XVI. *On the Relations of the Vomer, Ethmoid, and Intermaxillary Bones.*

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IN a paper read before the Royal Physical Society of Edinburgh, in March 1859*, I have drawn attention to the fact, not before noticed, that in Mammalia the lateral masses of the ethmoid always lie edge to edge with the dilated part of the vomer, and are usually united with it to form one bone. I have shown that in the human subject the sphenoidal spongy bones represent, in a disrupted and altered form, the plates by which in other mammals this union is effected; and these plates I have ventured to call the ethmovomerine laminæ.

A further inquiry into the variations of these bones and their development has not only confirmed my former statements, but led to other conclusions of most important morphological bearing.

It will be convenient to consider, in the first place, the typical connexions of the vomer in the mammal. We shall then examine the peculiar modifications which the vomer, ethmoid, and intermaxillaries undergo in the human subject. Afterwards we shall review in detail the varieties of their connexions in a number of mammalian families, and endeavour to deduce their morphological relations. Lastly, we shall glance at the arrangement of these bones in the other classes of Vertebrata, and draw such additional morphological conclusions as our observations shall seem to warrant.

Typical Connexions of the Mammalian Vomer.

In all young mammals the septal cartilage of the nose extends backwards to the presphenoid bone, and the vomer embraces its inferior edge. The vomer is known to be developed from two centres of ossification, one on each side; it always consists therefore fundamentally of two alæ; and between these a groove runs along its whole length, and is occupied by the septal cartilage.

Anteriorly it articulates generally with the mesial-palatine processes of the intermaxillaries. Sometimes this articulation does not take place, to wit, where the intermaxillaries have either no mesial-palatine processes or very short ones; but, when it exists, it is always of such a character that the vomerine groove is continued forwards by a groove between the intermaxillaries, while also the inferior aspect of the mesial processes of the intermaxillaries lies in a continuous line with the inferior edge of the vomer.

* Edinburgh New Philosophical Journal, October 1859.

Since the vomerine groove extends from the presphenoid to the intermaxillaries, it is obvious that the primary laminæ of the vomer (its alæ) can have no contact with the bones forming the back part of the palate. The articulation which the vomer forms usually with the maxillaries, and often with the palatals, is brought about by the production, downwards and backwards from the line of junction of the alæ, of a mesial plate, which is an after-development, and of varying extent in different species.

Between the vomer and the central plate of the ethmoid the only connexion that ever occurs is of a very secondary description. No doubt the appearances in human skulls are often such as would incline one to a different conclusion; but in the skulls of other animals there is, even in the adult condition, in the majority of cases, no contact between the two bones at all; and when there is, it is a contact of contiguity, not of continuity. The central plate of the ethmoid grows from above downwards at the expense of the septal cartilage, and is an ossification of that structure; while, on the other hand, the vomer only embraces the cartilage, never invades it.

But the most intimate and constant connexion of the vomer is with the lateral masses of the ethmoid; although no one who had confined his attention to the arrangement in adult human skulls would think that these bones were at all related. This connexion can be very well seen in the Dog, the Cat, the Sheep, or the Pig. In all these animals, and indeed, as far as I am aware, in all mammalia except Man, the Orang, the Horse, the Elephant, and the Giraffe (keeping the Cetacea out of view at present), the vomer and lateral masses of the ethmoid form one continuous bone. The free superior edge of each ala of the vomer can be traced all the way back in contact with the mesial structures embraced; and, forming a sharp angle with this edge when examined from above, but appearing to be gradually continuous with the ala when looked at from beneath, a very thin but often broad plate of bone passes outwards underneath the ethmoidal convolutions to the external inferior angle of the lateral mass of the ethmoid, and is continuous with the principal lamina which forms the framework of that bone. This plate is what I have called the ethmovomerine lamina. The vomer frequently extends some distance backwards beyond its junction with the ethmovomerine laminæ; but the position of the latter is so far constant that their posterior edges are always in contact with the sphenoidal processes of the palate-bones. The place of junction of the ethmovomerine lamina and ethmoid always corresponds to the upper margin of the internal aspect of the foramen called in human anatomy sphenopalatine, but which has only a seeming relation to the sphenoid bone in the human subject, and none whatever in other mammals, and which it will be better therefore in this paper to call the nasal foramen of the palate-bone.

The Vomer and Sphenoidal Spongy Bones in Man.

If we now proceed to examine the development of the vomer and the bones connected with it in the human subject, we shall see how beautifully the adult appearances are derived from conditions exactly corresponding to those just described. The key to these appearances is to be found principally in the sphenoidal spongy bones. These curious little bones reach their maximum of development at a very early age. Of four specimens beside me illustrating this condition, No. 1 (Plate IV. fig. 1) is from an infant possibly about a year old; No. 2 (fig. 2) from a child two or three years old; No. 3 (fig. 3) from a child which, judging from the appearances of the rest of the skull, may have been four years old; and No. 4 from an infant a few months old. In all these cases the body of the presphenoid is distinguishable from the postsphenoid by a mark at the line of junction, and projects forwards in continuation of it, in a somewhat rounded form, presenting little of that compression which has taken place to so great an extent in the adult. The presphenoid at this date is quite unconnected with the sphenoidal sinuses, and consists simply of the body just described, and the wings of INGRASSIAS. The body dips between the sphenoidal spongy bones, but is separated from them by some thickness of tissue. In Nos. 1 and 2, the sphenoidal spongy bones are already adherent to the ethmoid; in 3 and 4 they are unattached either to the sphenoid or ethmoid. They are of the shape of hollow pyramids with their apices directed backwards, and their inner aspects parallel to their fellows. Their cavities (the commencing sphenoidal sinuses) open at their bases in front into the nasal fossæ.

There are, I believe, three distinct ossifications which go to the formation, normally, of each sphenoidal spongy bone: certainly there are three portions which require description. A superior plate, very distinctly marked off in the specimens alluded to, limits the sphenoidal sinus more or less perfectly on the superior and internal aspects; it forms a convexity directed upwards and inwards, and lies in contact with the fibrous tissue which separates it from the body of the sphenoid. An inferior plate forms the whole or the greater part of the floor of the sphenoidal sinus, and may be said to be the only recognizable part in the adult. Internally this plate comes in contact with the lower margin of the superior plate, beneath which it is prolonged downwards so as to lie edge to edge with the corresponding lamina of the vomer, immediately in front of the thick dilated part. Posteriorly it lies above the sphenoidal process of the palate-bone. Besides these two plates, there enters properly into the formation of the sphenoidal spongy bone a third element (an orbital plate) connected with the anterior and external part of the inferior plate, and whose characteristic property is that by an aspect which articulates behind with the sphenoid, in front with the ethmoid, inferiorly with the palatals, and sometimes above with the frontal, it takes a small part in the formation of the orbit. It may be attached to the ethmoid, palatal, or sphenoid bone, instead of to the remainder of the sphenoidal spongy bone. In specimen No. 3 it is certainly unusually large and distinct, but it can be easily distinguished in Nos. 1 and 2 also. It is absent in No. 4; but there it exists incorporated with the orbital process of the palate-bone, at least that process projects upwards between the sphenoid and ethmoid. This enlarged form of the orbital process of the palate-bone is not at all uncommon; and that it arises from union with it of the orbital element of the sphenoidal spongy bone I am satisfied, from its occupying the position of that element. Moreover, in an adult specimen, in which I carefully disarticulated a palate-bone with an orbital process of that description, I found that that process had the whole sphenoidal spongy bone in union with it*.

It will be seen from this description that the sphenoidal spongy bone forms an arch of communication between the ethmoid and exactly that part of the vomer from which in other mammals the ethmovomerine lamina springs. Also it is it, and not the sphenoid, which completes with the palate-bone the sphenopalatine foramen; thus it agrees entirely with the ethmovomerine lamina in its relations. If there be yet any link wanting to prove its identity with that lamina, we shall find it supplied when we examine the skull of the young Orang.

In a fœtus of the third or fourth month, the vomer consists merely of two alæ which meet beneath the septal cartilage and form one bone. The inferior edge of the scooped bone so formed presents, in a fœtus of the fifth or sixth month, a broad surface marked by a raphe in the middle line for articulation with the maxillaries strictly so called, *i. e.* the part behind the anterior palatine foramen (fig. 4, B). This surface narrows behind into a mere edge to articulate with the palatals; while in front it ceases abruptly, and only the lamina bounding the groove is prolonged on the intermaxillary part of the palate. Already the intermaxillaries have begun to be elevated in the middle line above the level of the maxillaries, so as to form the crista incisiva, consisting of a process on each bone ("semicrista incisiva" of HENLE), and a groove between the two on such a level as to continue the groove of the vomer, which it does throughout life.

