartilaginous pre-sphenoidal centrum, as well as the process which forms the septum of the posterior nares, indicated the probability of the "vomer" being a still more complex bone. I have not met with the palatal plate as a separate bone in the Turtle, although in longitudinal sections I have observed faint indications of its having been so. I find, however, that in certain Tortoises, not only is the palatal plate connected by a distinct suture to the upper portion of the so-called "vomer," but it is divided by a similar suture in the mesial line of the palate into two halves. In these Tortoises, therefore, the separation of the posterior nares, the junction of the descending processes of the ethmoido-frontals, and the support of the cartilaginous bar-like centrum of the pre-sphenoid, are affected by a distinct bone, which, including its connections to the palatines, presents all the characters of the so-called "vomer" of the Bird. But I have already stated my belief, that the bone so-called is not the vomer of the Bird; and in the sequel I shall state the grounds on which I hold it to be the combined entopterygoids—the upper elements of the palatine arch.

*Ethmoidal Sclerotome in the Crocodiles.*—In the Crocodiles proper, and the Gavials, the lachrymal is interposed between the so-called pre-frontal and the maxillary. In the Alligators the maxillary resumes its connection with the pre-frontal, which it had lost in the two other families on account of the elongation of the snout. The pre-frontals in all the Crocodilians are separated from one another mesially by the passage backwards of narrow contiguous processes of the nasals, and by similar processes which pass forwards from the so-called "proper frontals"—in this respect resembling the so-called "nasals" of the Bird, which are separated from one another by the ascending processes of the inter-maxillaries.

Assuming the relations of the pre-frontals of the Crocodilian to the maxillary arch as evidence of their being the meta-neurapophyses of the ethmoidal sclerotome—that is, collectively, the homologue of the Mammalian frontal—the next elements of this sclerotome to be determined are its neurapophyses. At this point the type of ethmoidal sclerotome



exhibited by the Bird, and the modification of that type presented by the Chelonian, indicate its character in the Crocodilian. The descending processes of the pre-frontals of the Crocodiles are connected inferiorly to the ascending processes of the so-called "palate bones." Now, a bone connected to the homologue of the Mammalian frontal cannot well be considered as the palate bone, even although it be situated between and united by suture to the maxillary and pterygoid. But a bone with such relations, if viewed in the light of the corresponding relations of the ethmoidal neurapophyses of the Bird, indicates its own real nature. The ethmoidal neurapophyses of the Bird, connected above with the ethmoido-frontals, form below more or less of the palatine vault. The ethmoidal neurapophyses of the Chelonians, pushed away forwards and downwards from the ethmoido-frontal by the ento-pterygoid, still form a part of the vault of the palate. In like manner I recognise, in the so-called "palate bones" of the Crocodilian, the neurapophyses of its ethmoidal sclerotome. The ethmoido-frontals and neurapophyses of the Bird, form, along with their cartilaginous septum or centrum, a complete catacentric neural ring. The interposition of the ento-pterygoid of the Chelonian separates the meta-neurapophyses from the neurapophyses of the ethmoidal sclerotome, and at the same time separates the neural space into an upper portion, mesially divided by the cartilaginous septum or centrum for the passage of the olfactory nerves, and into an inferior, mesially divided by the ento-pterygoid itself for the right and left nasal passages. A similar but somewhat modified change is effected in the ethmoidal sclerotome of the Crocodilian, by the interposition of the anterior extremities of its pterygoids—which anterior processes I believe to be, in fact, the ento-pterygoids. These anterior, generally mesially united, processes of the pterygoids of the Crocodilian, were considered by Cuvier as representing the under portion of the Mammalian vomer. He describes them as two osseous pieces fixed to the inner margins of the "palate bones," in front of the "anterior frontals," and of that part of the pterygoid which covers the nasal canals. Professor Owen describes these pieces as the "vomer," and as being generally ankylosed to the forepart of the basi-sphenoid; but he adds the following very important observation, which I have verified, that they (the "vomer") form a distinct bone in a species of Alligator, which passes so far forward and downwards as to appear in the form of a plate in the vault of the palate, in front of the palate bones.

That this double bony splint is not a vomer, as Cuvier supposed, must be evident, if the vomer is to be considered as an element of the vomerine sclerotome. It cannot be, as Professor Owen states, a vomer united to the "basi-sphenoid;" because, in front of the elevated, laterally-compressed, quadrilateral process which passes forwards and upwards from the centrum of the post-sphenoid, the real axis of the skull is continued forward in the form of a compressed cartilaginous bar, which is the centrum of the pre-sphenoid, and which passes in front into the cartilaginous nasal septum, which constitutes the ethmoidal and vomerine centrams. The Crocodilian and Chelonian skulls are, in fact, entirely destitute of ossified central elements in front of their post-sphenoidal centrams, the superincumbent framework in these forms of cranium being supported along the base, not by ossified centrams, but by greatly expanded and modified pterygoids, ento-pterygoids, ethmoidal neurapophyses, maxillaries, and inter-maxillaries, immediately above which series of bones lies the persistent central axis of the primordial cranium, as far back as the ossified centrum of the post-sphenoidal sclerotome. In a mesial antero-posterior section of the macerated skull of the *Crocodilus vulgaris*, a suture will be found commencing in front of the common orifice of the



Eustachian tubes, and terminating at the lower part of the root of the laterally-compressed post-sphenoidal process already alluded to. In front of this suture, the section presents no traces of central elements, the pterygoids and so-called "palatals" taking their places. In a section of this kind in the Museum of the University of Edinburgh, the extremity of the anterior process of the pterygoid passes forwards and downwards, appearing in the suture between the two "palatines," about an inch from their anterior margins; the right and left portions exposed on the vault of the palate being separated from the "palatines" by surrounding suture, and forming together a narrow double surface, one-eighth of an inch in length. In the section to which I allude, and in similar sections, I observe traces of the line of anchylosis between these anterior processes and the pterygoids themselves. These lines run upwards and forwards, and appear to include the anterior and greater part of the pterygoidal portion of the nasal septum, and the thin plate which, on each side, passes up to be united to the descending process of the "pre-frontal." In disarticulating the skull of the Crocodile the pterygoids generally remain attached to the post-sphenoidal centrum, so that the prolonged anterior processes of the former present the appearance of being elongations of the latter, which they in fact are not.

From the foregoing considerations, and on grounds to be explained in the sequel, when the palatine arch, or hæmal arch of the pre-sphenoidal sclerotome comes to be examined, I recognise in the Crocodilian vomer of Cuvier and Owen the proximal or upper element of the pre-sphenoidal hæmal arch—the same element to which, when existing in certain Fishes, Professor Owen applies the sufficiently expressive term *ento-pterygoid*.

It will now be observed, that in consequence of the great development of the pterygoids, and of the *ento-pterygoids* in the Crocodilian, the latter extending forward into the neural space of the ethmoidal sclerotome roof over the greater part, and provide a septum for nearly the whole of that extent of the nasal fossæ, the sides and floors of which are formed by the so-called "palatals" or ethmoidal neurapophyses, and abut against the descending processes of the "pre-frontals" or ethmoido-frontals, without entirely extruding the neurapophyses from these processes, as in the Chelonian. There is another minor difference between these parts in the Crocodilian and Chelonian. In the Chelonian, as has been already stated, the *ento-pterygoids* having pushed the ethmoidal neurapophyses from their natural connection with the descending processes of the ethmoido-frontals, complete, by means of their ascending divergent processes, the triangular space for the olfactory nerves. In the Crocodilian, again, the descending processes of the ethmoido-frontals complete the space for the olfactory nerves, by means of a short process from each of them, which, passing inwards, meets its fellow of the opposite side a little above the junctions of the descending processes themselves with the *ento-pterygoids*. The space left between this transverse commissure above, the combined *ento-pterygoids* below, and the lower ends of the descending ethmoido-frontal processes laterally, is occupied by a prolongation forwards of the cartilaginous bar-like pre-sphenoidal centrum.

If the bones hitherto considered by comparative anatomists as the "palatines" in the Crocodilian, are in reality the neurapophyses of its ethmoidal sclerotome, the question arises—Where are the actual palate bones? This question comes to be examined in the sequel, when the hæmal arch of the pre-sphenoidal sclerotome, of which these bones are elements, is under consideration. At present I may state that the study of the crania of the Bird, Lacertian, and Ophidian, has led me to recognise as the palate bone that bone which Cuvier was induced to consider



peculiar to the Lizard and Serpent, and named "os transverse" or "pterygoide externe"; and which Professor Owen also names ecto-pterygoid.

*The Ethmoidal Neural Arch and Centrum in the Lacertians.*—The maxillaries of the typical Lacertians are invariably connected above to the so-called pre-frontals. These pre-frontals are widely separated from one another by the anterior extremities of the so-called "principal frontals," which pass forward, and bound laterally the divided or undivided nasals. The pre-frontals bound the anterior superior angles of the orbits, sending downwards on each side a plate which separates the orbit from the nasal cavity, is more or less intimately connected with the so-called "double vomer," and with the so-called "palatines." I shall, in the sequel, state the grounds on which I hold the "palatines" of the Lizard, Ophidian, and Amphibian, to be its ento-pterygoids, and to be the homologues of the bone or bones which in the Bird are considered as the "vomer." I believe the "transverse bones" of the Lizard to be actually its palate bones, pushed backwards and outwards by the greatly developed ento-pterygoids, and of its so-called "vomer." The so-called "vomer" of the Lizard consists of two bones, which form the floor of the nostrils, separated from, but at the same time connected to, one another by the lower margin of the cartilaginous nasal septum, abutting against the intermaxillaries in front, and the so-called "palatines" or ento-pterygoids behind, and leaving a space on each side, wider behind than before, between their outer margins and the maxillaries, for the posterior nares. In some Lizards the posterior extremities of the two halves of the "vomer" are separated from the transverse descending plates of the "pre-frontals" by the interposition of the anterior extremities of the ento-pterygoids, but in others they articulate with the pre-fronto-lachrymal. Anatomists appear to have been induced to look upon these two bones in the Lizard as the two halves of the vomer, by the same circumstance which has induced them to consider the ento-pterygoids of the Bird as its vomer, viz.,—their position between the posterior nares. But the general relations of the so-called double "vomer" of the Lizard, indicate that its two halves are homologous with the ethmoidal palate-plates of the Chelonian, with the so-called "palatines" or ethmoidal neurapophyses of the Crocodilian, with the corresponding cartilaginous or osseous pieces in the Bird, and with the lateral masses of the ethmoid in the Mammal. It appears to me that the ethmoidal neural arch and centrum form a cat-centric arrangement, the two compartments of which constitute the greater part of the nasal fossæ, the olfactory nerves entering through the mesially divided space between the descending or orbito-nasal processes of the meta-neurapophyses; and the posterior nares passing off on the outer sides, and between the neurapophyses and the maxillaries.

*The Ethmoidal Neural Arch and Centrum in Ophidians.*—The maxillaries of the Serpent are articulated or connected to the "pre-frontals." The latter are separated from one another mesially by the elongation of the nasals back to the "principal frontals." Each of the "pre-frontals," comparatively large, and ankylosed to the lachrymal, sends down a transverse orbito-nasal plate, notched on its inner margin for the olfactory nerve, but separated from its fellow of the opposite side by the pre-sphenoidal processes of attachment of the "palatines." The space roofed over by the nasals and "pre-frontals" is mesially divided above by the contiguous mesial descending laminae of the nasals, and below by the cartilaginous nasal septum. It is floored by the double "vomer," the two halves of which, connected by the lower margin of the cartilaginous septum, extend from the intermaxillaries in front to the centrum of the pre-sphenoidal sclerotome behind, being separated from



the orbito-nasal processes of the "pre-frontals" by the pre-sphenoidal processes of the "palatines."

From what has already been stated with reference to the corresponding parts in the Bird, the Chelonian, and Saurian Reptile, it will now be seen that I hold the so-called "pre-frontals" of the Serpent to be its actual frontals or ethmoido-frontals; its so-called double "vomer" to consist of the right and left neurapophyses, as the "pre-frontals" are the two halves of the meta-neurapophyses; and the cartilaginous nasal septum the centrum of its ethmoidal sclerotome.

*The Ethmoidal Neural Arch and Centrum in the Amphibians.*—The view which I take of these parts in the Amphibia will at once appear from the foregoing statements, and may be illustrated by the structure in the Frog. As in the Bird, the basis of the ethmoidal neural arch and centrum consists of that portion of the persistent primordial cranium which is situated behind the intermaxillary region, and immediately in front of the "os a ceinture." The mesial portion of this mass of cartilage forms the centrum of the sclerotome, as the posterior part of the nasal septum. The posterior portions of the nasal fossæ are hollowed out on its sides. Its upper surface is covered by the so-called "pre-frontals," which are, in fact, ethmoidal-frontals, or the two halves of the divided meta-neurapophysis. Its lower surface is supported by the two triangular bones, covered with teeth, and which are the neurapophyseal ethmoidal elements, already examined in the other Vertebrata. The posterior nares are situated behind, between the outer margins of these so-called vomerine bones and the maxillaries. The latter are, as usual, connected to the ethmoido-frontals.

*Of the views which have been hitherto taken of the Ethmoidal, or Nasal Vertebra, or Sclerotome.*—I am precluded in an abstract from entering upon the important but tangled morphological history of the nasal segment of the cranium. I shall only, therefore, on this department of the subject, make a few observations, in deference to the authority of Professor Owen, and in explanation of those points on which I find myself at variance with his doctrine. I have already so far stated, and in the sequel shall more fully state, the grounds on which I dissent from the doctrine of Oken and Bojanus, adopted by Professor Owen, that the nasals and vomer are respectively the neural spine and body of the nasal vertebra. What I intend more particularly to notice at present is that part of Professor Owen's doctrine which relates to the neurapophyseal elements of the nasal vertebra.

Professor Owen considers the middle plate of the Mammalian ethmoid to be the coalesced pre-frontals, and the two halves of the crebriform plate, the ethmoidal cellules, and turbinated laminae, to be collectively the greatly developed olfactory capsules. If the latter are kept out of view, as not entering, according to his doctrine, into the formation of the ethmoidal or nasal neural arch, the doctrine necessitates the conversion of the laterally-placed "pre-frontals" of the Fish and Reptile into a single mesial laminar bone. Here I would observe that, overlooking, for the present, the adoption by Professor Owen of the current statements as to the identity of the "pre-frontals" of the Fish with the "pre-frontals" of the Reptile, I cannot conceive how the "pre-frontals," either of the Fish or Reptile, can be homologous with a mesial bone. Embryologically, I cannot understand how the olfactory nerves, which in the Fish and Reptiles are situated mesiad of the "pre-frontals," can become placed in the Mammal on their outer aspects. The pair of "pre-frontals" in the Crocodile or Turtle can be legitimately enough conceived as coalescing mesially into a single bone; but this change presupposes the withdrawal or obliteration of the olfactory nerves; for, otherwise, two conditions



must be admitted, both of which are embryologically untenable—first, that the olfactory lobes of the Mammal are at one period in its development mesial to the right and left halves of its central ethmoidal plate; and secondly, that the nervous and sclerous structures change places, the former passing outwards through the latter, or the latter meeting in front of the former, and passing backwards between them. But the actual facts are these:—The mesial plate, or bar, of the Mammalian ethmoid is mesial from the first; and the olfactory bulbs, or nerves, are situated from the first on its lateral aspects. The mesial plate is the prolongation forward of the central bar of the primordial cranium; it is a true vertebral centrum, and is continued onwards and downwards into the vomerine portion of the cranial axis. The crebriform lamellæ are the only parts, therefore, of the Mammalian ethmoid which present in their embryo and adult conditions all the characters of neurapophyseal elements; connected below with their centrum, and laterally or above with their frontal meta-neurapophyses, they, along with the latter, and the centrum, close in the forepart of the encephalic portion of the cranial cavity, and enclose the olfactory lobes of the brain. That the olfactory, like the fifth nerve of the Mammal, leaves the encephalic cavity by more than one orifice, and that the olfactory “sense capsules” are united to the corresponding neurapophyses, are circumstances which afford no arguments against this determination, but, on the contrary, are in accordance with the union of the auditory capsules with their corresponding neurapophyses, and the exit of the auditory nerve from the encephalic cavity in divisions. It must also be observed, that if we are to look, with Professor Owen, upon the central lamina or bar of the Mammalian ethmoid as the result of the mesial union of a pair of “pre-frontals,” we must assign a morphological reason for the co-existence of a mesial cartilaginous septum with divided “pre-frontals” of the Reptile and Fish.

I am also obliged to dissent from Professor Owen’s determination of the so-called “ethmoid” of the Bird as the mesially-united neurapophyses of its nasal vertebra. Apparently influenced by its usual designation, and shut up to his own view of its homology by his determination of the “basi-sphenoid” as consisting of the connate centruns of the “mesencephalic” and “prosencephalic” vertebræ, Mr Owen has in the Bird, as in the Mammal, arranged this portion of his morphological system in opposition to embryological facts. The two olfactory nerves of the Bird pass forward on each side of the so-called “ethmoid” in shallow grooves; in certain instances only do they pass through notches or complete orifices formed by osseous development from the two surfaces of the bone. The two nerves in no instance pass forwards between the plates of the bone in any part of their extent. At no period during development are the olfactory nerves of the Bird situated mesial of any part of this bone; for it is originally a mesial cartilaginous plate, a portion of the axis of the primordial cranium, extending forwards and upwards from that part of the primordial axis which, when ossified, constitutes the anterior or acuminate extremity of the centrum of the post-sphenoidal sclerotome. In the sequel, I shall have to point out that this bone in the Bird, which anatomists have hitherto looked upon as the “ethmoid,” is, in fact, the body or centrum of the pre-sphenoidal sclerotome converted into a mesial plate extending up to, and flattened out at the upper surface of the cranium, in accordance with the catacentric character of the neural arch of the sclerotome, of which it is an element. Its corresponding neurapophyses are the pre-sphenoidal wings,—the “orbito-sphenoids” of Professor Owen,—which not only bound laterally the orifices for the optic, but also those for the olfactory nerves. The so-called “ethmoid” of the Bird is not therefore formed by the coalescence



of a pair of "pre-frontals," but is a mesial element belonging to another sclerotome. The Bird already possesses distinct or "divided" "pre-frontals," with all the characters of the "pre-frontals" of the Reptile in its so-called "nasals."

Dugés considered the "os en ceinture" of the Frog to be the ethmoid, from its giving passage to the olfactory nerves by two funnel-shaped orifices at its anterior extremity, and from its intimate connection with the nasal cartilage in front. Professor Owen, on the same grounds, while he holds the posterior part of this bone in the *Rana boans* to consist of the "orbito-sphenoids," looks upon its anterior part as the confluent "pre-frontals." But as the "os en ceinture" of the common Frog originates in a centre of ossification on each side of its fundamental portion of the primordial cranium; and as Professor Owen does not state the grounds on which he holds the "orbito-sphenoids" to be confluent with it in the Bull Frog; as I can find no trace of such confluence, either in the Bull Frog or common Frog; and as the forepart of the bone is divided by a mesial septum,—I look upon it as consisting of a single pair of neurapophyses and a catacentric septum. As this "os en ceinture" is situated upon the upper surface of the anterior acuminated portion of the centrum of the post-sphenoid, as in the Bird; and as it is covered above, and, in the common Frog, is united with the anterior portion of the so-called "parieto-frontal," it appears to me to constitute the neural arch and centrum of the pre-sphenoidal sclerotome, of which the orbito-sphenoids are the neurapophyses. The proper "os en ceinture" of Cuvier is in fact the homologous structure in the aneurous Batrachian with the so-called "ethmoid," and the orbito-sphenoids collectively in the Bird; the centrum being principally developed in the latter, the neurapophyseal elements in the former. On these grounds, and also because I hold, with Cuvier, the "nasals" of the Frog to be its "pre-frontals," I cannot assent to Professor Owen's doctrine, that the "os en ceinture" exhibits a stage in the mesial coalescence of a pair of "pre-frontals," the final effect of which is the formation of a mesial ethmoidal plate, or mesially united nasal neurapophyses.

*On the Actinapophyses of the Ethmoidal Sclerotome.*—As the radiating elements of the ethmoidal segment of the skull are numerous and important; and as their elucidation requires a more extended reference to corresponding elements in the succeeding sclerotomes than can be made before the examination of these has been entered upon, I shall at present make only a general statement on the subject.

In the Mammal we find a series of sclerous elements arranged from above downwards on each side of the ethmoidal sclerotome. On its upper or neural portion are the olfactory "capsule" and the lachrymal bone. On the lower or hæmal portion the cartilages of the eyelids, with the inferior turbinated and malar bones. If the secondary antero-posterior elongation of the maxillary be kept out of view; and if it be conceived in its fundamental developmentary form as a rib-like bone, the convexity of which is inclined outwards and backwards; and if, at the same time, the possibility of a double arrangement of actinapophyseal elements in each sclerotome be borne in view, it will be seen that the malar extends outwards and backwards from the anterior or outer; the inferior turbinal from the posterior or inner aspect of the bone. I have already stated that the actinopophyseal elements of the cranium are generally flattened or extended so as to abut against one another, and against the other bones of the skull. Thus the malar passes backwards in the fibrous membrane which extends across the orbital opening, and which covers in the temporal fossa. The final purpose of the malar is to afford an abutment against the squamosal so as to strengthen the flank of the Mammalian head. The malar, therefore, in many instances sends secondary processes upwards and inwards,



to abut against other bones. While I gladly avail myself of Professor Owen's term "squamosal," and fully agree with him as to the bone itself being a "radiating" element of the cranium; and while I more particularly assent to his very beautiful determination of it as the "quadrate jugal" of the Bird, I must, nevertheless, contend for the much greater probability of its being a radiating element of the mandibular than of the maxillary arch. Its intimate connection with the quadrate bone in the development of the chick, and the disunion of it and the malar in certain Mammalia, appear to me to indicate that they belong to distinct sclerotomes.

The extended attachment from above downwards of the inferior turbinal to the inner aspect of the maxillary of the foetal Ruminant, a form of attachment which is repeated in the lachrymal process of the bone in the human subject, indicate the primary actinapophyseal form of the bone. Its elongation backwards on the inner aspect of the palate bone, and its prolongation forward to abut against the cartilaginous actinapophysis of the vomerine hæmal arch, are secondary processes in the development of the bone, and steps towards the completion of that antero-posterior system of serially homologous actinapophyses which constitute what may be termed the inferior turbinal system. The inferior concha is peculiar to the nasal fossa of the Mammal. The sclerous elements, which constitute its skeleton in its most fully developed form, are posterior or inner actinapophyses of the rhinal, vomerine, and ethmoidal hæmal arches. These actinapophyses become included in the nasal fossa by the closure of the metasomatic clefts; and, as they subsequently elongate, they abut against one another in the antero-posterior direction.

I shall, in the sequel, show that the more or less defined space termed orbit, at the side of the Mammalian cranium, is fundamentally the metasomatic fissure between the ethmoidal and pre-sphenoidal sclerotomes. The upper part of this fissure continues permanently open as the lachrymal canal, and drains away the secretion which bathes the front of the eyeball, while that organ, supported by the sclerotic, which is a pre-sphenoidal neuractinapophysis, and surrounded by its accessory structures, is lodged in its dilated portion. From the upper, anterior, and lower orbital margins, which are formed by elements of the anterior of its two bounding primary sclerotomes, a fibrous membrane extends backwards, covered externally by the orbicular muscle, and closing in the contents of the orbit, with the exception of the front of the eye, exposed through the palpebral fissure. This fibrous membrane is a metasomatic or actinal lamina, extending very obliquely outwards and backwards, like an operculum over the orbit. The succeeding metasomatic membrane assumes the form of the tissue which separates the orbit from the temporal fossa, and which, passing backwards external to that fossa, forms the temporal fascia, which constitutes an operculum to that space. The temporal fossa itself is the upper portion of the metasomatic fissure, between the pre- and post-sphenoidal sclerotomes; occupied by the muscles of mastication and the homologous nerve; the lower part of the fissure on each side remaining permanently open as the mouth, or more correctly as the anterior opening of the isthmus of the fauces. By the extension of ossification from neighbouring bones into the anterior and external portion of this fibrous layer, the orbit may be more or less shut off from the temporal fossa.

The cartilaginous laminae which support the eyelids of the Mammal are developed in the fibrous layer which constitutes the operculum of the orbit, and lie in the same morphological plane as the malar and lachrymal bones. Their histological as well as morphological relations appear to me to indicate, not only that the palpebral cartilages are actinal elements



of the endo-sclerome, but also that they are anterior or external hæmapophyses of the ethmoidal sclerotome. This view of the morphological relations of the malar bone, palpebral cartilages, and opercular membrane of the orbit in the Mammal, is borne out by the corresponding arrangement in the Bird. A fibrous membrane extends backwards over the orbit, from the posterior extremity of the feebly developed maxillary, and from the posterior margin of the descending process of the ethmoido-frontal. In the lower part of this membrane the malar is imbedded; across its centre the palpebral cartilage; and at the antero-superior angle of the orbit, the lachrymal bone. These have all distinct actinapophyseal characters, which, in the case of the lachrymal, enables us to perceive more clearly how the Mammalian lachrymal, having become intercalated between its corresponding hæmapophysis and neurapophysis, retains only so much of its actinapophyseal character as is indicated in the anterior margin of its groove, the remainder of the bone being a secondary expansion.

The lachrymal bone of the Bird may extend into the orbital membrane along the outer margin of the so-called "principal frontal," or sphenoido-frontal, and become attached to that bone without losing its connection with the ethmoido-frontal. It may thus also form a union with the supra-orbital bone, when that bone is present, as in the Hawks. The lachrymal may, moreover, extend backwards under the eye to the post-frontal process, and may have a branch of communication with the antero-inferior projection of the mastoid, as in certain Parrots. It may also extend down to the malar, and may be connected in this direction with the transverse projection of the so-called "ethmoid," or presphenoidal centrum. The infra-ocular bony arch in the Maccaws and certain other Birds is not a zygomatic arch, although consisting like it of actinapophyseal elements. The proper zygomatic arch, as consisting of the malar and squamosal, exists in all Birds; the infra-ocular arch is ossified in comparatively few.

The reference of the lachrymal and the other bony formations round the orbit in Birds to a muco-dermal system by the continental anatomists and by Professor Owen, appears to me to be disproved by their relation to the soft parts. They are all developed in aponeurotic bands, which enter into the formation of the orbital fascia already alluded to. In a band extending along the margin of the sphenoido-frontal, the supra-orbital bone takes its rise, which may thus become connected with the lachrymal, when that bone, which is developed in the anterior extremity of the band, extends backwards in it. A second band extends downwards and backwards from the lachrymal to the malar, forming a ligament between the two bones, and along which ossification may extend. A third band extends from the post-frontal process downwards and forwards to the quadrate-jugal or squamosal, along which ossification may extend from above. In all birds a band connects the lachrymo-malar with the post-fronto-squamosal band, thus forming an arch below the under eyelid. The extension of ossification into this commissural band, probably from both extremities, completes the infra-orbital bony arch, and may approximate or unite it to the squamoso-jugal or proper zygomatic arch. A fibrous band, which extends downwards and forwards in the temporal fascia from the anterior process of the mastoid, becomes ossified in some Birds; and it is an extension of this ossification which appears to form the mastoidal limb, or attachment of the infra-ocular arch of the Maccaw. I shall, in the sequel, state the grounds on which I regard as actinapophyseal all the bones developed in the opercular membrane of the orbital of the Bird. I regard the lachrymal bone and the supra-orbital bone or bones of the Saurians, as referable to the same morphological category; and as due to arrangements in the fibrous operculum of the orbit, similar



to those in the Bird; as also the connection between the malar and the post-frontal of the Crocodilian, as well as the change in the direction of the jugal, and the peculiar position of the squamosal in the typical Lizards.

The supra-orbital bone or cartilage, with the infra-ocular bony arch, appear in various forms in the osseous Fish; and the arrangements presented by this form of cranium clearly indicate that these orbital bones are parts of a system of actinapophyseal elements referable respectively to the ethmoidal, pre- and post-sphenoidal, temporal, and occipital sclerotomes, peculiarly modified and connected in front for the protection of the orbit, and behind for the suspension of the pectoral girdle.

**THE PRE-SPHENOIDAL SCLEROTOME.**—*Its Centrum and Neural Arch.*—It has been already stated that this sclerotome is peculiar in the Mammal, in the absence of its meta-neurapophyses, while this mesial element is more or less fully and largely developed in the other forms of vertebrata. When the cerebrum proper is developed, the sphenoido-frontal bone is absent; when the cerebrum proper is a mere film, as in Birds and Reptiles, or is absent altogether, the sphenoido-frontal is present. As the evidence on which this statement is based is derived from the consideration of the varied relations of all the primary elements in the different forms of cranium, I am compelled, in this preliminary abstract, to refer those who are desirous of weighing that evidence to what has been already adduced with regard to the ethmoido-frontals, and to the statements to be afterwards made in regard to the meta-neurapophyses of the post-sphenoidal and temporal sclerotomes. In the meantime, I shall confine myself to a general exposition of the arrangement as I regard it.