In the skulls of young subjects (for example in the specimen referred to as No. 1 (fig. 1, B), the vomer is seen in its most characteristic form. The alæ have reached their maximum of development. At their posterior extremity is seen the thick dilated part which passes back beneath the sphenoid, and lies between the upper extremities of the pterygoids, which are sometimes called *vaginal processes*, but improperly, since they only lie edge to edge with the vomer and never sheath it. In front of the dilatation the margins of the alæ continue for some distance to ascend as they pass forwards, and it is at this part, as far forwards as the points at which they begin to slope downwards, that the sphenoidal spongy bones are in contact with them. Also, by the elongation of the face, the vomerine groove has become sloped, while the extremity which rests on the crista incisiva is, by the increased elevation of that process, raised above the level of the maxillaries; and the space thus left between the groove and the hard palate is spanned by a mesial plate, about one line deep in front and three behind. As the face developes further this mesial plate becomes deeper, and sometimes there is a process continuous with the anterior perpendicular edge of the mesial plate, sent downwards between the incisive foramina, behind the crista incisiva (fig. 4, A). This downward process is occasionally a separate bone, and is so in a specimen of mine taken from a subject

* HENLE mentions that the orbital process of the palate-bone "aids in closing the sphenoidal sinus when its wall is imperfect." The condition which he refers to is no doubt that mentioned in the text. See HENLE, Handbuch der System. Anat. des Menschen, i. 174.

possibly about ten or twelve years old. But apparently the most frequent arrangement in the adult is that the crista incisiva is prolonged backwards so as to articulate with the maxillaries behind the anterior palatine canal; and in that case, as the maxillary margin of the vomer falls short of the canal, the process in question does not exist.

At an early age the vomer begins to lose its characteristic form and its individuality; and the sphenoidal spongy bones lose theirs even sooner. In consequence of this, the ordinary descriptions, however faithfully they may give an account of the appearances in adult skulls, are imperfect as descriptions of these separate bones. The fact is that the maturity of a skull does not correspond with the period of most perfect development of the individual bones of which it is composed. This is recognized by us when we resort to young skulls for specimens of disarticulated bones, and would be acknowledged still more readily in describing an elephant's skull or a whale's; but, with regard to the bones in question, the period of this most characteristic condition is so early that it has escaped due attention, and the natural result has followed, that the adult appearances have not been properly understood.

The alterations which the sphenoidal spongy bones undergo take place in connexion with the increased hollowing out of the sphenoidal sinuses. As these sinuses dilate, the superior plates of the spongy bones are pressed against the body of the presphenoid, which also becomes narrowed and deepened, until, instead of a thick bone in the middle line and a lamina supporting it on each side, we meet with only one central lamina between two large sinuses, and that deviating often a great distance to one side. The processes which projected downwards to the vomer disappear by the dilatation of the sinuses, until there is nothing left of them but a slight ridge corresponding to the edge of the vomer; inside which, what was once a perpendicular lamina forms part of the convex floor of the sinus, and on reaching the middle line is incorporated with the body of the presphenoid to form the septum sphenoidale. Thus the sphenoidal spongy bones become blended with the sphenoid, while at the same time their appearance of continuity with the vomer is gradually effaced; so much so, that the latter is habitually and correctly described as resting, in the adult, against their under surface. In the Anatomical Museum of this University there is a skull, seemingly from a subject about twelve years of age, in which the descending processes of the sphenoidal spongy bones have at the fore part not yet begun to be rounded away, but articulate accurately edge to edge with the vomer.

The sphenoidal and other sinuses no doubt have the important function of serving as caves for the reverberation of the voice, but they are likewise useful in giving lightness to the bones they occupy; and though in old persons they cease to communicate with the nose, they nevertheless grow larger and larger as age advances and the bones grow denser, until, as in a specimen beside me, the antrum of HIGHMORE invades the malar bones, and the sphenoidal sinuses so hollow-out the sphenoid that the walls of the Vidian canals are laid bare and traverse them like tubes. In these aged subjects the septum sphenoidale is a very thin partition indeed, and is usually very much driven to one side.

The alterations which take place with growth in the form of the vomer are results of the peculiar conformation of the human face, which is developed with a view to speech and expression, and not, as in the lower animals, for the mere prehension of food. The more the maxilla projects the wider is the gape allowed; but in Man, especially in the civilized races, instead of there being any such projection, the palate is short and the incisors perpendicular; and, as adult life approaches, the nasal fossæ and antra of HIGHMORE are enlarged to such an extent by downward growth of the maxillæ as to render the perpendicular height of the posterior nares quite a distinctive characteristic of the human skull. In consequence of this elongation of the face, the distance between the cribriform plate and the palate is rapidly increased. This distance the central plate of the ethmoid and the vomer must span; and as they stretch to accomplish this object, they become attenuated and most frequently lose their symmetry. Often indeed the first degeneration from its typical form which the vomer undergoes is a deviation of its laminæ from the middle line. This is found even in children.

As the central plate of the ethmoid grows downwards, its edge, which is advancing at the expense of the septal cartilage, corresponds with that structure in thickness. But only the edge is so thick; the rest of the plate gets thinner and thinner as it becomes elongated, and may even present irregular perforations. The vomer, on the other hand, embraces the cartilage from below. But when the central plate of the ethmoid, growing down from above, comes in contact with the alæ as they stretch upwards in the perichondrium, the ossifications from above and below unite, and if the middle line has been perfectly preserved, the cartilage between them is surrounded above, below, and on each side by bone. Very rarely this vestige of cartilage disappears entirely, and there is then a thin lamina of bone extending from the cribriform plate to the palate, and in it a diagonal of stronger bone stretching from the crista incisiva to the sphenoid. Generally, however, the deviation from the middle line is considerable, and the central plate of the ethmoid, though anchylosed with both alæ at the back part, is in front united more with one lamina than the other (usually most with that on the concave side of the septum), while the other tends to undergo atrophy. The cartilage between them is thus left more exposed on one side than the other, or sometimes is exposed on one side at one part, and on the other side further back. Occasionally, even in old subjects, a thread of cartilage can be traced back into one of the sphenoidal sinuses.

When the vomer is described as only grooved at its upper and back part, and exhibiting a cul-de-sac for the reception of the rostrum, the description is that of an irregular piece of bone consisting of the vomer and part of the ethmoid. The specimens chosen for study by the describers have been taken from skulls in which the vomer has already become thoroughly united to the central plate; and when it has been sought to separate it, the central plate has given way at its weakest part. In other instances the fracture is effected through the alæ of the vomer. It is utterly impossible to separate a vomer accurately from the central plate after the two bones have come into contact. The ridge which one so frequently meets with on one side of the vomer in specimens purchased with disarticulated skulls, is formed by an atrophied ala of the vomer, or by the edge of the central plate of the ethmoid projecting to one side, which it may do in an infinite variety of ways.

The same cause accounts for the imperfect description of the inferior margin of the vomer. In particular, the projection which lies on the crista incisiva is very liable to be destroyed by anchylosis; and even when it is not anchylosed it often requires very careful disarticulation to exhibit it. Sometimes the crista itself undergoes changes. It may have the margins of its groove worn away, and present a flat surface having the fore part of the vomer imbedded between its halves; or it may be completely bent over to one side, so that one semicrista shall lie above the other, while the fore part of the vomer, lying between them, is necessarily distorted, but may yet admit of disarticulation. At an early age the united margins of the maxillaries behind the anterior palatine canal become elevated into a sharp ridge, and the margins of the originally flat surface of the vomer in contact with them bend down to grasp it, and become irregular, thin away, and disappear more or less completely. Vestiges of them, as they die away, may sometimes be seen still very distinct on careful disarticulation, even in adult subjects. The edges of the palate-bones often form a more prominent ridge than the maxillaries, rising into a spine a couple of lines or more in height; and the portion of vomer in contact with this is a thin edge.

These remarks, I believe, are sufficient to show that if the human vomer is to be described with accuracy in its character as a separate bone, it must be studied as it shows itself in early life*.

If it be asked why, even in the early condition, when its form and connexions most resemble the typical arrangement, the human vomer should yet differ from the arrangement in other mammals by having the arch of communication between it and the ethmoid a separate bone, some explanation will be arrived at by considering that in Man the ethmoid is very feebly developed, and that the distance between the ethmoid and vomer is increased,—circumstances which depend on the feeble development of the sense of smell, and on the rapid curvature of the arch of the cranium. To the cursory glance the human ethmoid presents a rather well-developed appearance, since it forms a large part of the inner wall of the orbit, and the orbital plate is a peculiarity confined to Man and the Quadrumana. Yet in Man the ethmoid is rudimentary, and in Monkeys still more so; and the existence of the orbital plate is a mere consequence of the great curvature of the cranial arch. In the generality of mammals the ethmoid is shielded by the frontal and palatals; but in Man the palatals are removed from it by the downward development of the face; while by the great size of the anterior lobes of the brain it is pushed from under the shelter of the frontal, and the cribriform plate is depressed into the horizontal plane, instead of occupying, as in the Cat, the Sheep, &c., an almost vertical position. But whereas in most mammalia the lateral masses of the ethmoid

* Of this the first Monro was well aware. See the Works of Alexander Monro, M.D., published by his son in 1781, p. 120.

are composed of large turbinations imbedded in a dense mass of small leaflets, and both leaflets and turbinations lie at right angles to the cribriform plate, in Man there are no such leaflets and only two stunted turbinated processes, which, instead of descending to fill the nasal cavity, immediately curve backwards so as to occupy as little room as possible. And not only is the ethmoid so rudimentary, but by the curvature of the cranial arch, the vomer is moved away from it; its anterior extremity sloping rapidly to a lower level, and its posterior being pushed backwards under the sphenoid. Of this latter fact we may be convinced by comparing the position of the human vomer with that of the same bone in the Cat. The Cat has got sphenoidal sinuses as well as Man, but they are floored-in entirely by projections downwards from the wings of INGRASSIAS; and the part of the vomer which is continued into the ethmovomerine laminæ lies, not underneath the sinuses, but underneath the ethmoid, immediately in front of the sinuses. Moreover, it is very important to keep in mind that the margin of the ethmoid which is placed posteriorly in the human skull is that which is morphologically inferior, and which corresponds to that to which the ethmovomerine lamina is habitually attached, and to which therefore it behoved that the human vomer should be connected. This will be best illustrated by using the vomer and ethmoid of the Sheep, Dog, or Rabbit for comparison. It will then be easily understood, on referring to Plate IV. fig. 5, how there comes to be a space left between the ethmoid and vomer, to bridge over which the large and peculiar development of ethmovomerine laminæ as sphenoidal spongy bones becomes necessary (fig. 5).

Varieties presented by the Vomer and Intermaxillaries in different Classes of Mammalia.

In the *Quadrumana* the vomer comes to a point anteriorly, which is so directed that the vomerine groove is continuous, as in other animals, with the upper surface of the intermaxillaries; but it never comes further forwards than just to touch them, and sometimes falls short of them by a slight interval. This is owing to a want of development of the mesial-palatine processes of the intermaxillaries, these bones having in the Quadrumana begun to suffer that atrophy which they undergo in the human subject; and as their bulk is occupied almost entirely by the sockets of the large incisor teeth, while, on the other hand, the cartilages of the nose are little developed, there is no appearance of the crista incisiva found in Man. The ethmoid and vomer are continuous, according to the normal plan, save only in the Orang; and we may therefore confine our attention to the arrangement in it and in the Chimpanzee. In two skulls of Chimpanzees in the University Museum, the posterior part of the vomer arches out on each side into a lamina which passes up in front of the sphenoid to be continuous with the orbital plate of the ethmoid, as in other Quadrumana; but both are skulls of animals of such an age that they present anchylosis of many sutures. In the Orang, however, there are certainly separate sphenoidal spongy bones. The examination of three young Orang skulls gives the following results. In the largest skull, the sphenoidal spongy bone is quite distinct on the right side, both from the orbital plate of the ethmoid and from the vomer; but on the left side their suture of connexion with the ethmoid has begun to disappear, and it scarcely comes into contact with the vomer. In the smallest skull, the sphenoidal spongy bones are perfectly free from the ethmoid on both sides, and also free from the vomer, though in contact with it; but while that on the left side is perfectly free from the sphenoid, the right one is anchylosed with the anterior inferior margin of that bone. In the remaining skull, the sphenoidal spongy bones are separate from the orbital plates of the ethmoid, but are anchylosed with the sphenoid both in front of the foramen opticum and below, also with the vomer, and with a turbination of the ethmoid. In all three cases the sphenoidal spongy bones take part in the formation of the orbit, while the palatal has no orbital plate.

The shape of the posterior extremity of the vomer affords us a very distinctive difference between the skulls of the Orang and Chimpanzee, which I believe has not hitherto been noticed. In the Orang it is expanded, flat, and with irregular edges. In the Chimpanzee it is thick, comparatively narrow, with straight edges, bifurcated, and fitted into a groove so as to leave a canal between it and the sphenoid. These characters are well marked even in the extremely young skull. In the Gorilla the posterior extremity of the vomer has expanded irregular edges as in the Orang, while it is bifurcated and a canal is left above it as in the Chimpanzee* (fig. 6).

In the *Bat*, the intermaxillaries are extremely small; they do not come together in the middle line, and have no mesial-palatine processes; they therefore have no connexion with the vomer.

In the *Carnivora*, the vomer and ethmoid are quite typical in their arrangement. In the Cats, the Dogs, and the Bears, the mesial plate of the vomer reaches a short way back upon the palatals. In the new-born Kitten the sphenoid, vomer, and intermaxillaries are seen in a very instructive condition. The body of the presphenoid is not yet compressed into a septum, and the two projections from the wings of INGRASSIAS, which afterwards meet beneath so as to enclose the sinuses, are as yet but little processes; the vomer passes forwards in a straight line from the front of the body of the presphenoid; and beyond the vomer this line is continued by the intermaxillaries, while the surface for articulation of the vomer with the maxillaries is as yet a mere knob. This arrangement is calculated strongly to suggest the idea of a series of centra (fig. 7, D).

* In the engraving of the base of the skull of a Chimpanzee in the Trans. Zool. Soc. vol. iii. pl. 60, illustrating Professor OWEN's paper, "Osteological Contributions to the Natural History of the Chimpanzee," the canal along the middle line of the sphenoid is represented as completed behind the vomer by junction of the roots of the pterygoid bones, or in other words, by the vaginal processes meeting together in the middle line. This completely conceals from view any parallel-bordered part of the vomer which may be supposed to rest between these and the body of the sphenoid. The skull represented is that of a male. The representation of the vomer of the Gorilla in pl. 63, illustrating the same paper, agrees with the description given above. My sketch was taken from a Gorilla's skull in the Museum of the Jardin des Plantes, Paris.

In the skull of a young male Chimpanzee in Dr. ALLEN THOMSON's possession the pterygoids have already almost met in the middle line, as represented in Professor OWEN's drawing, while the vomer is compressed between them. Most probably this is a sexual characteristic.

The posterior extremity of the feline vomer, as I have observed it in the Lion, Tiger, Leopard, and Cat (fig. 7, A), is of a well-marked constant form, viz. the posterior margin of the ethmovomerine laminæ is a straight line across, and behind it the vomer sends back a narrow process between the palatals. In the canine family the ethmovomerine laminæ are very broad, and their posterior margins slope backwards and inwards to the posterior extremity of the vomer (fig. 8).

In the Bears and their allies the mesial-palatine processes of the intermaxillaries come in contact with the lateral plates of the same bones behind the incisive foramina, and in the middle line between them there is also a characteristic foramen (fig. 9). This foramen varies very much in different species, and also in individuals. The *Ursus ornatus*, in three specimens in the Museum at the Jardin des Plantes at Paris, has it larger than any other bear's skull in that collection. The *Ursus maritimus* has it always of considerable size. In *Ursus arctos* and *Ursus americanus* it is small and variable. The Coati Mondi has this foramen very large; and I observe it, but small, in the Weasel, the Marten, the Glutton, and the Hyæna, very small in the Badger, and not at all in the Civet and the Otter. The inferior margin of the vomer of the Weasel, notwithstanding the length of the hard palate, is very short; it articulates with the intermaxillaries, and only for a very short distance with the maxillaries.

In the Seal the ethmoid is so compressed that the elements of which it is composed are brought close together; so close that beneath the nasal bones the central plate, which is slightly flattened out above, comes in contact with and is soldered to the outer plates of the lateral masses (fig. 10). There is no need in this instance of a special ethmovomerine lamina to unite the vomer and lateral mass; they are in contact, and are anchylosed directly with one another. At an early age the central plate of the ethmoid of the Seal becomes closely connected with the vomer; yet even after it has extended down to the vomerine groove, one can mark this distinction, viz. that the central plate replaces the septal cartilage, while the vomer surrounds it. The vomer merely touches the intermaxillaries, and does not reach back to the palate bones.

The arrangement in the Hedgehog is interesting in this respect,—that, owing, I presume, to the unarched form of the head, the inferior margin of the central plate of the ethmoid intervenes for about a third of an inch between the vomer and presphenoid; so that if the maxillary and palate bones be removed from a hedgehog's skull, there are seen extending in a straight line forwards, the bodies of the occipital, postsphenoid, and presphenoid bones, the central plate of the ethmoid with a slightly flattened edge lying between the ethmovomerine laminæ, then the vomer, and lastly, the mesial-palatine processes of the intermaxillaries; the whole presenting the appearance of a series of homologous elements (fig. 11).