The anterior part of the body of the human sphenoid, and the corresponding pre-sphenoidal piece in the Mammalia generally, constitutes an undoubted centrum, to which the lesser, anterior, or orbito-sphenoidal wings, are the corresponding neurapophyses.

How far we may be entitled to assume the frequent "triquetral" bones in the coronal suture in the human, and in certain other Mammalian crania, and the separately developed antlers of the giraffe, as indications of the missing bone, remains to be determined. I would only observe at present, that the great extent and permanency of the anterior fontanelle appear to be connected with the deficiency in question.

I have already stated that I regard the so-called "principal frontal" of the Bird as the missing frontal of the Mammal. Distinguishing it as sphenoido-frontal, it is the divided meta-neurapophysis corresponding to the feebly developed "orbito-sphenoids," which, bounding the optic and olfactory orifices, constitute the neurapophyses, and to the so-called "ethmoid" as the centrum of the pre-sphenoidal sclerotome. Assuming for the present the signification I have attached to the "principal frontals," and holding the neurapophyseal character of the orbito-sphenoids as incontestable, I would only add a few remarks regarding the central element. The determination of the "ethmoid" of the Birds as the centrum of the pre-sphenoidal segment of the cranium, while it does not require Professor Owen's hypothesis of connation of this element with the centrum behind, presents the element under a form similar to that exhibited by the ethmoidal and vomerine centruns. It resembles these in being an ossified portion of the primordial axis of the cranium, in being flattened into a horizontal plate at its upper margin, in extending down to the line of the base of the skull, and in thus presenting a catacentric relation to its neural arch. The passage of the anterior acuminate extremity of the centrum behind beneath the lower margin of the pre-sphenoidal centrum, so as to support it, is merely an example of that longitudinal obliquity in the setting of cranial cen-



trums against one another, which may be considered as the rule rather than an exception. The posterior margin of the bone is oblique from below upwards and forwards; gives attachment to the orbito-sphenoids, or to their membranous neurapophyseal substitutes, which bound or give passage to the orbital and olfactory nerves. The obliquity of this margin of the bone corresponds with the similar obliquity of the forepart of the basis of the brain of the Bird, a remarkable feature in its configuration. The flattened upper edge of the bone may be more or less exposed on the upper surface of the cranium; and when the intermaxillaries, ethmoido and sphenoido-frontals are removed, this flattened margin is found to be similar to and continuous with the flattened upper margin of the ethmoidal and vomerine cartilaginous septum. The anterior margin may be nearly perpendicular, but is generally oblique from below upwards and forwards, concave or concavo-convex, sharp, and generally free, being connected to the posterior margin of the ethmoidal cartilaginous septum by membrane, thus permitting more or less movement of the upper mandible, that is of the combined ethmoidal and vomerine sclerotomes on the pre-sphenoidal.

In the majority of Birds a laminar process projects outwards and downwards from the lower and forepart of this bone. This process, variously developed, forms, along with the descending process of the lachrymal, the anterior wall of the orbit, separating it from the nasal space, and permitting the passage of the olfactory nerve through a notch or hole in its upper edge. I regard this process on each side of the pre-sphenoidal centrum as of the same nature as the process which will be found projecting from each side of the lower part of the ethmoidal septum or centrum, and which, abutting against the descending process of the ethmoido-frontal, forms a wall or rampart across the floor of the nasal passage, extending nearly half way up to its roof, immediately behind the external nostril, thus converting that part of the nasal chamber in front of it into a vestibule. This process is largely developed in the ossified ethmoido-vomerine septum of the Hawks and Owls.

I would here observe, that the "*os en forme de cuiller*" of Cuvier, which he considers as the inferior turbinal of the Lizard, and which forms the forepart of the floor of the nostril on each side, and the convex anterior part of which stretches like a buttress across the cavity, between the septum and the maxillary, immediately behind the external nostril, appears to me to be, with its fellow of the opposite side, merely the ossified lower portion of the ethmoidal centrum. These so-called "*cornets inferieurs*" of the Lizard form the floor, and do not, therefore, project from the outer wall of the nasal passage in the manner of the inferior turbinals; and I believe anatomists will, in reviewing the subject, admit that the inferior turbinal accompanies the fully completed maxillary arch, and only exists, therefore, in the Mammal.

I regard these lateral processes of the ethmoidal and pre-sphenoidal centruns of the Bird as homologous with the pterygoid processes of the post-sphenoidal centrum, and generally with those processes which, under various forms, project downwards from the sides of the lower or hæmal aspects of the occipital and succeeding centruns in certain Fish, or with those processes termed "*hypopophyses*" by Professor Owen.

Before dismissing the consideration of this important centrum in the Bird, I would direct attention to certain interesting modifications which it may undergo. In the first place, it may, like many other bones in the cranium of the Bird, become greatly dilated and altered in form by the development of air-cells in its interior. The pneumatic openings are two in number, one on each side of the anterior margin below the su-



perior horizontal plate. The pneumatic excavation and dilatation extends backwards more or less in certain species; and in some Owls the bone presents the form of a cubical cellular mass. This peculiarity of form might be adduced in support of Professor Owen's doctrine of the formation of this bone from the coalescence of the pre-frontals; but then it will be observed that the increased breadth of the bone is not due to incomplete mesial fusion of lateral parts, but to expansion from the mesial plane, for the olfactory nerves still run forwards in grooves on its lateral aspects, although these may be deep in front, and, posteriorly, their margins may overlap the nerves. The expansion of the pre-sphenoidal centrum also produces a remarkable separation of the optic foramina. As explanatory of this effect, I would observe, that the development of this bone in the Chick shows that it forms the posterior border of the common optic foramen by means of a pair of processes which project from its posterior inferior angle like the limbs of the letter Y. When, therefore, the bone takes on transverse dimension, the single optic chasm separates into two optic foramina, which, in *Strix flammea*, are three-eighths of an inch asunder.

The separation of the optic foramina from the pneumatic expansion of the pre-sphenoidal centrum leads me, in the second place, to observe, that the characteristic separation of these orifices in the extinct forms Dido, Dinornis, Palapteryx, did not depend entirely on pneumatic expansion of the pre-sphenoidal centrum, nor on such width of that bone as might be attributed to incomplete mesial fusion of a pair of "pre-frontals," but on the remarkable prolongation backwards on each of its sides of the neurapophyseal walls of the ethmoidal olfactory chambers.

Professor Owen, in his series of graphic and valuable memoirs on these three extinct forms, and in his memoirs on Apteryx, assuming the pre-frontal doctrine regarding the bone in question, and directing special attention to the more or less complete passage backwards of the nasal chambers to the anterior or inferior wall of the cranial cavity, and to the passage of the olfactory nerves into these by a number of orifices, apparently recognises in Apteryx for instance (although he does not directly make the statement), a completed Mammalian ethmoid. Now, recalling attention again to the embryological considerations from which the formation of neither the Mammalian ethmoidal septum, nor the so-called ethmoid of the Ostrich, Dinornis, Dodo, nor Apteryx, can be conceived as resulting from coalesced pre-frontals, I would remark, that the arrangement of the nasal fossæ in Apteryx, instead of being Mammalian, presents the peculiar Ornithic character of its parts, fully brought out; all the phases in the development of which may be observed in the series of Birds. In all Birds, the posterior extremities of the cartilaginous pouch-like ethmoido-neural, or olfactory chambers, approach or encroach upon the sides of the pre-sphenoidal centrum; so that the membrane which connects its anterior margin to the cartilaginous nasal septum, and a certain extent of both its surfaces, separate the two pouches from one another. The laminar or hypopophyseal process on each side of the bone, variously modified in form, limits, posteriorly and inferiorly, the olfactory portion of the lateral surface of the bone, and, folded over the pouch, walls it in more or less from below; while the lachrymal from above passes down on its outer side. The gradual environment of the pouch may be traced in the series of Birds; and I find in the Asiatic Cassowary, the stage immediately preceding the completion of the process in Apteryx. In this Bird, the pair of deep fossæ in the interior of the skull, which lodge the olfactory lobes, are separated from one another by the posterior margin of the pre-sphenoidal centrum, which here represents the crista-



galli. The plate of bone which forms the floor of each fossa, instead of being crebriform as in *Apteryx*, is perforated by a single star-like foramen, a form due to the partial shooting across of bony processes from its margin.

*In the Chelonian.*—The neural arch and centrum of the Chelonian are represented in the dry skull by the pair of bones usually considered as the "proper frontals," but which I regard as sphenoido-frontals. In the recent condition the centrum appears in the form of a compressed cartilaginous bar, continuous posteriorly with the compressed anterior part of the post-sphenoidal centrum, resting below on the conjoined pterygoids and ento-ptyerygoids, continuous in front with the cartilaginous ethmoidal septum or centrum, and thus presenting all the relations of the pre-sphenoidal centrum of the Bird. It is continued upwards, and represents the orbito-sphenoids, or neurapophyses, in the form of a double fibro-cartilaginous membrane, the two laminae of which separate to unite with the posterior margins of the orbito-nasal processes of the ethmoido-frontals, with the two parallel descending ridges of the sphenoido-frontals, and with the anterior margins of the peculiar descending processes of the so-called "parietals." The olfactory nerves pass forwards between these neurapophyseal laminae above; and the optic with the other orbital nerves perforate them.

*In the Crocodilian.*—In the Crocodiles, the sphenoido-frontals have coalesced; but the cartilaginous centrum, and neurapophyseal interorbital laminae, present exactly the same relations as in the Chelonian; the only difference being the result of the union of the orbito-nasal processes of the sphenoido-frontals near their lower extremities, and the consequent space left between this bony bridge, and the deep furrow formed by the inclined upper surfaces of the ento-ptyerygoideal portions of the pterygoids.

*In the Lacertians.*—In the Lizards, the sphenoido-frontal is again double. In consequence of the mesial separation of the ento-ptyerygoids ("palatals") and pterygoids, the elongated fibro-cartilaginous centrum and neurapophyseal interorbital laminae, are left unsupported below; to which circumstance is probably due the formation in the inter-orbital laminae, of a pair of delicate triradial osseous neurapophyses, which pass off from the upper margins of the optic foramina.

*In the Ophidian and Batrachian.*—Leaving the further consideration of the special homology of the anterior sphenoidal wing in the Reptiles, and more especially in the Crocodiles, until the posterior sphenoidal wing, and the so-called "petrosal," have been examined, I would observe, that the grounds on which Professor Owen distinguishes the "os en ceinture" of the Frog, from that segment in the Python which includes the so-called "frontals," appear to me somewhat arbitrary. This segment in the Serpent consists of a pair of neurapophyses, or orbito-sphenoids, which are distinct, as cartilages at least, in the embryo; of a double meta-neurapophysis (sphenoido-frontals), which not only occupy on each side the positions of the neurapophyses, but extend the forepart of their inner margins downwards, back to back, in the mesial plane, on the sides of the compressed centrum; which thus, along with them, divides the neural chamber in front, for the transmission of the olfactory nerves. The sides of the "os en ceinture" are formed by neurapophyses; while the so-called "frontals" of the Serpent occupy the greater part at least of the sides of their segment; in other respects, their relations are similar. They are both catacentric; the centrum, in both, resting, as in the Bird, on the upper surface of the anterior acuminate extremity of the post-sphenoidal centrum, and in the plane of the ethmoidal centrum in front. I regard, therefore, the "os en ceinture" in the Batrachian, along with the anterior segments of its "parieto-frontals," as consisting of the centrum,



neurapophyses, and meta-neurapophyses of the pre-sphenoidal sclerotome; and, therefore, also as homologous with that segment in the Ophidian which includes its "frontals," but exclusive of the elongated anterior prolongation of the post-sphenoidal centrum.

*The Pre-Sphenoidal Centrum and Neural Arch in the Fish.*—The bone which predominates over every other in the cranium of the Fish is the so-called "principal frontal"; which, however, as already stated, I do not regard as the frontal or ethmoido-frontal of the Mammal, but as a sphenoido-frontal. It is the pre-sphenoidal meta-neurapophysis of the Fish, presenting all the relations of the corresponding bone or bones in the Bird, Chelonian, and Lizard, except that the ethmoido-frontals anterior to it have coalesced in the middle line; while the ethmoidal neurapophyses have become so much developed, exposed, and connected to it laterally, as to assume the position of the so-called "nasals" and pre-frontals" in the Bird and Reptile. The enormous development of this bone in the Fish and Bird appears to depend on the great bulk of the organs of vision. There is, therefore, in both, an extended inter-orbital space to be filled up. In the Fish, as in the Bird, this is variously effected by means of fibro-cartilage and bone. The extreme forms of the inter-orbital arrangement may be illustrated by the Gadoid and Cyprioid Fishes. In the Cod the greater part of the so-called inter-orbital septum consists, as in the Chelonian and Lizard, of a double fibrous membrane, which extends upwards from the anterior prolongation of the post-sphenoidal centrum to the margins of the mesial grooves on the under surface of the sphenoido-frontal. The two laminae of this membrane thus bound the sides of the compressed neural space, along the upper part of which the olfactory nerves pass forward. In the posterior superior part of each of these neurapophyseal fibrous laminae, a comparatively small plate of bone is developed, while the centrum consists of the bar of persistent cartilage, which extends along the grooved upper surface of the anterior portion of the post-sphenoidal centrum, and terminates above the ethmoidal centrum ("vomer"). The optic nerves pierce the membranes so far back as to notch very deeply the anterior margins of the post-sphenoidal neurapophyses, or post-sphenoidal wings.

In the Carp, again, the inter-orbital space is occupied above by a considerable descent of the margins of the sphenoido-frontal groove; in front, by complete ossification of the fibrous membranes, which thus become pre-sphenoidal neurapophyses; behind, by the passage forwards of the post-sphenoidal wings ("ali-sphenoids"), through which, during development, the optic nerves have passed back, to be lodged in notches in their posterior margins; and below, by the bar of semi-ossified cartilage situated upon the upper surfaces of the posterior sphenoidal and ethmoidal centruns.