Ruminantia.—In the Ox, the Sheep (fig. 12), the Deer, the Camel, and the Alpaca, the vomer has the typical arrangement. The inferior margin is not prolonged back sufficiently far to articulate with the palate bones, and its anterior extremity is scarcely prolonged upon the intermaxillaries, but fits on to them in such a way as to make their mesial processes continuous with it. In the Giraffe, however, there is an exception to the usual connexions; the superior parts of the palatals floor-in the greater part of the ethmoidal turbinations, and the alæ of the vomer only come in contact for a very short distance in front of the palatals with prolongations inwards from the framework of the lateral masses of the ethmoid, but are not anchylosed to them. The arrangement is extremely similar to that in the Horse, even in the shape of the back part of the vomer.

There are some interesting varieties in the intermaxillaries of ruminants. In the animals which we have hitherto examined, the angle of junction of the mesial-palatine and lateral plates of the intermaxillary has been the most anterior part of that bone, and the groove for the septal cartilage has been open in front, so that, as in the human subject, the cartilage could be prolonged forwards beyond the intermaxillaries. But in the Sheep there is a slight, a very slight inclination of the lateral plates to prolong themselves forwards beyond the points at which the mesial palatine processes come off from them (fig. 13). These points are at a little distance from the middle line, and the prolongations forwards of the lateral plates are inclined inwards, so that in front of the mesial plates there is a little space left in the middle line. Into this space the anterior extremity of the septal cartilage, slightly dilated, dips down, and the tendency of the tips of the intermaxillaries is to embrace it. This arrangement is so faint in the Sheep that it would appear unworthy of attention, were it not that in the Camel and the Alpaca it is carried out to a most distinct and unmistakeable extent. In them the mesial-palatine processes, which are but slender in comparison with the lateral plates, arise at such a distance from the middle line that at their bases they are first directed inwards to meet one another before they are directed backwards. The space for the extremity of the septal cartilage is large, and almost converted into a foramen by the prolonged tips of the lateral plates approaching the middle line in front of it; and as they do so, they turn their inner aspects downwards, and embrace the cartilage on its upper border. Thus there can remain no doubt that the portion of the cartilage which projects through the space into the palate is really its anterior extremity (Plate V. fig. 14).

In the Giraffe this relationship of the intermaxillaries to the septal cartilage is very distinct. The mesial-palatine processes are very large, while the lateral plates are comparatively slender; but the continuation forwards of the latter to embrace the septal cartilage is well marked (Plate IV. fig. 15).

Pachydermata.—In the Horse, as already mentioned, the connexion of the vomer with the lateral masses of the ethmoid is of an exceptionally slight description. The leaflets of the ethmoid, which in most instances lie in contact for a considerable extent with the ethmovomerine laminæ, are in this case floored-in completely by the superior parts of the palate bones. But even in these circumstances a slender lamina, immediately in front of the palate bone, and in contact with its nasal foramen, passes downwards and inwards on each side from the ethmoidal turbinations, and articulates with the ala of the vomer, though it is not anchylosed to it (fig. 16). These peculiar relations in the skull of the Horse seem principally to depend on the palate bones being pushed further forwards than usual; a circumstance which is probably connected with the habitual nasal respiration of the Horse*, as, by the posterior nares being placed well forwards, the most direct and free connexion between the nasal passages and respiratory organs is obtained. The lateral plates of the intermaxillaries of the Horse meet for some distance in the middle line in front of the septal cartilage, in the same way as we have seen them tending to do in the Camel; but the mesial-palatine processes arise quite from the fore part, and are in contact with each other at their origins, so that the extremity of the cartilage is enclosed completely in a cul-de-sac, and does not project into the palate (Plate V. fig. 17).

In the Pigs, the vomer articulates with the intermaxillaries, maxillaries, and palatals below, and forms one bone with the lateral masses of the ethmoid, according to the typical mode. The posterior extremity of the vomer is always very narrow, and the intermaxillaries are as in the Carnivora. We may notice also the little bone developed in the anterior extremity of the septal cartilage, in connexion with the snout.

In the skull of a sucking-pig, I have observed to advantage some of the more important morphological relations of the vomer (Plate IV. fig. 18). The central and cribriform plates of the ethmoid have not yet begun to ossify; there are separate centres of ossification in a number of the leaflets of the lateral masses, and larger ones in the great turbinated processes; and on each side the vomer is continuous (with only a slight trace of the junction) with a mass of bone consisting of the ethmovomerine lamina and part of the lateral mass of the ethmoid. It is but fair to add, that already the vomer is anchylosed to the body of the sphenoid. The articular surface on the inferior edge of the vomer for the maxillaries is flat, with a raphe in the middle line, and abruptly ceases where the intermaxillaries fit on; and the inferior surface of the mesial processes of the intermaxillaries is continuous with the maxillary surface of the vomer; a state of matters exactly similar to what we have noticed in the young human subject, and which may also be seen in the skull of a new-born puppy.

The Hippopotamus has the vomer and intermaxillaries arranged like those of the Pig. The ethmovomerine laminæ are broad, but in the specimen which I examined, although it was a well-grown one, there were suture markings between them and the vomer.

In the young Elephant (Plate V. fig. 19) the intermaxillaries come in contact with one another by means of large triangular surfaces, which reach to a considerable height above the level of the floor of the nares behind. They have no mesial-palatine processes. There is a small anterior palatine canal between them and the maxillaries in the middle line. The vomer is but a slightly developed bone: in the specimen before me it presents in the greater part of its extent superiorly a mere edge to articulate with the septal cartilage, and no vestiges of alæ. At the posterior part, however, it is bifurcated, and comes in contact with the lateral masses of the ethmoid, but is not anchylosed to them. At its

* Pointed out by Sir Charles Bell in his 'Anatomy and Philosophy of Expression,' 3rd edit. pp. 126 and 134.

anterior extremity it presents two processes; one passing into the anterior palatine canal, the other inclined somewhat upwards behind the surfaces of contact of the intermaxillaries. The superior and inferior margins of the vomer are thus rendered continuous with those of the intermaxillaries.

In the two-horned species of Rhinoceros the intermaxillaries are very small, and consist merely of lateral plates, without vestige of mesial-palatine processes; while the anterior extremity of the vomer stops short on the palate plates of the maxillaries, some distance behind their anterior margin. But in *Rhinoceros indicus* (which unfortunately I have not examined) a process of considerable size is described as arising from behind the superior margin of the intermaxillary; and in *R. tichorhinus*, not only is the osseous septum of the nose rendered complete by this process reaching up to the nasal bone, but the thick nasals are prolonged downwards to the level of the palate, and articulate with the anterior extremities of the intermaxillaries, so as to form a complete arch of bone in front of the nostrils, the only instance of this among Mammals*.

In the Tapir we have another instance of intermaxillaries without any mesial-palatine processes, and the anterior extremity of the vomer stopping short upon the maxillary bones; the intermaxillaries, however, are of considerable size, and come in contact with one another for a considerable distance in front of and above the septal cartilage, exactly as in the case of the Horse, only much more extensively (fig. 20).

Rodentia.—In the Rodentia the vomer is remarkable for the very little tendency it evinces to articulate with the maxillaries. Its superior connexions are typical, *i. e.* it is continuous with the lateral masses of the ethmoid, and the margin of junction of the ethmoid and ethmovomerine lamina enters into the formation of the nasal foramen of the palate bone, as seen from within. In all those that I have examined the vomer is bifid in front, and fits on edge to edge with those parts of the mesial processes of the intermaxillaries which bound the groove for the septal cartilage. The mesial processes of the intermaxillaries are well developed, and are expanded laterally in connexion with Jacobson's organs in a very characteristic fashion. The edges for articulation with the vomer are sometimes, as for instance in the Hare, very minute: but in other species with strong incisors they are well developed; thus they are of considerable size in the Paca (fig. 21); while in the Porcupine they are remarkably elevated, and the vomer sends down a process from its mesial plate between them.

In the Rat, the Beaver, the Porcupine, and the Paca, the vomer comes in contact with the anterior extremity of the maxillary part of the palate plate by a little, slightly dilated point; in the Squirrel it scarcely comes in contact. But the most interesting condition is seen in the Hare and Rabbit: they have only one single large foramen incisivum; for although the mesial-palatine processes of the intermaxillaries project well backwards, the palate plates of the maxillaries do not come far enough forwards to meet them: the vomer does not even approach the maxillaries, but its posterior margin terminates inferiorly in a thickened angle, which articulates with the intermaxillaries in such a manner as to be

* Cuvier, Ossemens Fossiles, tom. ii. Meckel, Anatomie Comparée (traduit), tom. iv. p. 273.

continuous with their inferior margin; and between this angle and the point where the vomerine groove is continued on to the intermaxillaries, there intervenes a considerable space in which the vomer comes in contact with the intermaxillaries by the edge of a triangular development of mesial plate (fig. 22).

In the *Edentata* the vomer has its superior connexions typical. In *Orycteropus* its inferior margin reaches back to the palatals, in *Manis* and *Myrmecophaga* it does not; and in *Bradypus* it only articulates with the anterior part of the maxillaries. The intermaxillaries are very small. They are smallest in *Bradypus*. In *B. didactylis* and *B. torquatus* they are separate; in *B. tridactylis* they are fused into one little plate, which is in contact with the maxillaries by its posterior and lateral angles, and anteriorly turns upwards upon the septal cartilage. In *Myrmecophaga* the intermaxillaries are somewhat better developed, but the incisive foramina being large, the mesial-palatine processes do not quite come in contact with the vomer, even though the latter projects some distance forwards beyond the maxillaries.

The intermaxillaries of the Armadillo are very characteristic. Their lateral plates are broad, and meet together in the middle line of the palate behind the incisive foramina. These foramina are small; and the mesial-palatine processes which separate them are slender, but are prolonged back upon the superior aspect of the line of junction of the lateral plates, so that thus the vomer rests upon the mesial-palatine processes, according to the general rule, and does not come in contact with the lateral plates.

In the *Marsupiata* the relations of the vomer are normal. Sometimes, as in the Koala, the inferior margin articulates with the palatals; sometimes, as in the Kangaroo, it does not. The groove for the septal cartilage is open in front, as in the Carnivora. In the Kangaroo (fig. 23) the ethmovomerine laminæ are very broad: the vomer exhibits on each side a peculiar lateral ridge, which extends forwards from the point where the ethmo vomerine lamina comes off, and articulates in front with a very long prolongation backwards of the mesial process of the intermaxillary, which extends between it and the maxillary. This ridge exists also in the Wombat, the Phalangers, and the Opossum; probably it is a constant marsupiate characteristic.

Cetacea.—In the Manati and Dugong we again meet with the arrangement of the vomer and intermaxillaries which we found in the Tapir, viz. the vomer is quite unconnected with the intermaxillaries, and the latter have no traces of mesial-palatine processes. The lateral plates of the intermaxillaries are very well developed, and meet each other above and in front of the septal cartilage, as they do in the Horse and the Tapir. In the Manati the anterior extremity of the vomer projects beyond the anterior margin of the maxillaries; in the Dugong it falls considerably short of it. In the Dugong the turbinations of the lateral masses of the ethmoid are very slight; but their framework is strong, and united by ethmovomerine laminæ to the vomer (fig. 24). In the Manati the lateral masses of the ethmoid are considerably more developed; they also are united to the vomer.

In the carnivorous Cetacea the vomer is largely developed, and its inferior margin extends back the whole length of the palate. The intermaxillaries prolong the vomerine groove for a greater or less distance according to the genus. The distinctness of the central plate of the ethmoid from the vomer is very clearly seen, inasmuch as the former terminates abruptly where it becomes continuous with the cartilage in front, while the grooved surface of the latter is continued smoothly forwards. In vertical sections of skulls of the Dolphin and Grampus in the Museum of this University, although many sutures are obliterated, a straight line passing forwards from the inferior margin of the presphenoid indicates distinctly the place of contact of the still separate vomer and central plate of the ethmoid (fig. 25). The olfactory apparatus and lateral masses of the ethmoid are entirely absent; but the posterior parts of the alæ of the vomer are enormously expanded to take their place, and pass up on each side of the central plate of the ethmoid in front of the frontals, even as far as the nasals, forming the whole posterior wall of the nares, viz. the whole of that wall which in other Mammals is formed by the ethmoid. I notice also in *Deductor globiceps* that the expanded margin of the vomer, with the assistance of an angle of the maxillary, completes for the palate bone its nasal foramen (fig. 26).

Monotremata.—In the Ornithorhynchus the inferior margin of the vomer extends quite back to the posterior extremity of the hard palate, which is formed by the meeting of the pterygoids. In the Echidna it does not extend back so far. The condition of the intermaxillaries in the Ornithorhynchus is extremely interesting. The large bones which extend forwards from the maxillaries at a considerable distance from one another, and which give the form to the broad flat bill, are beyond all question intermaxillaries, and correspond exactly to the intermaxillaries of the Bat, or any other animal in which the mesial-palatine processes of these bones are not developed. Utterly unconnected with these, in front of the vomer, and continuing on its upper aspect the vomerine groove, is the little bone which has been recognized both by CUVIER and MECKEL as corresponding with the mesial-palatine processes of intermaxillaries, which it no doubt does; but it is very interesting to find these represented by a bone so distinctly separated from the lateral plates of the intermaxillaries. It leads us to the consideration of the remarkable arrangement which exists in cases of cleft palate in the human subject, contrasted with the natural arrangement.

In cases of *complete cleft palate in the human subject* the inferior margin of the vomer is free, and is seen in the middle line of the open roof of the mouth. The intermaxillaries, fused or separate, articulate with its anterior extremity, and continue forwards in the same straight line, and support the incisor teeth when they are developed. They are entirely disconnected from the maxillaries, and are developed on the under aspect of the septal cartilage, which is a mesial structure; while the maxillaries are developed in lateral laminæ which, in these instances, fail to reach the middle line. Yet in the normal condition, marvellous as it may appear, the intermaxillary grows from the same centre of ossification as the maxillary *, and therefore must be con-

* See on this subject, in the 'Comptes Rendus' (Dec. 1858 and Jan. 1859), various papers by M. EM.

sidered as at least commencing from what had originally been a lateral lamina. On the one hand, in the normal condition, the mesial processes of the intermaxillaries are obviously present; and in the cleft-palate condition, on the other hand, there can be no doubt that the lateral plates are represented as well as the mesial processes, since the incisor teeth are developed on the mesial bone. Thus it is certain that, according as the palate is completely closed or remains cleft, the whole intermaxillary—both mesial and lateral portion—comes from one or other of two parts which at an early period are always quite distinct. This is a fact of great importance.

Morphological Conclusions respecting the Vomer, Ethmoid, and Intermaxillaries in Mammals.

I had desired that this paper should be as strictly observational and as little theoretical or controversial in its character as might be; but I find it is impossible, now that I have arrived at this point, to refrain from indicating in what direction the observations just made appear to tend. I am conscious that by entering on this theme I render myself liable to the charge of presumption, in asking to be heard upon matters which have been discussed by the greatest authorities. My excuse is, that it is the observational part of my subject which compels me into the theoretical: and in venturing an opinion upon certain segments of the skull, I shall endeavour to limit myself as much as possible to what seem to me to be deductions to which the facts discussed inevitably lead; facts, some of them at least, not hitherto known, or not previously collated, and therefore not till now at the disposal of the theorist; but a knowledge of which, I cannot help thinking, is indispensable to the just conception of the segments to which they relate.

I gladly embrace this opportunity of acknowledging my obligations to Professor Goodsir for the use of books and specimens placed at my disposal, and for valuable information bearing upon topics treated of in this paper; and if, for the reason just mentioned, I have taken it upon me to adopt conclusions differing from his in certain details (although not more than from those of others), I do not forget that to him entirely I owe my morphological training; nor am I the less sensible of the advantage which I have enjoyed in being frequently indoctrinated by him in those great principles of Morphology which he illustrated in his communications to the British Association in 1856 *.

1. The first proposition which I shall make is, that the whole septum of the nose is continued forwards from the line of centra formed by the basilar process of the occipital and the bodies of the postsphenoid and presphenoid †. This statement can be best verified in some animal in which the body of the presphenoid is more developed than in

Rousseau, showing that the intermaxillaries are at no period normally separate from the maxillaries; and by M. Larcher, showing that in cleft palate they are distinct.

* Edinburgh New Philosophical Journal, Jan. 1857, pp. 118–181.

† The embryological aspect of this proposition is considered below at page 315.

Man. Take, for example, the Cat (fig. 7, B & C). The posterior aspect of the body of the presphenoid in the Cat exactly corresponds to the anterior extremity of the postsphenoid, presenting an appearance exactly similar to what the body of a vertebra exhibits on removal of its epiphyses; viz. a part in the middle, broad below and narrow above, formed by the centrum, and the two superior angles formed by the alæ. If we look at the same bone from the front, we see plainly that the septum between the sphenoidal sinuses consists entirely of the anterior extremity of the centrum greatly compressed; and just as the posterior extremity of the presphenoidal centrum is continuous with the postsphenoidal, so is its anterior extremity continuous with the septal cartilage of the nose and the central plate of the ethmoid. This continuity is in some respects even better seen in the new-born Kitten, as above described. Now we know that, morphologically, it is of little importance whether cranial bones are developed in the primordial cartilage of the skull, of which the septal cartilage is the remains, or are developed round it. The basisphenoid in fishes, for example, is developed round it, while in mammals it is developed in it. Therefore the central plate of the ethmoid, the vomer, and the mesial processes of the intermaxillaries all claim from their position to be centra as much as the basioccipital and basisphenoid. With regard to the mesial processes of the intermaxillaries, that they play the part of a centrum is shown, not merely by their constant relation to the septal cartilage, but by their articulation with the vomer being of such a description as to make them continuous with that bone both on the upper and under aspect, and by their condition in cleft-palate.

2. The vomer, lateral masses of the ethmoid, and palate-bones belong to one segment. This seems to be an altogether unavoidable conclusion, from the constant connexion of these bones in so invariable a manner.