*Of the Hæmal Arch and Hæmactinapophyses of the Pre-sphenoidal Sclerotome.*—The palatine arch, between which and the mandibular the mouth is situated, and which terminates therefore posteriorly the pre-stomal series of hæmal arches, may be presumed to undergo very varied modifications in connection with the olfactory, the respiratory, and the digestive functions. In the present instance, as in many others, the anatomy of the human body, instead of leading astray by complexity and extreme modification of its parts, supplies the key for their morphological solution by affording an example of the employment of the fundamental type of structure for the fulfilment of the most complex functional purposes.

The human pre-sphenoidal centrum, hollowed out by nasal air-cells, as in certain Birds, is bounded below and in front by a pair of separate triangular-curved bony plates, which, limiting the size of the right and



left pneumatic orifices, bring these into communication with the posterior ethmoidal air-cells or sinuses. These "sphenoidal turbinated bones," or "bones of Bertin," in contact along their outer margins, and outer part of their inferior aspects, with the sphenoidal processes of the palate bones, constitute the upper elements or suspensory extremities of the inverted arch, completed by the meeting of the palate bones themselves in the posterior part of the mesial line of the palatal vault. The right and left pterygoids are attached, as a pair of actinapophyses, to this arch. They pass off backwards and outwards from the posterior margins of the perpendicular plates of the palate bones, and abut in the embryo against the upper and fore part of the mandibular arch, retaining in the tympanic processes of their adult form, indications of their early connection with that arch. The most important secondary connection of the pterygoids in the human adult is with the pterygoid processes of the post-sphenoid; and it is this sphenoidal connection which is most frequently repeated in the animal series.

I shall not enter at present into the question of the probable existence of "bones of Bertin" in the Mammalia generally; nor enquire whether the separate orbital pieces of the palate bones in the herbivorous Cetacea, according to Cuvier, and the separate anterior portions of the pterygoids of the young Dolphin, as described by Meckel and Rapp, may be indications of the upper elements of the palatal arch; but pass on to the consideration of the palatal arch in the lower Vertebrata, in which the two elements of which it appears to consist on each side, are distinctly developed.

*The Palatal Arch and Pterygoids in the Bird.*—The bone hitherto considered by all anatomists as the vomer of the Bird, is a more or less elongated narrow plate, the margins of which are bent upwards so as to convert its upper surface into a groove, which is applied against the under surface of the acuminate anterior extremity of the post-sphenoidal centrum, which is therefore interposed between it and the pre-sphenoidal centrum. This bone, more or less compressed or extended laterally, separates the posterior nostrils from one another. Its anterior extremity reaches the anterior limits of these orifices, or, passing forwards into the palate between the ethmoidal neurapophyseal and maxillary palatal laminae, and concealed more or less by them, may terminate on the surface of the palate between the intermaxillary palatal plates. When this bone is much compressed it is single throughout; when flattened, it is more or less extensively divided in the mesial line.

The palate bones of the Bird, more or less elongated, extend anteriorly under the maxillary palatal laminae, to which in general they are only slightly connected, forward to the intermaxillary palate plates, with which they are anchylosed or articulated, separated from one another in front, to form the lateral boundaries of the posterior nares, the palate bones become broader posteriorly, approach one another, and are either attached to, or anchylosed with, the posterior extremity of the so-called "vomer." Their posterior extremities are provided with facets for articulation with the bar-like pterygoids, which extend from them, outwards and backwards, to articulate with the quadrate bone on each side. The pterygoids of certain Birds have also secondary connections; they articulate with processes which project from the post-sphenoidal centrum in some part of its extent; and on which their shafts glide, rotate, or vibrate.

The reciprocal relations of the so-called "vomer," the palatines, and pterygoids of the Bird, are extremely interesting and important. At present, I can only direct attention to those relations which bear upon my subject. When the palate bones are greatly developed, the "vomer" diminishes. When, again, the "vomer" is much developed, the palatines are in an atrophied condition. The pterygoids present phases of develop-



ment dependent on the variations of the palatines and pterygoids. The two extremes may be observed in the Parrots and the Struthious Birds. In the former, the palatines are enormously developed, while the "vomer" has disappeared. In the latter, the "vomer" is greatly elongated and developed, while the palatines present the relation, and exhibit the form of the "transverse" or "adgustal" bones of the Reptile.

*The Palatal Arch and the Pterygoids in Reptiles and Amphibians.*—The three bones on each side, which form the palatal system of the ordinary Lizard, present the same relations, and almost the same form as the "vomer," palatines, and pterygoids of the Struthious Bird. The pterygoids are in every respect similar. The "transverse bones" of the Lizard are also, in relations and almost in form, like the palatines of these Birds. The so-called "palatals" of the Lizard, while they exhibit all those relations to the "transverse" and pterygoids, which the "vomer" of the bird presents, differ from that double bone in this respect, that although in contact at the mesial line, they are comparatively so much broader, occupying so much of the comparatively narrow palatal space that they touch the maxillaries by their anterior external angles. They bound, therefore, the internal nares posteriorly; but like the so-called vomer in the Bird, separate them from one another, passing forward like that double bone to the ethmoidal neurapophyseal plates, which constitute the so-called "vomer" of the Lizard. In the monitors, these so-called "palatines," like the pterygoids, are evidently separated in the middle line, and forced backwards along the inner margin of the maxillary towards the transverse bones, by the development and elongation of the ethmoidal neurapophyseal elements. In the Crocodiles, again, the full development of maxillary palatal plates, and more especially of the ethmoidal neurapophyses, has forced backwards and towards the middle line, not only the bone called "palatal" in the Lizard, but also the pterygoids; and as the latter also exhibit that remarkable tubular development, various phases of which are perceptible in the Chelonians, Birds, and Mammalia, the former again presents the ornithic vomerine aspect.

In the Ophidia the two halves of the palatal system are widely separated at the middle line. The so-called "palatals," elongated forwards into the ethmoidal region, articulated by ascending processes to the pre-sphenoid, slightly attached externally to the maxillaries, as in the Lizards, bound as in these Reptiles, the nostrils posteriorly, but do not separate them mesially.

In the Frog, the so-called "palatals" extend transversely outwards from the "os en ceinture" to the maxillaries, being also connected at their outer extremities with the pterygoids. The latter are articulated posteriorly to the post-sphenoid and to the quadrate bone. The "os transversum" has disappeared at the junction of the so-called palatal, pterygoid, and maxillary.

The modifications presented by these bones in Reptiles and Amphibia are much too numerous to be followed in detail at present. I have, therefore, selected those which are essential for the elucidation of my subject; and shall sum up the conclusions I draw from them, by a comparison of them with the corresponding elements in Chelonians.

The Chelonians, we are told, have no "transverse bone." They are distinguished in this respect from all the other Reptiles. But if we examine the skull of a Tortoise, we shall find all the elements which enter into the formation of the palatine aspect in that of the Crocodile. In front are the intermaxillaries, immediately behind which, in the median line, is the double bony plate, which is usually described and



figured as the forepart of the so-called "vomer," but to which I have already directed attention as the combined ethmoidal neurapophyseal elements. In the Turtles the maxillaries meet across the palatal vault in front of the united ethmoidal neurapophyses, so that the latter are pushed backwards, and are in contact laterally with the palatals in the vault of the palate; while in the Tortoise the latter want entirely the palatal processes, consisting, as Cuvier expressed it, only of their upper portions, and extending outwards on each side from the outer margins of the so-called "vomer," and of the pterygoids, to the inner margins of maxillaries. Now, let the base of the skull of a Tortoise, a Turtle, and a Crocodile, be examined side by side. In all three we shall find the intermaxillaries in front. The maxillaries, although they do not meet across the palate of the Tortoise, do so in that of the Turtle, and thus, as in the Crocodile, bound posteriorly the intermaxillary segment of the palate. The transverse union of the maxillaries in the Turtle and Crocodile, pushes back the ethmoidal neurapophyses (which are in contact with the intermaxillaries in the Tortoise), but to such an extent in the Crocodile that the ethmoidal neurapophyses, also themselves much elongated, carry back the pterygoids, so that the latter almost entirely conceal the post-sphenoidal centrum. The outer margins of the pterygoids, already curved downwards in the Tortoise and Turtle, pass downwards and inwards in the Crocodile, so as to meet again in the mesial line of the palatal vault. The bony septum of the pterygo-ethmoidal portion of the nostrils of the Crocodile is at the same time seen to be the result of the extension downwards in the mesial plane of the middle ridge of the so-called "vomer" of the Tortoise or Turtle, and of the connection of the anterior part of that double bone with the ethmoidal neurapophyses. It will thus be observed, that if the maxillaries of the Tortoise were united across the palate, in front of its ethmoidal neurapophyses, to a considerable extent backwards; if the ethmoidal neurapophyses were also elongated in the same direction; and if the outer margins of the pterygoids, below the palatines, were to meet in the mesial line, the latter would be forced backwards and outwards; so that, still retaining their connections with the pterygoids and maxillaries, but leaving those with the "vomer" in front and internally, to abut against the malar behind and externally—the palatal aspect of the skull of the Tortoise would present the arrangement of the corresponding region in that of the Crocodile, the palate bones assuming the form and relations of "transverse bones."

If to the skulls of the Tortoise, Turtle, and Crocodile, those of a Serpent, a Lizard, a Frog, and an Ostrich be added, it will be observed, that the palate bones have disappeared in the Frog; that they have assumed the form and relations of "transverse bones" in the Lizard, Crocodile, and Serpent; that they are essentially "transverse bones" in the Struthious Bird, while in the Tortoise, but especially in the Turtle, they present the Mammalian character and form. It will also be observed, that the bones in the Turtle, Tortoise, Crocodile, and Bird, hitherto denominated "vomer," are the same bones which in the Frog, Lizard, and Serpent are named "palatals," the term "vomer" being applied in these animals to those two bones collectively, which are situated under the ethmoidal portion of the skull. It will also be noted that the bones called "vomer" in the Turtle, Tortoise, Crocodile, and Bird, and the bones called "palatals" in the Frog, Lizard, and Serpent, are related to the others, along with which they have been examined, exactly as the "bones of Bertin," in the human cranium, are to the palate bones and pterygoids.

*The Pre-sphenoidal Hæmal Arch and Hæmactinapophysis of the*



*Fish.*—In the osseous Fish a fibrous membrane extends outwards and downwards on each side from the suborbital bar-like portion of the basis of the cranium. In most Fishes there will be found in this membrane, where it passes off from the pre-sphenoidal portion of the cranium, a more or less elongated scale-like bone on each side. This is the “*pterygoïdien interne*” of Cuvier, the “*hérisséal*” of St Hilaire, the “*ento-pterygoid*” of Professor Owen. The palate bone, connected by the same fibrous membrane to the outer margin of the ento-pterygoid, extends forwards to the side of the so-called “*vomer*,” or to the ethmoidal centrum and neurapophysis, to which, as also to the maxillary and intermaxillary, it is variously attached directly and indirectly. The corresponding actinapophyseal element or pterygoid in the Fish is firmly connected in front to the palate bone, and less intimately to the ento-pterygoid, and, extending backwards, downwards, and outwards, abuts against the anterior margin of the “*hypo-tympanic*” and “*pre-tympanic*” bones, as the pterygoid of the Bird and Reptile does against the so-called “*quadrate*,” or “*tympanie*” bone. If, then, the basal aspect of the cranium of the osseous Fish is placed in series with those of the Bird, Lizard, Serpent, Tortoise, and Frog, it will be observed, that while its palatals and pterygoids may be at once associated with the corresponding bones, as already determined, in the Bird and Reptile, the ento-pterygoid of the Fish presents all the relation of the double bone, usually called “*vomer*” in the Bird; of the posterior or horizontal portion of the bone called “*vomer*” in the Tortoise; and of the bones called “*palatals*” in the Lizard, Serpent, and Frog. It will also be observed, that while the toothed bone, called “*vomer*” in the Fish, has, from a catacentric change, disappeared from the under aspect of the cranium in the Bird, Reptile, and Batrachian, the two bones, called in the Fish “*pre-frontals*”—its ethmoidal neurapophyses—present the same relations to its ento-pterygoids as the ethmoidal neurapophyses of the Bird to its so-called “*vomer*,” and as those of the Tortoise to the posterior portion of its so-called “*vomer*,” and as those of the Lizard, Serpent, and Frog to the bones hitherto called “*palatal*” in these three forms. I therefore apply provisionally the term ento-pterygoid to the so-called “*vomer*” of the Bird, to the posterior part of the so-called “*vomer*” of the Chelonian, to the corresponding bony piece in the Crocodiles, to the so-called “*palatals*” of the Ophidian, Lacertian, and Batrachian, to the “*bones of Bertin*,” and their representatives in the Mammal.

*The constitution of the Nasal Fossæ, and the relative positions of the External and Internal Nares.*—The details necessary for the morphological examination of the rhinal, vomerine, ethmoidal, and pre-sphenoidal sclerotomes, have involved a number of facts connected with the varied constitution of the nasal fossæ in the different vertebrate forms. As, however, the constitution of these fossæ has important bearings on the morphology of the entire cranium, I shall briefly direct attention to the subject.

The only perfect form of nasal fossæ is that presented by the Mammal. They consist of the entire neuro-hæmal cavities of the rhinal and vomerine, combined with the hæmal cavities of the ethmoidal and pre-sphenoidal sclerotomes. That portion of the combined nasal fossæ which consists of the cavities of the rhinal and vomerine sclerotomes, is divided in the mesial plane by the centruns of those sclerotomes; while the dependent portion of the ethmoidal centrum, and the posterior portion of the vomerine centrum, divide in the same manner that part of the combined fossæ which consists of the hæmal cavities of the ethmoidal and pre-sphenoidal sclerotomes. The Mammalian nasal fossæ are therefore bounded in front by the walls of the neuro-hæmal chambers of two catacentric sclerotomes;



and, posteriorly, by the catacentrically divided hæmal chambers of a demi-catacentric and diacentric sclerotome.

As the hæmal portions of the cephalic somatomes are separated from one another in their early embryo condition by meta-somatonic clefts, we may expect to find traces of these clefts in the walls of the adult nasal fossæ.

The first or anterior pair of meta-somatonic clefts of the embryo head, that is the clefts between the rhinal and intermaxillary lobe of the "median frontal process," are retained in the adult as the external nares. These openings in the non-proboscidian Mammal, are situated therefore between the ali-nasal cartilages and the intermaxillary bones. In the proboscidian Mammals, they are probably situated between the ultimate and penultimate, or, at least, between two of the distal somatomes of the proboscis.

The second pair of meta-somatonic clefts, situated between the external angles of the median frontal process and the lateral frontal processes, may disappear entirely in the course of development; but they occasionally remain under the form of Stenson's ducts, which pass obliquely through the so-called "incisive spaces," or "foramina," from the mouth to the nasal fossæ, between the intermaxillaries and maxillaries. The mucous walls of the canals of Stenson are supported by cartilaginous tubular folds, which are continuous superiorly with cartilaginous laminae, which, passing off laterally from the lower margin of the nasal septum and vomer, cover more or less of the floor of the nasal fossæ, upper part of the incisive fissures, and spaces between the intermaxillaries and maxillaries. The "organs" or "sacs of Jacobson," supplied by the olfactory and fifth nerves, lined by glandular integument, sheathed by a continuation of the cartilaginous laminae already alluded to, and opening into the canals of Stenson, when these are present, are, whatever their function may be, morphologically connected with the second pair of meta-somatonic clefts.

The next pair of meta-somatonic clefts, situated between the lateral frontal processes and the so-called "superior maxillary" deflection of the "first visceral lamina," continue pervious in all the Mammalia except the Cetacea. The lachrymal canals which connect the anterior pouches of the conjunctivæ with the nasal fossæ, consist of the persistent upper portions of these clefts. Their outer or lower portions are obliterated, but the corresponding inter-scleratomic space, much dilated, constitutes that part of the orbit formed by elements of the ethmoidal and pre-sphenoidal sclerotomes, while the spheno-palatine and posterior palatine foramina and fissures, are also enclosed portions of the space between these two sclerotomes, retained for the passage of vessels and nerves.

The posterior nares are not meta-somatonic openings, they are merely the communications between the catacentric hæmal space of the pre-sphenoidal, and the corresponding but undivided hæmal spaces of the succeeding somatomes.

The mouth is the persistent and developed form of the great cleft between the pre- and post-sphenoidal somatomes. It is situated therefore morphologically in the same transverse plane as the posterior nares. Its fundamental or morphological relations are retained and represented by the posterior isthmus of the fauces. The buccal chamber is a vestibule superadded to the alimentary tube, by the anterior elongation of the lower jaw, and by the development of the floor of the mouth and of the tongue, with the consequent inclusion of the vault of the palate; so that the latter, instead of forming the anterior portion of the hæmal or sternal aspect of the head, becomes apparently a portion of the wall of the visceral tube.

The complete development of the vomer characteristic, as already stated



of the Mammalian head, is also a characteristic feature of the nasal fossæ in the Mammal. As the centrum of that sclerotome, of which the intermaxillaries are the hæmapophyses, it extends back from them to abut against the pre-sphenoidal centrum, forming a beam which adds to the antero-posterior strength of the entire arrangement, and which supports the more feebly developed ethmoidal and rhinal portions of the nasal septum. All these relations of the vomer are retained in the remarkably modified nasal passages and snout in the Cetacea.

The seat of the olfactory sense is limited to the upper part of the ethmoidal portion of the nasal fossæ. However complex the arrangement of the ethmoidal turbinal laminae may be, they invariably present the general character of folded laminar neuractinapophyses, connected to their corresponding neurapophyses, after the type of the cartilaginous sessile olfactory cups in the Plagiostomes.

As already stated, the so-called inferior turbinals consist of an antero-posteriorly arranged series or system of mutually abutting hæmactinapophyses, enclosed during development within the nasal fossæ. The inferior turbinal system is peculiar to the Mammal, and consists of elements which, in developed forms of the system, are derived from, and attached to, the rhinal, vomerine, and ethmoidal hæmapophyses. The palate bone, or distal pre-sphenoidal hæmapophysis, supports the posterior extremity of the turbinal system, but I have not had occasion to observe any turbinal element supplied by it.

As the rhinal sclerotome has disappeared in the Bird, the neuro-hæmal chambers of the vomerine sclerotome become closed in front, and the external nostrils are supplied by those metasomatic clefts between the vomerine and ethmoidal sclerotomes, which in the Mammal form the "incisive foramina," the "canals of Stenson," and the "organs of Jacobson."

As the anterior nares are removed one somatome back in the Bird, so the posterior nares are removed one somatome forwards. They are situated between the maxillary and incomplete palatine arches, the ento-pterygoids separating them, while the palatines are on their outer sides. The posterior nares, instead of being directed backwards in a plane at right angles to the axis of the alimentary tube, open downwards in the plane of its upper wall. This direction of the posterior nares is due to the following circumstances:—1. that the intermaxillaries, although completing their arch below, are principally developed upwards and backwards; 2. that the maxillaries, even when they meet partially across the middle line, have the space which they enclose occupied by the neurapophyses, centrum, and sense capsules of their own sclerotome—in other words, they are in contact with the central and neurapophyseal aspect of their own sclerotome; 3. that the palatines do not form an arch at all, but lie in the horizontal plane of the under surfaces of the centruns of the cephalic sclerotomes behind them.

The Bird, in fact, does not possess nasal fossæ in the same sense as the Mammal, that is, it does not present nasal chambers, formed by the completed hæmal arches of a certain number of sclerotomes. Its nasal fossæ consist only of the catacentric-hæmal or neuro-hæmal spaces of the vomerine sclerotome, and of the combined neural and "sense capsule" spaces of the ethmoidal sclerotome, which occupy the space enclosed by its hæmal arch. They differ therefore from the Mammalian nasal fossa, not only in wanting rhinal compartments, but also in the deficiency of ethmoidal and pre-sphenoidal hæmal spaces. The palate of the Bird, instead of being like that of the Mammal, situated in a plane inferior and parallel to that in which the vertebral column lies, is in the plane of the latter, like that of the Fish. The palate of the Fish is in the horizontal



plane of the vertebral column, because its nasal fossæ are absent, the constituent hæmal arches being all incomplete; and because the cavities of its olfactory capsules open externally. The palate of the Bird is in the horizontal plane of the vertebral column for reasons already stated, and also because the olfactory capsules, instead of being situated external to the cavities of their sclerotome as in the Fish, or in its hæmal cavity as in the Mammal, have become involved in, or have taken the place of its neural chamber, and have therefore their inner orifices or posterior nares directed downwards, on the central aspect.

The mode in which the walls and cavities of the olfactory capsules of the Bird become involved or lost in its ethmoidal neural chamber and walls, may be morphologically conceived, if the structure is compared with the corresponding segment of the cranium of a Ray. The cranium of the Plagiostome is modelled on the form of the "primordial cranium" of the Mammal and Bird. The laterally projecting sessile cartilaginous olfactory cups communicate each by a wide orifice with the cranial cavity. If the orifices be conceived as much enlarged, and the walls of the capsules as withdrawn into, or becoming continuous with, those of the cranium; or if the latter be conceived as disappearing, while the former take their places, the general arrangement of the ethmoidal section of the persistent "primordial cranium" of the Ray will be seen to be similar to that sclerotome in the Bird's skull, which retains most of the primordial character. The development of the imperfect maxillaries in contact with the lower aspect of the slightly ossified inferior wall of the combined capsular and neural mass, and the formation of the ethmoido-frontals in the perichondrium which covers its upper surface, would reduce the entire arrangement to the type of the corresponding parts in the Bird.

By a similar process, the sessile cartilaginous auditory capsules of the Cyclostome may be conceived to become buried in the temporal portions of the cranial wall in the Plagiostome, while in the osseous Fish, after the primordial cranium has become enveloped in the bony plates which are formed in its substance and in its fibrous covering, the auditory capsules pass into the cranial cavity, having been enclosed by the neurapophyseal and metaneurapophyseal bony pieces of their own and neighbouring sclerotomes.

The external nostrils of the Lacertian, Ophidian, and Amphibian, are situated, as in the Bird, between the vomerine and ethmoidal sclerotomes; the intermaxillaries being closed in front and below. The so-called nasal fossæ in their vertebrate forms are also, as in the Bird, merely olfactory chambers, occupying the neural space of the ethmoidal sclerotome. The posterior nares, too, open as in the Bird, between the ethmoidal and pre-sphenoidal sclerotomes, but with the following subordinate differences:—In the Lizard they are separated by the anterior extremities of the ento-ptyergoids, and are bounded behind by the maxillary processes of these bones, and externally by the maxillaries themselves. In the Ophidian they are separated by the free margin of the ethmoidal catacentric plates; anteriorly by the posterior margins of the ethmoidal neurapophyses, externally by the anterior projecting portions of the ento-ptyergoids, and behind by the pre-sphenoidal attachments of the latter. In the Frog they open between the ethmoidal neurapophyses ("vomer"), the ento-ptyergoids ("palatals"), and the maxillaries.

We again approach the Mammalian type of nasal fossæ, through the Tortoises, Turtles, and Crocodiles.

It has been already stated that the anterior nostrils of the Chelonian appear to possess more of the Ornithic than Mammalian conformation. The primordial cartilaginous lining of the olfactory fossæ project in some



Turtles through the anterior nasal opening of the cranium in the form of a double proboscis. The posterior nares in the Tortoises are separated by the combined ento-pterygoids (upper and back part of the "vomer") and are bounded by the maxillaries and the palatines, the latter remaining open or ununited across the vault of the palate. In the Turtles, the vault of the palate and the posterior nares present more of the Mammalian aspect, although still formed essentially on the type of the corresponding parts in the Bird. This is effected by the ethmoidal neurapophyseal plates (palatal plate of the "vomer"), which lie somewhat above the level of the vault of the palate in the Tortoises, passing down into, and forming an area of it in the Turtles, extending from its posterior margin half way, or quite up to the intermaxillary palate plates. In the latter arrangement the ethmoidal area is hexagonal, and separates the palatal plates of the maxillaries from one another. In the former it is pentagonal; and the palatal maxillary plates meet in the mesial line in front of it. The palatal plates of the palatines are more or less developed in the Turtles; and many approach one another at the free margin of the vault, but are always separated by the posterior or free margin of the ethmoidal area.

The arrangement of the vault of the palate in the Turtles, and the peculiar Chelonian configuration of the pterygoids, lead to the very remarkable combination of Ornithic and Mammalian structure presented by the nasal fossæ and palatal vault of the Crocodiles. The Mammalian characteristics are the full development of the inter-maxillary and nasal bones, with the extensive, although cartilaginous, vomer. The vomerine sclerotome of the Crocodile is not closed anteriorly as in all the other Lacertians, in the Ophidians, Amphibians, and Birds; but presents a completely perforated catacentric arrangement. This complete form of the vomerine necessitates a rhinal sclerotome, which, accordingly, feebly represented in the Crocodiles and Alligators, appears to be more fully developed in the Gavials. The extensive and complete Crocodilian palatal vault is only apparently Mammalian, it is partially Ornithic or Chelonian in its constitution. As in the Mammal the anterior extremity of the vault is formed by the pair of fully formed palatal inter-maxillary plates. Except in the Alligators in which there is a slight intrusion of the ento-pterygoids, the palatal plates of the maxillaries meeting along the mesial line, form the second and most extensive area of the palatal vault. The next area of the vault consists, as in the Turtles, of the ethmoidal neurapophyses (the so-called "palatals"), united along the mesial line, and much elongated backwards. The posterior margin of the combined ethmoidal neurapophyses of the Turtle forms the central part of the free margin of the palate; but the completion in the Crocodile of the deflected outer margin and central ridge of the pterygoids into a double tube, or pterygoidean prolongation backwards of the nasal fossæ, produces a corresponding elongation of the palatal vault; which accordingly presents, behind its ethmoidal, an extensive and broad pterygoidean area, which thus completes the vault behind, as in certain Cetacea and Edentata. Among the Mammalia the great elongation backwards of the combined maxillary palatal plates, the corresponding elongation of the combined ethmoidal neurapophyses, and the great breadth of the pterygoidean area, have displaced the palate bones so far backwards and outwards, that, separated from the ento-pterygoids and the ethmoidal neurapophyses by a wide chasm, but retaining their connections with the maxillaries and pterygoids, and coming into contact with the malar, they are, in fact, extended from the walls of the nasal fossæ, and from the palatal vault, and, thus disguised, have been hitherto known only as "transverse bones," "adgustal bones," "pterygoïdes externes," "ecto-pterygoids."



*The Nasal Passage of the Cyclostomous Fishes.*—The cyclostomes differ from all other Fishes in possessing a tubular passage, which, opening externally above the oral disk, passes backwards to the combined olfactory capsules, and behind which it terminates in a cul-de-sac in the Lamprey, but in the Myxine and Bdellostoma, communicates with the alimentary and respiratory tract.

The form and arrangement of the cartilages, which enter into the formation of the walls of this tubular passage, have been figured and minutely described in the classical memoirs of Joh. Müller, on the Cyclostomous Fishes. It becomes a point of much interest to ascertain the morphological character of this tubular passage, and to determine the morphological relations of its cartilaginous elements.

The olfactory capsules of the Myxine, Bdellostoma, and Lamprey, are completely fused into one another at the mesial plane, so as to form a single chamber, situated immediately in front of, and in a line with, the cranial cavity. The common olfactory chamber communicates with the cranial cavity by two orifices perforated in the fibro-cartilaginous transverse septum, for the passage forwards of the olfactory nerves. The olfactory chamber opens below into the naso-pharyngeal passage. In the Lamprey this passage is membranous throughout, the portion in front of the olfactory chamber lying above the posterior superior oral shield, its posterior portion passing back between the base of the cranium and the central part of the palatal cartilage, terminates in a cul-de-sac at its pharyngeal extremity. In the Myxine and Bdellostoma the posterior portion of the passage is a membranous canal situated between the base of the cranium and the mesial palatal cartilage, and opens posteriorly into the pharynx. That portion of the naso-pharyngeal passage in front of the olfactory chamber is supported above and laterally by a series of ten cartilaginous rings, incomplete below—the entire arrangement closely resembling a Mammalian trachea. The membranous floor of this part of the passage is supported by the anterior portion of the central, and the transverse junction of the lateral palatal cartilages, and in front by the mesial and transverse superior oral cartilages.

The morphological constitution of this remarkable nasal skeleton appears to be similar to that of the nasal fossæ of the higher Vertebrata. The olfactory capsules have passed inwards, as in the Bird and Reptile, so that, instead of projecting from the sides of the cranium, like the auditory capsules, they occupy the space of the corresponding cranial segment. The incomplete cartilaginous rings of the nasal tube, viewed in their relations to the cranium and conjoined olfactory capsules, are in the position of a superadded series of neural arches, similar to the neural portions of the rhinal and vomerine Mammalian scleratomes, destitute, however, of centrums, but supported below by the peculiarly developed palatine and maxillary elements which have passed forward beneath them. The entire arrangement presents the general characters, or is developed on the plan of the nasal fossæ of the Reptile, Bird, and Mammal, with the additional peculiarity of an increase in the number of constituent segments, similar to that which apparently exists in the proboscidean Mammals.