What meaning can be attached to the remarkable way in which, in the human subject, the vomer and lateral masses of the ethmoid, notwithstanding their altered forms and positions, preserve the relations to one another which they exhibit in other animals, but that they are members of one segment? And how else can we explain that the place of the flattened ethmoid and ethmovomerine laminæ of the Dugong is occupied in the Delphinidæ by expansions of the vomer, which both form the posterior walls of the nostrils and articulate with the palatals?

This conception of the construction of the ethmoidal segment, as well as the reasons just mentioned for considering that the mesial-palatine processes of the intermaxillaries play the part of a centrum, is at variance with the view of Professor GOODSIR, that the vomer and the intermaxillaries are members of one "sclerotome*."

Also if the connexions of the vomer and lateral masses of the ethmoid recorded above are considered sufficient to prove that these bones are parts of one segment, it will at once appear evident that the lateral masses of the ethmoid and the ethmovomerine laminæ form an incomplete neural arch. In that case we must differ from Professor

* *Op. cit.* p. 138.

OWEN, who considers that the central plate of the ethmoid represents in a coalesced condition the prefrontals of the fish or reptile*, and plays the part which we allot to the lateral masses in the neural arch of the vomerine segment. It cannot do so, for these reasons: 1st, that while the lateral masses of the ethmoid are continuous with the vomer, the central plate is never truly continuous, but only contiguous to the vomer; 2ndly, that the central plate must, for reasons above stated, play the part of a centrum; and 3rdly, that, as Professor GOODSIR has shown, Professor OWEN's view is inconsistent with the relation of the olfactory nerves to the central plate †.

3. The frontal and the central plate of the ethmoid belong to one segment. The fact of the central plate of the ethmoid having no early connexion with the vomer, as well as its tendency to remain distinct even after the vomer and it have come in contact, shows that it is not part of the same centrum as the vomer; therefore, inasmuch as we have already concluded that it is a centrum, it can form no part of the vomerine segment. On the other hand, the presphenoidal centrum is complete without it. In these circumstances it becomes apparent that the central plate of the ethmoid is the centrum of a segment intervening between the vomerine and presphenoidal. This opinion is strengthened by our remembering that in the Sheep the central plate of the ethmoid is anchylosed to the centrum of the presphenoid before uniting with the lateral masses, and that in the Hedgehog it appears on the base of the skull for a considerable distance between the presphenoid and vomer. The frontal forms the neural arch belonging to this centrum, and is in constant connexion with it. But if, as above proved, that margin of the os planum of the human subject which lies superiorly is morphologically posterior, then the margin of the frontal which articulates with it, viz. the inner edge of the orbital plate, is morphologically anterior; and therefore not only the foramen cæcum, as Professor GOODSIR believes ‡, but also the space occupied by the cribriform lamina, lies within the arch formed by the frontal and the central plate of the ethmoid. Thus the cribriform lamina, which in point of development is a mere lateral expansion of the central plate, forms a screen across the entrance into the cavity of the ethmovomerine arch in the plane of segmentation, and has no further morphological importance than may be supposed to attach to the tentorium cerebelli. By the turning up of its anterior extremity to touch the frontals and nasals, the central plate of the ethmoid divides the neural arch of the segment to which it belongs, as well as those in front of it, into a

* OWEN 'On the Archetype and Homologies of the Vertebrate Skeleton,' pp. 131 & 135.

† *Op. cit.* p. 149. The strength of Professor GOODSIR's argument rests in this: that, according to Professor OWEN's theory, the olfactory nerves in the mammal are made to lie outside a neural arch, through which they pass in the reptile and fish; which involves the supposition that the points of egress of the olfactory nerves have been moved in the mammal one segment backwards. According to the theory advanced in this communication, although no doubt the bone corresponding to the mammalian central plate of the ethmoid passes upwards on the outside of the olfactory nerves, and does not rise up between them, yet in both fishes and mammals the olfactory nerves are contained within the neural arch of the segment.

‡ *Op. cit.* p. 142.

right and left portion, exactly as the vomer, by a prolongation downwards, divides the anterior hæmal arches.

4. The intermaxillaries, maxillaries, and nasals are the osseous elements of one segment. Of this we might find sufficient evidence in their relations in mammals; and indeed the proposition does not stand in need of much proof, if it be once considered certain that the vomer, lateral masses of the ethmoid, and palatals belong to one segment, and that the mesial-palatine processes of the intermaxillaries are the centrum of the segment following. But that we may fully understand the parts played by the intermaxillaries, maxillaries, and nasals respectively, we must defer our remarks on this subject till we have examined the arrangements in other classes.

We shall now glance for a single moment at the manner in which this explanation of the anterior segments of the skull affects the general view of the cranial segmentation.

That there is an occipital segment, and that the postsphenoid and parietals are portions of another segment, is generally admitted; and we have concluded that the frontal and central plate of the ethmoid are elements of a third segment. These then are the three segments which roof-in the cranial cavity. They are all complete above. Their centra are successively smaller in their order from behind; and the floor of the neural arches which they form gradually turns upwards as it passes forwards.

In front of the occipital segment lie the petrous bones*, and connected with them are the organs of hearing. In front of the parietal segment lies the presphenoid, connected with which are the organs of vision. In front of the frontal segment lies the ethmo-vomerine segment, and connected with it are the organs of smell. None of the three segments connected with the special senses has a complete neural arch. With the most posterior of them no centrum is connected; the second (the presphenoid) has a small centrum; and the most anterior has a larger centrum—the vomer: and the tendency of these centra, contrary to the tendency of the centra of the brain-protecting segments, is to curve downwards as they pass forwards. Thus there are two alternating sets of sclerotomes, which may be distinguished as the protective and the sensory; while foremost of all is an imperfect and peculiar seventh and terminal sclerotome—the facial, which may be considered as binding these two sets together. On this seven-segmented plan I believe the head to be formed in all vertebrata; and although it be true that in certain cases there are no sclerous elements of the cranium developed in connexion with either the ear or the eye, these organs are nevertheless themselves portions of segments lying between those in connexion with which the neighbouring protective sclerotomes are developed. The upward tendency of the protective, and the downward tendency of the sensory sclerotomes, is not seen at all in the fish, but becomes more and more observable as we ascend to reptiles, birds, and mammals; and is exhibited best of all in man, in whose structure the idea of vertebrate creation is completed (fig. 27).

These few and imperfect remarks have been necessitated by the consideration that no

* It is unnecessary for the purpose of this argument to discuss the positions of the interparietal, mastoid, or squamous.

segment of the skull can be properly viewed apart from the others. While on the other hand, were I to enter into further details, I should be led far beyond the subject of this paper, and such details are not required for the elucidation of the points under consideration.

Birds, Reptiles, and Fishes.

The Vomer and Intermaxillary in the Bird.—There is only one intermaxillary in the bird. It sends no mesial processes backwards on the palate. Its lateral plates articulate with the maxillaries exactly as the mammalian intermaxillaries do. Its distinctive peculiarity is, that from the place of union of its two halves in front it sends up long processes between the nostrils, which reach back to the roof of the skull. These processes close-in the septal cartilage above and in front, exactly as it is closed in by the intermaxillaries in the Horse, the Tapir, and the Dugong. If the parts of the intermaxillaries of the Dugong which meet in the middle line were prolonged back to the frontal, their arrangement would altogether resemble the intermaxillary of the bird, for they are situated as much in front of the nostril as it is. The arrangement also in *Rhinoceros tichorhinus* only differs from the beak of the bird, in that the bones roofing the nostrils are prolonged down to the intermaxillaries, instead of the latter passing up to the former. The nostrils of the bird, therefore, correspond to those of the mammal, and the bones which roof them (ethmoido-frontals of GOODSIR) are the nasals.

Fortunately, opinions are agreed as to which bones are the palatals of the bird. They approach each other behind and come in contact in the middle line, and form by their junction a grooved surface, which glides backwards and forwards on the basisphenoid. But very frequently a small bone (the vomer of CUVIER, OWEN, &c., the entopterygoid of GOODSIR) is intercalated between them, so situated as to furnish a continuation of this groove along the inferior edge of the septal cartilage; and with this little bone the palatals articulate edge to edge. It is often absent, as in the Gallinaceæ, and in different birds it presents different shapes: thus it is broad in the Crow, and a vertical plate of considerable size in the Duck (fig. 28); and in the Gull and Guillemot, as well as in the Albatros, which has it of very large size, it bears a most striking resemblance to the mammalian vomer. That it belongs to the same segment as the palatals is as obvious as that the vomer, lateral masses of the ethmoid, and palatals in the mammal belong to one segment; and if that proposition has been proved by the foregoing observations, there can be no further doubt that this bone in the bird's skull is the vomer.