*POST-STOMAL CEPHALIC SCLEROTOMES.*—*Their Central and Neural Elements.*—As the discrimination of the constituent central and neural elements of the three post-stomal segments of the skull demands a constant reference from the one segment to the other, I shall examine them together. Of these three segments, the post-sphenoidal, the temporal, and the occipital, the second has not hitherto been recognised except by Carus, whose system includes a temporal intervertebra.



My attention was directed to the temporal segment of the cranium by the remarkable indications of it presented by the human skull. The human occipital bone, in addition to that upper angular portion of its squamous plate, which presents the relations of the interparietal, exhibits all the characteristics of a vertebral centrum, in combination with neural- and meta-neurapophyses. The inferior articular processes of this cranial segment are largely developed, in relation to the atlas. But it has not been hitherto noted, that the so-called jugular processes are in fact its upper or anterior pair of articular processes; and that, consequently, the jugular processes on the posterior margins of the petrosal portions of the temporals must be the zygapophyses of the succeeding cranial segment. These occipital and temporal jugular articular processes, like the corresponding processes in the column below, present distinct cartilaginous articular facets, and are contiguous to the "foramina lacera posteriora" or "intervertebral foramina," formed by the conjunction of the temporal and occipital jugular fossæ, and which transmit, as in the spine, vessels and nerves. But the petrous portion of the human temporal bone has, in addition, a pair of distinct pro-zygapophyses. They are situated on the anterior margins of the petrous portions where these margins form the angles with the squamous portions, in which are situated the openings of the Eustachian tubes. The articular surfaces of these processes are perpendicularly striated, and are applied against corresponding surfaces of the so-called styloid processes of the sphenoid at the posterior angles of its great wings. These "styloid processes" are therefore the zygapophyses of the post-sphenoidal sclerotome. The pro-zygapophyses of the post-sphenoidal and the zygapophyses of the pre-sphenoidal may be observed at the forepart of the pterygo-palatine groove in the foetal bone, but are more remarkably developed in the young Ruminant; in which also may be observed the zygapophyseal connection of the pre-sphenoidal with the ethmoidal neurapophyses.

We have, therefore, in these zygapophyseal connections distinct evidence of five cranial segments—an ethmoidal, pre-sphenoidal, post-sphenoidal, temporal, and occipital, in addition to the vomerine and rhinal.

For the further development of this subject, the cranium of a Cyprinoid Fish should next be selected. If the lateral wall of the cranium be examined, either from the external or mesial aspect, five serially arranged neurapophyseal plates will be recognised, connected to one another by four distinct zygapophyseal articulations. These plates are, from before backwards, the so-called "pre-frontal," the "cranial ethmoid," the "orbito-sphenoid" of Owen, the "ali-sphenoid" of Owen, and the lateral occipital. I have already stated the grounds on which I believe we must look upon the "pre-frontals" of the Fish as the neurapophyses of the ethmoidal, and the "cranial ethmoid," as the combined neurapophyses of the pre-sphenoidal neural arches. If so, then, the succeeding plate must be the "ali-sphenoid," and not the "orbito-sphenoid," as Professor Owen considers it to be; and, therefore, as there has never been a question regarding the lateral occipital, the plate interposed between the latter and the former, as it has all the characters of a neurapophysis, indicates the existence of a cranial segment between the post-sphenoidal and occipital. I shall not at present allude to the various opinions entertained regarding this plate, but shall merely distinguish it as the inferior temporal neurapophysis.

Proceeding now to the consideration of the centrams corresponding to this series of neurapophyses, it must be observed that in no osseous Fish in any stage of development have more than three osseous pieces been observed in the basis of the cranium from the so-called "vomer" to the



"basi-occipital" included. The assumed "connation" of the centruns of the pre- and post-sphenoids, as held by Professor Owen, has at present no support from embryology; the missing centrum or centruns must, therefore, be accounted for otherwise than by a hypothetical division of the "basi-sphenoid." Professor Owen appears, indeed, to a certain extent to admit this, for in certain Fishes he considers the symmetrical Y-shaped ossicle marked in his diagrams 9<sup>1</sup>, and superimposed on the pre-sphenoidal process of his basi-sphenoid, as the central part; while that process itself he holds to be the capsular portion of the ossified notochord.

That mutual elongation and overlapping of the cranial centruns formerly alluded to, is strongly marked in Fishes, the sphenoidal centrum being dovetailed into and elongated beneath the occipital behind, and above the ethmoidal ("vomer") in front. The manner in which the anterior elongated portion of the post-sphenoidal centrum of the Bird elevates and carries on its upper surface the compressed pre-sphenoidal centrum, has already been stated; and I must again observe, that it appears to me that the pre-sphenoidal centrum exists in certain Fishes only in the form of a bar of cartilage—a portion of the "primordial cranium" situated on the upper surface of the anterior prolongation of the post-sphenoidal centrum, and terminating on the upper surface of the ethmoidal centrum or so-called "vomer;" and that in Fishes with an "ossified orbital septum" or "cranial ethmoid," it is to be recognised in the half-ossified cartilaginous mass which unites the right and left plates of that "septum," and which have been already indicated as its corresponding neurapophyses. The pre-sphenoidal is an undeveloped centrum in the Fish, retaining more or less of its "primordial" texture and form, and elevated, therefore, above, or carried inwards, so as to be covered by the fully developed ethmoidal and post-sphenoidal centruns.

I am acquainted with no example of a fully developed temporal centrum. It is represented in the "primordial cranium" by the quadrilateral cartilaginous plate, bounded laterally by the ear capsules, behind by the portion corresponding to the cartilaginous lateral occipitals, and in front by the part in which the post-sphenoidal centrum first appears. In all vertebrate animals this portion of the basis of the primordial cranium is of great comparative extent, and is encroached upon by the advancing ossification of the occipital and post-sphenoidal centruns in modes which vary in the different vertebrate forms. In Mammals, the occipital advances into it at the expense of the post-sphenoidal centrum. In Birds and Fishes, the post-sphenoidal passes more backwards. In the Reptiles, the two centruns appear to share it equally. In all the forms, I believe that traces of the intermediate or temporal centrum may be detected, either in the cartilaginous or osseous condition. In Fishes, more or less of the primordial cartilage remains above the junction of the occipital centrum, post-sphenoidal centrum, and temporal neurapophyses ("petrosals"), and covered more or less internally, or towards the cranial cavity, by the internal prolongations of the occipital centrum, and of the temporal and post-sphenoidal neurapophyses. The peculiar canal for the muscles of the orbit existing in certain fishes, and which is roofed over principally by the "petrosals," or temporal neurapophyses, appears to be hollowed out principally in the primordial temporal centrum, and to be lined by its constituent cartilage. The peculiar Y-shaped bone met with in the pike, perch, and salmon, marked 9<sup>1</sup> by Professor Owen, and \* by Hallman, and considered by the former as that portion of the pre-sphenoidal centrum which results from the ossification of the corresponding central portion of the notochord, appears to me to be a central element; but referable rather to the post-sphenoidal or temporal, than to the pre-sphenoidal segment. For, in the



first place, it may be questioned whether the *corda dorsalis* of the Fish reaches the region of the pre-sphenoid; and, in the second place, if I am correct in my determination of the post-sphenoidal and temporal neurapophyses of the Fish, the two ascending limbs of this bone abut against these latter elements, and are not at all connected with the pre-sphenoidal neurapophyses. As, moreover, these ascending limbs of the bone in question are more intimately connected with the bones which Professor Owen considers to be the ali-sphenoids, but which I must hold to be the inferior temporal neurapophyses, I am inclined to conceive it an ossified portion of the temporal centrum.

With regard to the bone termed by Hallman *os innominatum*, which is small but well marked in the carp, and larger in the perch, and which Professor Owen considers to be the petrosal, I quite agree with him. But while I do so, I make a distinction between an ossified portion of the auditory capsule and the bone which constitutes the corresponding neurapophysis, in the same manner as I find myself compelled to admit the independent existence of the ethmoidal neurapophysis and the olfactory capsules, whether fibrous, cartilaginous, or osseous, and the corresponding independent existence of the variously modified sclerotics and the orbito-sphenoids.

Proceeding now to the examination of the remaining elements of the post-stomal neural arches in the Fish, I would observe that if we put aside those conceptions of the constitution of the arches in question, derived from previous study of the cranium of the Mammal, the constitution of the corresponding arches in the Fish, which naturally suggests itself, is the following:—

1. Over the occipital centrum, the lateral occipitals and the external occipitals—as two pairs of neurapophyses; and the superior occipital—as a single meta-neurapophyses.

2. Over the position of the temporal centrum, the bones termed petrosals by the continental anatomists, but by Professor Owen petrosals in the cod, and ali-sphenoids in the carp, and over these the mastoids, these “petrosals” or “ali-sphenoids,” along with the mastoids—as two pairs of neurapophyses; and the contiguous or separated bones usually termed “parietals,” as a divided meta-neurapophysis.

3. Over the great basi-sphenoid, the bones termed by Professor Owen orbito-sphenoids in the carp, and ali-sphenoids in the cod, with the post-frontals—as two pairs of neurapophyses, the meta-neurapophyses being absent.

Before making any statements in support of this view of the constitution of the post-stomal neural arches in the cranium of the osseous Fish, I would direct attention to the corresponding parts in the other Vertebrata, from the same point of view.

In the Bird the occipital neural arch wants the ex-occipitals. The temporal arch possesses no centrum, but the petrosals, mastoids, and parietals, are placed one over the other as two pairs of neurapophyses and a divided meta-neurapophysis. The post-sphenoidal centrum is surmounted by the post-sphenoidal wings and the feebly-developed post-frontals—as two pairs of neurapophyses; while the meta-neurapophysis is deficient.

In the Crocodiles, the occipital arch, as in the Birds, has lost the upper pair of neurapophyses. The temporal centrum is not developed, but the two pairs of neurapophyses, and an undivided meta-neurapophyses—the petrosals (ali-sphenoids of Owen), mastoids, and so-called parietal—form a continuous arch. The post-sphenoidal centrum is again found to carry two pairs of neurapophyses, the great sphenoidal wings (orbito-sphenoids of Owen), and the post-frontals. The meta-neurapophysis is missing.

In the Chelonians, the occipital arch consists of one pair of neurapophyses and a meta-neurapophysis surmounting a centrum. The tem-



poral centrum is not developed. The inferior pair of neurapophyses, the so-called ex-occipitals, abut externally against the mastoids, and are thus connected with the largely developed so-called "parietals." These "parietals" not only form a large part of the cranial and temporal vaults, but send down laminae to rest on the pterygoids, and thus enter into the formation of the lateral walls of the cranial cavity in front of the post-sphenoidal wings. Above the post-sphenoidal centrum, the post-sphenoidal wings and the post-frontals rise in connection with one another, as two pairs of neurapophyses, but the meta-neurapophysis is again wanting.

In the Ophidians, the occipital centrum is again surmounted by one pair of neurapophyses and a meta-neurapophysis. The temporal centrum has disappeared behind the basi-sphenoid; but the well-developed so-called "petrosals," the ali-sphenoids of Professor Owen, are surmounted by the elongated and nearly extruded mastoids; while the single meta-neurapophysis, the undivided "parietal," is so largely developed, that, passing down as in the Chelonian to the basis of the cranium, it rests upon the post-sphenoidal centrum over a great extent in front of its own neurapophyses, so as altogether to obliterate the post-sphenoidal wing. The post-sphenoidal centrum is there cut off from the post-frontals, which constitute the only remaining elements of its neural arch.

In the Lacertians, the occipital centrum, with its pair of neurapophyses and single neurapophysis, is followed by a temporal arch, without a centrum, but with two pairs of neurapophyses, "petrosals," and mastoids, and an undivided meta-neurapophysis or "parietal," generally single in front, but projecting backwards, with the mastoids on each side behind. The post-sphenoidal centrum is not surmounted by ali-sphenoids, except the parietal columella represent these elements. The post-frontals again appear; but without a corresponding meta-neurapophysis.

In the Frogs, the occipital centrum and the corresponding meta-neurapophyses have disappeared; a single pair of neurapophyses constituting the sole osseous elements of the arch. The temporal centrum appears in the primordial cartilage which extends across on the upper surface of the posterior part of the much-elongated "basi-sphenoid," and between the cartilaginous auditory capsules. The latter are intimately connected to the inferior temporal neurapophyses, the ali-sphenoids of Professor Owen, with which feebly developed mastoids or superior neurapophyses are conjoined; the whole being surmounted by the greatly developed antero-posteriorly elongated so-called "parietals," which dip down slightly at their margins, in front of the temporal region towards the "basi-sphenoid," as in the Chelonians and Ophidians. The portions of the post-sphenoidal wings and the post-frontals are occupied by fibrous texture; the "basi-sphenoid" or post-sphenoidal centrum extending forwards below; and the "parietals" taking the place of the deficient meta-neurapophyses.

The preceding view of the arrangement of the centrams and neural arches of the post-stomal sclerotomes of the lower forms of cranium, is that which would appear naturally to suggest itself to a mind uninfluenced by the arrangement of the corresponding region of the Mammalian skull. It is assumed throughout, that there are more or less complete cartilaginous or osseous auditory capsules in addition to corresponding neurapophyses; and that these neurapophyses are not post-sphenoidal but temporal, as evinced by their zygapophyseal connections in the human cranium. No reference has been made to the relations of the contested "petrosals" and "ali-sphenoids" to the fifth nerve, because, while the fundamental relation of that nerve to the post-sphenoidal sclerotome is admitted, the divisions of the nerve exhibit the same tendency to vary in their points of exit, as is presented by the other cerebral nerves; moving backwards more or less across the corresponding neurapophyses, and notching or perforating the neurapo-



physes behind. In fact, until a more minute investigation of the development of the cranium in its relations to the cerebral nerves has afforded some explanation of the varied relations of these parts in the series, we cannot, in my opinion, attach much weight to the determination of a "petrosal" or an "ali-sphenoid" by means of their relations to the trigeminal nerve.

Proceeding now to the examination of the post-stomal centrums and neural arches of the Mammalian cranium, let the Human skull be selected for examination. The occipital centrum is surmounted by a pair of neurapophyses and a double meta-neurapophysis. But again, surmounting the meta-neurapophyses there is a double piece, which occasionally remains permanently separate from the "occipital bone." This double piece, or pair of bones, present the relations of the interparietal bones in lower Mammalia. They may extend laterally to join the "mastoids," or they may be connected to the latter by a more or less continuous chain of "triquetral bones" in the line of the lambdoidal suture.