The framework of the lateral masses of the ethmoid of the mammal is not represented in the bird; but the turbinations for the distribution of the olfactory nerves, which in the mammal are attached to that framework, are in the bird, when they are ossified, usually in close connexion with the palatals, which are members of the same segment. This can be seen in the Gull and in the Albatros. In the Parrot there is an exception to the rule.

If the nasals of the bird correspond with the nasals of the mammal, then the frontals of the bird (sphenoido-frontals of GOODSIR) must correspond with the frontals of the mammal; and indeed they have the same relation to the cranial cavity, and are met, like those of the mammal, by the anterior extremity of a bone belonging to the series of centra. But if they are the frontals, then the bone which meets them, viz. the interorbital plate (prefrontal of OWEN), corresponds to the mammalian central plate of the ethmoid, at least in the anterior part of its extent *.

The Vomer in Reptiles and Fishes.—Of the vomer in reptiles and fishes it is not necessary, for the purposes of this paper, to say much. If the vomer, palatals, and lateral masses of the ethmoid in the mammal form one segment, and if this segment is that to which the olfactory nerves belong, then it requires no argument to prove that these bones must be respectively represented in reptiles and fishes by the vomer and palatals of CUVIER and OWEN, and the prefrontals; for these comply with all the necessary conditions. The prefrontals and palatals are always in contact, and sometimes, as in the Crocodilia, in such a way as to indicate in the strongest manner that they are parts of one sclerotome; while the vomer articulates always with one or other of these two pairs of bones, and sometimes with both. Moreover the vomer in reptiles and fishes always lies along the inferior margin of the septal cartilage (or middle frontal process of the primordial cranium). In reptiles, however, it presents a series of variations. While in the Turtle it is a single bone, and disposed much as in the mammal, except that inferiorly it appears prominently in the palate †, in other reptilia it is in two parts—a right and a left. In the Crocodile these parts lie side by side, and inferiorly articulate with the palate plates of the palatals, while superiorly they curve outwards and come in contact edge to edge with the superior extremities of the same bones. On the other hand, in the Serpents it is the inferior edges of the vomerine bones which curve outwards. In the Lizards they merely come in contact in the middle line; and in the Batrachia they do not even meet.

If it be asked, what corresponds in reptiles and fishes to the central plate of the ethmoid, I reply that it is the interorbital septum. This structure is frequently completely ossified in fishes so as to form a single distinct bone; and, as Professor GOODSIR has pointed out ‡, it completes a neural ring with the great frontal. According to the theory now advanced, it differs from the central plate of the mammalian ethmoid only in that it stretches outwards and upwards to meet the frontal, instead of the frontal stretching downwards, spanning the whole arch to meet it; and in that it does not project upwards in the middle line so as to divide the arch into lateral halves.

According to this view the centrum of the frontal segment always lies between the

* The posterior part of the interorbital plate appears to belong to the presphenoid, as has been pointed out by Professor HUXLEY in his Lecture "On the Theory of the Vertebrate Skull," pp. 10 & 11. See Royal Society's Proceedings, Nov. 18, 1858.

† The vomer appears, however, in the palate of even some mammalia, viz. in certain Cetacea. In *Hyperoodon* it even appears at two different places.

‡ *Op. cit.* p. 158.

orbits; and the peculiarity of its position in the mammal consists merely in this,—that by the curving downwards of the frontal and vomerine neural arches, and the curving upwards of the frontal centrum, the latter is entirely concealed by the former.

The Intermaxillaries in Reptiles and Osseous Fishes.—We now approach a most interesting series of intermaxillaries, which afford the clue to the explanation of the segment to which these bones belong. In the Crocodiles the arrangement of the intermaxillaries is like that in the mammalia, but by the great elongation of the maxillaries they are far removed from the vomerine bones. The articulation of their anterior extremities is like that in the Horse; they pass up in front of the septal cartilage and close it in. In the Chelonians the nasals are absent; and the intermaxillaries are united into a single bone, which is placed between the anterior extremities of the maxillaries, and in the Tortoise articulates with the vomer. From the Chelonians we pass to the Lizards, and in them also we find the intermaxillary single and articulating with the anterior extremities of the maxillaries; but it differs from the chelonian intermaxillary by sending upwards and backwards in the middle line a process to articulate with the nasals, which corresponds to the processes projected upwards by the intermaxillary of the bird, and which is often the most developed part of the bone. In *Varanus* and others the nasals are represented by a single bone.

In the Serpents we again meet with a single intermaxillary which articulates in the middle line with the nasals; and as it is but loosely connected with the maxillaries, and forms the anterior extremity of the line of centra, it puts one strongly in mind of the arrangement in cases of cleft-palate in the human subject.

It greatly resembles also another bone, viz. the nasal in fishes (nasal of OWEN); and the resemblance consists in this, that, like the reptilian intermaxillary, the nasal of the fish, when present, forms the anterior member of the series of centra.

Sometimes this relation of the nasal in fishes is very much disguised by the thickening of the vomer which takes place in connexion with the development of vomerine teeth,—a thickening which gives to the vomer the appearance of projecting downwards, and which often looks as if it formed the termination of the line of centra, while the extremity of the nasal appears to be situated altogether above that line. This is the case, for example, in the Cod; but when, in the fresh state, a vertical section is made through the nasal and vomer, it is seen that, not the vomer, but the extremity of the nasal bounds anteriorly the cartilaginous bar of the base of the skull (fig. 29). There is, in addition, a nodule of cartilage * attached in front of the nasal, in the Cod and many other fishes, which seems to be a portion of that bar, separated from the main part by the interruption of the nasal. But that the nasal lies in the line of centra is best seen in some of the fishes which have no vomerine teeth. It is beautifully seen in *Malapterurus*, in which the whole shape of the nasal singularly resembles the intermaxillary of *Boa* or *Python* (fig. 30).

One might well believe from its relation to the line of centra that the nasal of the fish

* Recognized as the vomer by Professor GOODSIR, *op. cit.* p. 140.

was the true intermaxillary, were it not that the bones universally acknowledged as intermaxillaries in the fish have claims to the name which cannot be set aside, inasmuch as a complete chain of forms of intermaxillaries, of which they form one link, can be traced from reptiles to fishes through the Batrachia. The position therefore which I maintain is this, that in the sclerotome formed by the nasals, intermaxillaries, and maxillaries, when the centrum is represented by a bony formation, it is derived in mammals, birds, and reptiles from the intermaxillaries, and in fishes from the nasal: the Ornithorhynchus being the only animal, as far as I know, in which it is a separate bone.

If it be repugnant to any preconceived notion to believe that the same morphological element (the centrum) can be derived in one instance from one developmental element, and in another instance from a different one in the same segment, we have only to keep in memory the exactly analogous instance of the intermaxillaries in the human subject, which usually arise from the maxillaries, and yet in certain conditions of development take origin in connexion with the septal cartilage (see above, p. 303).

To return to the series of forms of intermaxillaries in reptiles and fishes: the intermaxillaries of the Frog are two small bones articulating with one another in the middle line, and externally with the anterior extremities of the elongated maxillaries; they give off processes towards the nasals, and very slight mesial-palatine processes. Exactly in the same way do the intermaxillaries of the Salmon articulate with one another, and with the maxillaries; the only difference being that the maxillaries hang downwards instead of being directed horizontally backwards. In most fishes the intermaxillaries have superior mesial processes, which pass backwards over the nasal, and evidently correspond with the superior mesial processes in frogs, lizards, and birds. Frequently, as in the Cod, the maxillaries and intermaxillaries are so loosely connected, that the idea is given of two separate arches; but, on the other hand, it is to be remembered that not only is this looseness of connexion (considered apart from the question of development, to be afterwards noticed) no reason why they may not be members of one segment, but also that the intermaxillaries are always in contact with one another in the middle line, while the maxillaries are not so; that the arrangement is often such as has just been mentioned as existing in the Salmon; and that sometimes the maxillary and intermaxillary are even more closely soldered into one arch, of which the intermaxillary forms the proximal, the maxillary the distal part.

Morphological Conclusions respecting the Construction of the Facial Segment throughout the Vertebrata.

Ere endeavouring to discover from the above data in what precise manner the maxillaries, intermaxillaries, and nasals unite to form the facial sclerotome, it will be well to state distinctly that they cannot be considered as forming in the mammal a continuous neural ring behind the nostrils, however tempting at first sight that idea may appear; for such an hypothesis would render inexplicable the union of the intermaxillaries above the anterior extremity of the septal cartilage, which occurs in the Dugong, Tapir, &c., besides that it could not be applied to other than mammalian forms.

The real constitution of the facial segment will become evident if we consider the series of appearances assumed by it, passing upwards from the fish. In the fish the intermaxillaries and maxillaries hanging downwards form a sufficiently evident incomplete hæmal arch; while the ideal cylinder formed by the series of neural arches is brought to a close in front by the nasal, which rests, like the nasals in the other classes, upon the cartilage in connexion with which the centra are developed; and when the centrum of this sclerotome is represented by a plate of bone, it is a process of the nasal which represents it. Obviously the nostril of the fish lies behind the facial segment, for both the intermaxillaries and maxillaries lie in front of the nostril (fig. 31).