The zygopophyseal attachments of the "petrous portions of the temporal bone" indicate these masses to be neurapophyses enveloping the ossified auditory capsules. Keeping out of view the "squamous," "tympanic," and "styloid" portions of the "temporal bones," the "mastoidal portions" become early and intimately connected with the "petrous portions." Commencing with the "petrous portions," as an inferior pair of temporal neurapophyses, they are surmounted, as in the lower Vertebrata, by the "mastoidal portions" as a second pair of neurapophyses, while the arch is closed by the double element which forms the upper angle of the "occipital bone," as a meta-neurapophysis. There are well-marked indications of a temporal centrum in the human cranium. The irregularly truncated apices of the "petrous portions," directed obliquely forwards and inwards, are continuous, by means of the fibro-cartilaginous remains of the basis of the "primordial cranium," which occupy the "foramina lacera media," with the inclined plate of bone which, in the plane of the "basilar process of the occipital" or occipital centrum, forms the back part of the "body of the sphenoid," including the "posterior clinoid processes." This plate of bone is frequently surrounded by a deep groove, the posterior part of which lodges the "transverse venous sinus," and I have seen it nearly detached.

The feebly developed post-frontals in the Bird have disappeared in the Mammal, so that the post-sphenoidal centrum is surmounted by the "ali-sphenoids," as a single pair of neurapophyses; and by the enormously expanded double meta-neurapophysis in the Human subject, or the less developed form of parietals in the Mammalia generally.

The fundamental facts on which the preceding determination of the comparative constitution of the post-stomal neural arches of the cranium depends, are the zygopophyseal connections of the human "petrosals." If the "petrosals" even in one species can be proved to present the characters of neurapophyses, the sclerotome to which they belong must exist in addition to those to which the "ali-sphenoids" and "orbito-sphenoids" are referable. The existence of temporal neurapophyses explains the existence of interparietal, in addition to parietal bones in the Mammal; both of these meta-neurapophyses taking part in the protection of the developed cerebrum; while the non-appearance of the anterior or sphenoparietal in the Bird, Reptile, and Fish, accords with the complete development of the posterior or temporo-parietal, repressed in the former by the influence of the cerebrum, and by the full development of the ethmoido-frontal. I base my determination of the separate existence and reciprocal development of ethmoido-frontals and sphenoparietals, of sphenoparietals and temporo-parietals, not only on my analysis of the bones them-



selves in the series, but also on the evident reciprocal influence which the superimposed cerebral mass in the Mammal, and the bulky organs of sense and uncovered sense-ganglions of the lower Vertebrata have on the cranial neural arches. I believe also, that in this as in other departments of inquiry, we are apt to look for greater simplicity and uniformity in details than actually exist. The simplicity of natural law consists in the comprehensiveness of its general principles. In tracing these principles into details, the complexity is found to be infinite.

*The Hæmal Arches of the Post-Stomal Cephalic Sclerotomes.*—The clue by means of which we can alone be safely guided to the morphological constitution of these arches, in the midst of the varied complexity which they present to the comparative anatomist, is afforded by embryology. The hæmal arches of the post-stomal sclerotomes are developed each in the corresponding pair of "visceral laminae." By endeavouring to ascertain, therefore, in which of these post-stomal "visceral laminae" the sclerous elements of the varied forms of the post-stomal hæmal arches are originally formed, the morphological constitution of the individual hæmal arches may reasonably be anticipated. If, again, I am correct in my determination of the constitution of the pre-stomal sclerotomes, the allocation of the individual post-stomal hæmal arches to their proper centrums and neural arches follows as a matter of course.

From the observations more particularly of Rathke and Reichart, the formation of the osseous elements of the post-stomal hæmal arches in the "visceral laminae," is preceded in each by a more or less distinct and continuous cartilaginous streak or band. Rathke found seven pairs of these cartilaginous streaks loosely connected to the basis of the embryo head of the *Blennius viviparus* and corresponding to the mandibular, hyoidean, first, second, third, and fourth branchial and pharyngeal arches. In the Adder the same indefatigable embryologist and comparative anatomist found a cartilaginous style, with a process directed forward in the position of the maxillary, palate, and pterygoid bones, embedded in the first visceral lamina and its "superior maxillary process," and attached to the side of the basis of the primordial cranium in front of its auditory region; a similar style lay in the second visceral lamina, and was firmly attached to the base of the cartilaginous cranium behind, and external to the auditory capsule; a third style lay in the third visceral lamina, and was also firmly attached like a rib to the occipital region of the primordial cranium. Similar primordial hæmal arches have been found by Reichart in the visceral laminae of the Mammal and Bird, and by numerous observers in the Amphibia. It is important to observe again at this point, that the relations of all these seven pairs of primordial hæmal arches are similar. Firstly, all the visceral laminae in which they are developed appear to consist of the serous, vascular, and mucous layers united; secondly, the cartilaginous streaks are formed towards their inner surfaces, under the mucous layer; thirdly, the heart and vascular arches are on their exterior, under the serous layer.

*First Post-Stomal Hæmal Arch.*—The constitution of this arch must be determined by the examination of the development of the first post-stomal visceral lamina. It has been already stated that the process usually considered as the upper part of the so-called "first visceral lamina" is, if its general relations be taken into account, the posterior pre-stomal visceral lamina in which the pre-sphenoidal hæmal arch is developed.

The cartilaginous streak in the first post-stomal visceral lamina of the Mammal divides into two portions. The superior and smaller of the two becomes the incus. The long inferior portion is the cartilage of Meckel; around the lower part of which the corresponding half of the lower jaw is developed; the upper part forms the slender process and the



head of the malleus. As the Eustachian tube, the tympanum, and the external auditory passage, consist of the persistent upper portion of the first visceral cleft, the cartilage of the Eustachian tube, and the tympanic bone, which are continuous with one another, and form the floor of these three spaces, are developed in blastema deposited near the upper extremity of the cleft. This blastema also forms the membrane of the tympanum, into which the handle of the malleus shoots. It is to be observed that this lower jaw and tympanic bone do not originate in the primordial cartilaginous streak, but in blastema deposited around it. The tympanic bone forms at first an inverted arch across the visceral cleft, or a ring incomplete above, which supports the membrane of the tympanum on the outer side of the attenuated portion of Meckel's cartilage, which connects the malleus to the inner side of the jaw. It then extends inwards, so as to form the floor of the tympanum and Eustachian tube, folding up before and behind, and thus inclosing the incus and malleus leaves, the latter connected to the jaw through the tympanic fissure.

The development of the first post-stomal visceral lamina appears, therefore, to indicate at least four elements on each side of the mandibular hæmal arch in the Mammal. The tympanic element is probably complex; the mandibular consists of at least two portions, one on the outer, the other on the inner side of the corresponding portion of Meckel's cartilage.

In the Bird the omoid and palate bones are formed like the pterygoid and palate bones of the Mammal, in the so-called "superior maxillary process." In the proper first post-stomal visceral lamina, the primordial cartilaginous streak divides, as in the Mammal, into two portions. The upper and smaller of the two becomes the quadrate bone; the lower and longer portion—Meckel's cartilage—becomes enveloped in the corresponding half of the lower jaw; but instead of the upper end of this portion forming the slender process of a malleus, it remains as the peculiarly-formed articular piece of the jaw itself. The original intimate connection of the rudiment of the pterygoid bone, in the so-called "superior maxillary process," with the upper or incudal portion of the primordial cartilaginous streak of the first post-stomal visceral lamina of the Mammal, speedily diminishes; but in the Bird, not only does the pterygoid or omoid bone rapidly increase in relative size and configuration; but the quadrate portion of the first visceral streak does so likewise. The latter also exhibits, attached to its outer side, as the omoid is to its internal process, a styliform ossicle, the rudiment of the quadrate-jugal bone, which again is connected anteriorly to the jugal.

Reichart, who has minutely described and figured the development of this visceral lamina in the Bird, makes no allusion to the remarkable indication which it affords of the signification of the quadrate bone, and articular piece of the lower jaw. It affords, as it appears to me, sufficient evidence that the quadrate bone of the Bird is the homologue of the Mammalian incus, and that the articular piece of its lower jaw is the homologue of that ossified portion of the upper end of Meckel's cartilage, which in the Mammal forms the slender process of the malleus.

The quadrate bone has been hitherto considered as the homologue of the tympanic bone in the Mammal, not only from the proximity of the latter to the condyle of the jaw, but chiefly from its presumed absence in the skull of the Bird. But there appears to me to be sufficient evidence of its existence, not only in the fibro-cartilaginous frame which connects the margin of the tympanic membrane to the mastoid, lateral occipital, and basi-sphenoid, but more particularly in the thin well-defined lamina of bone, which, apparently united to its fellow of the opposite side, forms the floor of the tympanic cellular space in the broad posterior portion of the basi-sphenoid. As these apparently united laminæ are continuous with the



single cartilaginous Eustachian tube, below the single or double osseous Eustachian orifice, I am induced to believe that they will turn out to be the feebly developed representatives of the tympanic bones of the Mammal.

By a very beautiful analysis Professor Owen has proved that the quadrate-jugal bone of the Bird is the homologue of the squamous portion of the Mammalian temporal. I cannot, however, give my assent to his determination of its special homology, as a portion of the subdivided radiating appendage of the maxillary arch. Its relations in Birds and Crocodiles, in which it presents all its fundamental connections, appear to me to show that it is an anterior actinapophysis of the mandibular arch; passing forwards to abut against the malar, which I have already stated to be a posterior actinapophysis of the ethmoidal hæmal arch, or as in the Lacertians against the post-frontals. The squamous portion of the quadrate-jugal bone is a Mammalian superaddition, to adapt it to the part it takes in the formation of the cranial wall. It is withdrawn therefore from the quadrate or incudal portion of the mandibular arch (which portion diminishes relatively), and passes—as the entire bone does in the Lizards—upwards to be connected with the cranial wall. The development of the first post-stomal visceral lamina in the Bird appears therefore to afford evidence that the mandibular hæmal arch in the Bird and Mammal includes a tympanic element, a quadrate or incudal, a malleal or articular, and the elements of the corresponding side of the lower jaw.

On the same grounds I am inclined to believe that the articular piece of the lower jaw of the Reptile and Amphibian is malleal like the corresponding piece in the Bird, and not the homologue of the condyle of the Mammalian jaw. They are all malleal portions of Meckel's cartilage retained in connection with the jaw. In like manner, I am inclined to believe that the so-called tympanic bone of the Reptile and Amphibian, like the quadrate or so-called tympanic bone of the Bird, is not the homologue of the tympanic bone in the Mammal, but of the incus. The incus of the Mammal has been set free from its fundamental quadrate-jugal and pterygoid connections to co-operate with the similarly released malleus in the economy of the ear. The absence of proper tympanic bones in the Reptile and Amphibian is explained by the absence or feeble development of the tympanic cavity. I am inclined to think, however, that traces of them may be detected under and between the basi-sphenoid and occipital of the Crocodile, in the walls of those canals which connect, as Professor Owen has shown, by a common tubular communication, the sella turcica and the tympanic cavities with the basis of the cranium.

The tympanic systems and lower jaw of the osseous Fish form together a well-marked hæmal arch, developed in the first post-stomal visceral lamina of the embryo. From what has already been stated regarding the sclerous elements which result from the development of this visceral lamina in the other vertebrata, Professor Owen's view of the tympanic system of the osseous Fish, as the teleologically divided homologue of the quadrate bone of the Bird, and tympanic bone of the Reptile, would appear to require additional evidence. We are not yet in possession of materials for a rigorous determination; but it appears extremely probable that the tympanic bones of the osseous Fish are morphological, as well as teleological elements. If the articular piece of the lower jaw be assumed as the malleal portion of the persistent cartilage of Meckel, the hypo-tympanic occupies the position of the incudal element, connected, as usual, with the pterygoid. The epi-tympanic is in the position of the proper tympanic element of the Mammal, while the pre-tympanic, in its relations to the hypo-tympanic and pterygoid, closely resembles the quadrate-jugal or synamosal.

The opercular bones form on each side of the mandibular arch a series



of actinapophyseal elements, which, from the view already taken of such elements, would appear to be posterior, as the quadrate-jugal or squamosal is anterior in relation to the sclerotome. With regard to any traces of these opercular or actinapophyseal elements in the mandibular hæmal arch of the higher vertebrata, I must agree with Carus in considering the cartilages of the external ear in the Mammalia as homologous with them. The objection of Rathke to this determination of Carus—that the cartilage of the concha is attached to the tympanic bone so as to be situated at the back of the auditory foramen, that is, at the posterior margins of the first visceral cleft—appears to me to be met by taking into account the peculiar curved form which the tympanic element assumes in passing from before backwards across the cleft.

The allocation of the mandibular hæmal arch to the post-sphenoidal, or first post-stomal sclerotome, follows from the analysis already made of the pre-stomal sclerotomes.

*The Second and Third Post-Stomal Hæmal Arches.*—As the researches, more especially of Rathke and Reichart, on the development of the first visceral lamina, afford a clue to the constitution of the corresponding hæmal arch; the labours of these observers in like manner indicate the nature of the second and third arches. These arches are developed in the second and third visceral laminæ, and, from the varied forms which they present in the series, could only have been determined by an appeal to embryology.

In the Mammal the primordial cartilaginous streak in the second visceral lamina, and which is attached superiorly to the auditory region, divides into segments, the uppermost of which becomes the stapes; while the succeeding become, in succession with the intermediate soft portions, the “stapedius muscle,” the pyramid and its prolongation downwards, the styloid process, the stylo-hyoid ligament, and the series of sclerous elements which terminates below in the anterior horn of the hyoid.

The primordial cartilaginous streak in the third visceral lamina is attached to the occipital region, breaking up into four segments; the two upper disappear; the two lower become respectively the posterior horn and corresponding half of the body of the hyoid.

In the second visceral lamina of the Bird, in like manner, the auditory columella is developed superiorly, and the feeble anterior horn of the hyoid below, while the elements of the suspensory or posterior horn of the hyoid are formed in the third visceral lamina. The fibrous septum of the tongue and the epiglottis of the Mammal make their appearance in the line of junction of the second and third visceral laminæ. The respective share taken by these two laminæ in the formation of the so-called basiglosso- and uro-hyals in the Bird remains to be determined.

The precise observations of Rathke have shown that the lateral halves of the feebly-developed hyoid of the Ophidian are formed by the lower portions of the primordial cartilaginous streaks of the second pair of visceral laminæ, while the auditory columellæ are formed in their upper portions. Rathke also found that the primordial cartilaginous streaks of the third pair of visceral laminæ, and which are attached to the occipital region, disappear altogether.

There are no embryological observations in sufficient detail to indicate the morphological relations of the more or less complex hyoid apparatus in the Chelonian and Lacertian. The so-called hyoid, or suspensory arch of the branchial apparatus in the Amphibia is developed in the second pair of visceral laminæ. The corresponding arch in the Tadpole, and the anterior or suspensory horn of the so-called “hyoid” of the Frog, are also developed in this pair of visceral laminæ. The suspensory arch of the branchial apparatus is attached to the quadrate, or so-called



"tympanic" piece of the mandibular arch, and not to the base of the cranium. Rathke had observed a filament extending between the auditory region of the cranium and the quadrate cartilage of the Tadpole. He found that the so-called "malleus and incus" are developed in this filament. According to Reichart, this filament appears to be the upper part of the second primordial cartilaginous streak, which, in consequence of the peculiar manner in which it curves forward superiorly towards the quadrate cartilage (a curvature of the same kind towards the quadrate bone has been observed by Rathke in the Adder), becomes attached to it. In consequence of this attachment, the hyoidean arch becomes suspended to the quadrate portion of the mandibular; and the upper portion, between the quadrate cartilage and the auditory region of the skull, becomes converted into those elements in the Frog, which have their homologues in the stapes of the Mammal, and the columella, with its cartilaginous extremities, in the Bird and Reptile.

As the cartilaginous branchial arches of the Tadpole, and of the other Amphibia, are formed in the succeeding visceral laminae, it would appear to follow, as a necessary consequence, that the suspensory or hyoidean arch of the Amphibian, with its inferior mesial element, and along with the auditory ossicles, is homologous with the anterior or suspensory part of the hyoid, along with the stirrup-bones in the Mammal, and with the corresponding structures in the Bird and Serpent; and that the first branchial arch of the Amphibian, with its corresponding inferior mesial elements, are homologous with the posterior horns and body of the hyoid in the Mammal, and with the posterior or suspensory horns, with the corresponding inferior mesial elements of the hyoid in the Bird. The so-called posterior horns of the hyoid of the Frog cannot, therefore, be the homologues, as Professor Owen's statements might lead us to infer, of the posterior horns of the hyoid of the Mammal or Bird. The posterior horns of the hyoid of the Frog are the remains of its posterior pair of branchial arches, or enlargements of the posterior angles of its basi-hyals. They are developed therefore in its posterior visceral laminae; while the posterior hyoidean horns of the Mammal and Bird are developed in the third pair of visceral laminae.

As the skeleton of the hyoidean and branchial apparatus of the Fish is developed in the form of a series of inverted arches in the corresponding visceral laminae, from the second inclusive, we are obliged to conclude that its hyoidean arch is the homologue of the stylo-hyoidean arch, with the stirrup-bones,—or second post-stomal arch—in the Mammal; and of the corresponding portion of the hyoidean apparatus in the Bird, with the columellae; and of the entire hyoid in the Serpent, with the columellae; and that the first branchial arch in the Fish is the homologue of the corresponding arch in the Amphibian; of the posterior horns of the hyoid, and their associated elements in the Bird; and of the posterior horns and body of the hyoid in the Mammal.

It has not yet been determined upon what developmental change the suspension of the hyoidean arch of the Fish to its mandibular arch depends. It is probably of the same nature as that which occurs in the Tadpole, with this difference, that the upper portion of the hyoidean arch disappears in the Fish, without developing a stapedial ossicle; while its lower portion remains permanently connected to the mandibular arch, instead of regaining an attachment to the cranium.

The hyoidean and branchial arches of the Fish are provided, as has been already stated, with a well-developed double series of actinapophyses, for the support of the branchiostegal membrane, and the branchial laminae. These actinapophyses in the Fish are foreshadowed in the Tadpole by the tubercular margins of its branchial styles.



The question may now be put—if we are brought by reference to the development of the parts to allocate to the three post-stomal sclerotomes, hæmal arches, consisting respectively of the sclerous parts developed in the three anterior post-stomal visceral laminæ, to what sclerotomes are we to refer the potential or actual hæmal arches in the remaining visceral laminæ? For reasons already stated, they cannot be disposed of by referring them to a splanchno-skeleton, because in that case the hyoidean arch or arches, and apparently the mandibular arch also, must be referred to the same category. Neither can they be referred to any of the cervical, or trunk sclerotomes; because it would appear that the visceral walls of the head are alone perforated by clefts. We are not yet prepared to answer the question. It involves, as it appears to me, the investigation of a residual quantity, the solution of which will require some information in reference to certain points, regarding which we cannot at present be said to possess any. First, the development of the Cyclostomes, but more especially of Branchiostoma; secondly, the mode in which the trunk sclerotomes increase in number and become arranged in groups; thirdly, the mode in which the same changes proceed in the cranium; fourthly, the determination of the series of cephalic nervous centres, with their corresponding nerves (neurotomes), more especially in the medulla oblongata, with the causes which determine the grouping and order in which the cerebral nerves pass through the walls of the cranium.

If there appears to be no sufficient developmental grounds for making a distinction between the branchial arches of the Amphibian and Fish, as belonging to a splanchno-skeleton, and the hyoidean and mandibular as referable to the neuro- or endo-skeleton, it becomes important to determine the signification of the sclerous elements of the larynx, trachea, and bronchial tubes. Without presuming to anticipate the minute observation of the development of the parts themselves necessary for the solution of a question of this kind, I would venture to suggest that the proper cartilages of the larynx are developed from the inferior or mesial extremities of certain of the visceral laminæ; and that the cartilages of the trachea and bronchial tubes are a pair of highly developed actinapophyseal systems, referable to one of the posterior visceral arches.

*Post-stomal neuractinopophyses.*—In addition to the auditory capsules, I recognise as post-stomal neuractinopophyses more particularly those ossicles attached to the post-frontals, mastoids, and external occipitals of Fishes. Those attached to the post-frontals may enter into the formation of the infra-ocular bony arch. Those, again, which are developed on the temporal and occipital sclerotomes are modified so as to co-operate in the cranial suspension of the scapular girdle.

In conclusion, Goethe was the first to indicate the intermaxillaries, the maxillaries, and palatals, as elements of three distinct cranial segments. In the course of my investigation of the development of the teeth I became early aware of the correctness of Goethe's views on this subject, and have found myself, therefore, unable to coincide with the doctrine of Professor Owen as to the constitution of his palato-maxillary or nasal hæmal arch.

### 3. On the Morphological Constitution of Limbs.

Carus, maintaining generally the doctrine of cephalic limbs, originally propounded by Oken, has at the same time given much greater precision to the conception of the skeleton of a limb, by viewing it as a system of elements radiating from the exterior of a costiform arch. Professor Owen, while he rejects with British and the majority of Foreign anatomists, the fantastic doctrine of Oken and his immediate followers with regard to cephalic limbs, has adopted the general doctrine of the skeleton



of the limb as propounded by Carus, and has developed and applied it with much ingenuity to the illustration of actual structure. Professor Owen has, however, at the same time, by his allocation of the scapular girdle to the occipital segment of the cranium, as its hæmal arch, and by the view which he takes of the opercular and brancheostegal elements, actually reproduced the doctrine of cephalic limbs in another form. I do not propose in this communication to examine in detail the grounds on which Professor Owen's general doctrine of limbs is based, but shall merely state categorically those considerations which appear to me to render it untenable.

1. It is highly improbable that the sclerous elements of a limb should be derived from one, or at most two, sclerotomes, while its other elements, and more especially its nerves, are supplied by a greater number of somatomes.

2. It appears to be highly improbable that the bones which enter into the structure of an arm or leg, or that the corresponding sclerous parts in the lower animals should be the result of teleological subdivision of a single "diverging appendage" or "archetypal element." Professor Owen virtually admits that these "teleological" elements have a morphological value when he institutes an inquiry into their "special" and "serial homologies."

3. It appears to me that the scapular girdle cannot be the hæmal arch of the occipital segment of the head—firstly, because that segment is already provided with a hæmal arch in the series of transitory and persistent sclerous elements developed in the third pair of visceral laminae; secondly, because the scapular girdle is invariably found to be developed at or in the immediate neighbourhood of that part of the trunk of the animal where it is ultimately situated; and, thirdly, because it is improbable that the exceptions to a general law should be more numerous than the instances in which it is adhered to.\*

The germs of the limbs make their appearance when the ventral laminae of the primordial vertebral system are passing down towards the hæmal margin. At first they resemble lappet-like projections of the inferior margins of these laminae; they extend along at least four or five of their segments, and are situated in those regions of the body to which the future limb is attached, viz., in the pelvic and posterior region of the neck, except in the Fish, in which the pectoral lappets are situated close behind the head. As the ventral laminae extend downwards, the lappets retain a position more or less elevated on the side of the trunk. At this stage they also begin to exhibit a change in their form and position. They become first sessile, then pedunculated, and the peduncle then indicates by an angle at its centre the formation of the central joint of the shaft of the future limb—the elbow or knee-joint. At the same time, what I term the plane of the limb is changed. The lappet was originally developed in a plane, which is coincident with the axis of the corda dorsalis. This is the primary or fundamental plane of the limb; and when in this plane the lappet presents its radial or tibial margin forwards towards the head, and its ulnar or fibular margin backwards. When the limb leaves its primary position, it lies in its secondary plane, which cuts the corda dorsalis more or less obliquely, so that the radial or tibial margins of the limb are directed more or less forwards and inwards, and the ulnar and fibular backwards and outwards. The permanently sessile pectoral lappets or fins of the osseous Fish exhibit a peculiar modification of the same movement;

\* It is somewhat remarkable that the only embryological evidence which Professor Owen adduces in support of that portion of his Doctrine of Limbs, in which the anterior limb is assumed to be developed at or close to the head, is a reference to a passage in Rathke's *Entwicklung der Schildkröten*, in which the author adduces the *fundamental position* of the bones of the shoulder—viz., the posterior region of the neck—as a circumstance tending to explain their ultimate passage into the thoracic cavity.



they rotate on a transverse axis, so that their anterior or radial margins are directed downwards and their ulnar margins upwards. In the Sharks and Rays the pectoral and abdominal fins continue permanently in the primary plane.

While the lappet is still in its primary plane, the rudiments of the girdle of the future limb may be detected under the integumentary covering, and therefore external to the proper mass of the visceral wall of the body. In the primordial condition of the lappet of the wing of the Chick, Remak has detected four parallel streaks running to its outer margin, and continuous internally with the rudimentary nervous structures of the four primordial vertebræ, with which the attached margin of the lappet is connected.

Guided by embryological facts and conclusions, to the more important of which I have just alluded, I have endeavoured to detect, more particularly in the osseous Fishes, Plagiostomes, Amphibians, and Reptiles, the principle which lies at the basis of the morphology of limbs. The view which this inquiry has induced me to take of the subject I shall, in conclusion, state very briefly.

1. A limb does not necessarily derive its elements from one somatome—about fifty segments of the trunk appear to contribute towards the structure of the great pectoral fin in the Ray.

2. The nervous elements of the limbs appear, as in other parts of the vertebrate animal, to indicate most distinctly the morphological constitution of the sclerous elements. About fifty spinal nerves contribute the greater part of their hæmal divisions to the pectoral fin of the Ray; and there are about one hundred fin-rays—a pair of fin-rays to each nerve, and derived from each sclerotome. This correspondence does not apparently exist between the fin-rays and nerves of the osseous fish; but it may be fairly assumed that when we have detected the developmental circumstances which induce the attachment of the pectoral girdle of the osseous Fish to its cranium, as well as those peculiarities exhibited by its anterior trunk sclerotomes, this discrepancy will be explained. A more careful analysis than we yet possess of the number of spinal nerves which supply branches to the limbs of the higher Vertebrata is still a desideratum in this department of the subject; but it appears to be extremely probable, that in the Mammalia, at least five spinal nerves transmit filaments to the five distal divisions of the limb. It would appear, too, that, notwithstanding their plexiform arrangement at the attached end of the limb, the greater number of the filaments of each nerve reach their own morphological district at the distal part of the limb. The radial and the ulnar nerves are formed principally by the upper and lower roots of the human brachial plexus, that is, from the nerves of the upper and lower primordial segments with which the embryo limb was connected, and from which it derived its various elements.

3. The nerves supplied to a limb are not the inferior or hæmal divisions of the spinal nerves, but radiating on actinal branches of these divisions. The intercostal nerves are not the nerves serially homologous with the roots of the brachial plexus. The thoracic nerves, serially homologous with these roots, are the intercosto-humeral and the succeeding middle intercosto-cutaneous.

4. Each sclerotome supplying elements to the structure of a limb supplies as a sclerous element a single actinapophysis; or, as in the Rays, an anterior and a posterior—that is, a pair of actinapophyses.

5. From the structure of the mesial and lateral fin-rays of the Fish, the actinapophyseal elements of a limb may be assumed as primordially segmented.

6. The fin-rays in the Fish, and the phalangeal, metacarpal, and metatarsal bones of the higher vertebrata, are more or less persistent con-



ditions of the distal segments of the primordial actinapophyseal elements of a limb.

7. By atrophy, or otherwise, one or more of the segments in the successive transverse rows of actinapophyseal elements disappear, so as to leave in Man, *e.g.*, four elements in each carpal row ; two in the fore-arm ; one in the arm ; two in the next row for the coracoid and clavicle ; one in the proximal row for the scapula.

8. The nature of the subsequent changes, which the elements of the limb undergo, up as far as the shoulder or hip, may be inferred from an examination of the paddle of the Enaliosaur or Cetacean.

9. A careful application of the hypothesis to the limb girdles of the cartilaginous Fishes, Amphibia, and Reptiles, leaves me strongly inclined to believe that the coracoid is an actinapophyseal segment between the humerus and scapula, prolonged downwards, towards the hæmal margin of the body ; that the scapula is a proximal element, elongated towards the neural margin of the body ; that the clavicle is the only other retained element in the same transverse row as the coracoid, in front of it, and elongated like it in the hæmal direction ; and that the corresponding elements of the posterior limb have a similar morphological signification.



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The Journal of the American Medical Association is a weekly publication that contains a wide variety of articles, including original research, clinical reports, and reviews. The Journal is one of the most important sources of information for medical practitioners and is read by thousands of physicians and surgeons throughout the United States. The Journal is also a valuable source of information for the general public, as it contains many articles that deal with the latest developments in medicine and the health of the community.

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