The facial segment of the Frog differs from that of the fish in that the maxillaries are directed horizontally backwards, and come in contact with bones behind; and in that the centrum of the segment is represented by a process derived, not from the nasals, but from the intermaxillaries. Further, the nasals of the Frog differ from the nasal of the fish in being expanded to protect the nostrils, like those of most reptilia, birds, and mammals. The exact signification of this expansion we shall consider anon.

The relation of the nostril of the Frog to the facial segment is the same as in the fish, but inasmuch as it communicates with the mucous surface, and this communication lies between the maxillary and the palatal, we can now see distinctly that the nostril is a passage lying between the segments to which these bones belong,—what has been named by Professor Goodsir a "metasomatomic" opening*.

In lizards, serpents, and birds the facial sclerotome is constituted as in the Frog; and the hæmal arch has still, as in the Frog, its distal extremities directed backwards instead of downwards. According to this view the superior mesial processes of the intermaxillaries are to be considered morphologically as projecting not so much upwards as backwards, and as lying above the nostrils, while the hæmal arch lies in front of the nostrils.

Lastly, in the mammalia, by the union of the palate plates of the maxillaries the hæmal arch is completed, and the ring of bone which surrounds the incisive foramina is the anterior extremity of the ideal cylinder formed by the series of hæmal arches (fig. 27). This is best conceived of by looking at this ring in the Hare or the Rabbit. There we see the single incisive foramen bounded in the middle line in front by the mesial-palatine processes of the intermaxillaries, while extending backwards from them is the hæmal arch formed by intermaxillaries and maxillaries exactly as in other classes, except that it is complete.

The fact that in certain mammals the intermaxillaries limit the anterior extremity of the septal cartilage as much as they do in birds and lizards, embracing it at a point morphologically anterior to the nostrils, appears to me to prove that this is the true explanation of the facial sclerotome in the mammalia, and that the nostrils throughout the vertebrata are intersegmental openings lying between the two most anterior segments of the skull.

* To Professor Goodsir we are also indebted for the terms "sclerotome, myotome," &c. and other additions to explicit morphological nomenclature.

If these conclusions are correct, the connexion of the nasals with the intermaxillaries and maxillaries behind the nostrils, although so constant, is of altogether secondary morphological importance. But it is undeniable that by the great extent of this connexion in mammals, and by the non-development, in most of them, of any part of the intermaxillaries above the septal cartilage, and the separation of the nasals from the intermaxillaries in the middle line, where in birds and lizards they come in contact, there is a marked attempt, so to speak, on the part of Nature to convert the nasals, intermaxillaries, and maxillaries of the mammal into a neural arch behind the nostrils. This tendency reaches its maximum in the human skull, in which the hæmal ring of the facial sclerotome has almost, if not altogether, disappeared, and the whole bulk of the elements of the hæmal arch may be said to be devoted to the formation of what we may call the pseudo-arch behind the nostrils. It may be described as an effort to open up the closed extremity of the neural cylinder, and at the same time to close the open extremity of the hæmal cylinder*.

Still, however, the morphological interpretation of the mammalian nostrils is that they are intersegmental clefts. They are similar clefts to those in which the eye and ear are developed; and the alar cartilages pass round the olfactory clefts exactly as the tarsal cartilages pass round the optic clefts, and the pinna of the ear and the tympanic bone round the auditory clefts.

Thus these structures are morphologically as well as functionally comparable; they encircle openings which pass from the dermal to the mucous surface, and which primarily lie in the transverse plane; although in Mammalia the malar, which belongs to the facial segment†, passes backwards and sends up a process behind the orbit, and, in a similar manner, the intermaxillary and maxillary send up processes behind the nostril. That these processes, however, are not situated so entirely behind the nostril as might on first thoughts be supposed, will be perceived if we take into consideration that the arch formed by the intermaxillaries and maxillaries lies in the plane of the palate, and that processes pointing upwards at right angles to that plane are therefore directed ideally backwards. Thus the nasal process of the maxillary is ideally inferior to the nostril, in the same way as we have seen that the superior mesial process of the intermaxillary of the bird or lizard is ideally superior to the nostril.

Let it not be supposed that such a structure as the trunk of the Elephant presents any obstacle to the theory of the nostrils here offered. The fusion in the middle line of structures undoubtedly lateral in their ideal position is well exemplified in cases of sympodia; and in those monsters in which the head is only developed as far forwards as the ears, the pinnæ of the ears are united at their bases, forming a short tube.

* If we take into consideration that the facial segment is the segment especially engaged in expression, I think that I shall not be considered too fanciful in saying that the gradual closing of the hæmal cylinder and opening of the neural cylinder by the disposition of the bones of the facial segment is in harmony with the increasing development of innervation from fishes up to man.

† This statement, made in passing, is illustrated by the attachment to the maxillaries alone of the largely developed malars of the Sloth family and of the vestiges of malars in *Myrmecophaga*.

With regard to the nasals: to understand the exact morphological part which is played by them, we must have recourse to embryology. The only theory of the segmentation of the skull, as far as I know, in which the teachings of embryology have been taken into account and been sought to be explained, is that of Professor GOODSIR. He is of opinion that the maxillaries are developed, not, as has been supposed, in the maxillary lobes, but in the lateral frontal processes of REICHART*; and certainly, if the maxillary lobes are homotypic with the pair of visceral laminæ behind them, this hypothesis presents the only escape from a most serious difficulty; for, while the maxillary lobe arises from behind the eye, all theories agree in representing the maxillary bone as belonging to a segment in front of the eye. But although it is with the utmost diffidence that I would express an opinion differing from Professor GOODSIR'S, I take courage to do so in the present instance, inasmuch as his view does not agree with the conclusions arrived at above from the consideration of adult forms, and because, from observations made on embryo lambs, I am convinced that embryologists have been right in considering that the maxillary bones are developed from the maxillary lobes. I believe that the true solution, and that which will be found to explain all the phenomena, is this: that the cleft between the maxillary lobe of the embryo and the lateral frontal process is not transverse in position, but longitudinal; that it does not separate an anterior from a posterior segment, but that it divides the inferior elements of more than one segment from the corresponding superior elements. It will be observed that if the maxillary bone belongs to a segment in front of the eye, and if it is really developed from the maxillary lobe, it follows as a necessary consequence that the nature of the cleft between the maxillary lobe and lateral frontal process is as now stated. For on one side of the cleft is the blastema in which the palatal and maxillary afterwards appear, while on the other side is that in which appear the frontal and nasal, and doubtless also the lateral mass of the ethmoid. Moreover, this idea of the fusion of segments by longitudinal cleft is by no means an unwarranted assumption, as may possibly be alleged. In support of it we observe,—

1st. The maxillary lobe, as it grows, runs alongside of the lateral frontal and middle frontal processes, and does not strike out at right angles to them.

2nd. The permanent severance of the pterygoid of the fish from the base of the skull is an instance of longitudinal fission of at least one sclerotome, remaining throughout life.

3rd. The hypothesis of fission of segments by longitudinal clefts is necessary to explain the peculiar condition of the elements of the face in cartilaginous fishes, if the head is to be considered as segmented at all; for no one can suppose that the upper jaw of the cartilaginous fish, and the parts which unite it to the skull, are all parts of one segment. According to my hypothesis, the condition is merely an arrestment of development; for I judge from the maxillary lobe in mammals being originally separate from the superior parts of the face, and afterwards united to them, that longitudinal fission is a symptom of degeneration at the extremity of the series of segments, which

* *Op. cit.* p. 120.

tends to disappear as the segments involved become more fully developed*. I believe, therefore, that the palatals and maxillaries combine to form the upper jaw of the cartilaginous fish (as may be seen to advantage in the Sturgeon), and that the extremity of the snout represents the intermaxillary†; and that thus, for example, the weapon borne by the Sawfish is an intermaxillary bearing teeth. Among mammals, to a certain extent similar is the arrangement in Cyclopian monsters: the nose is represented in them by a proboscis above the single eye, and the maxillary forms no superior connexion in front of the eye.

4th. Tendency to longitudinal fission of the anterior cranial segments is exhibited in the permanent duplicity, in many animals, of the vomer and of the intermaxillaries; also in the compression of the septum of the nose, and separation of the segments into two alternating sets, as above described. Moreover, the flattening at the base of the skull of the substance surrounding the chorda dorsalis, and its division into two trabeculæ where the chorda ceases, are phenomena, as it appears to me, indicating the same thing; and in this last case also the divided parts unite as development proceeds‡.

In deference to the opinions of Professor HUXLEY§, I may here state that I cannot think that the cessation of the notochord is proof of the immediate cessation of segmentation. The keenest advocate of the segmentation of the cranium will admit that in the face the segment or segments are of a degenerated description. So are those at the caudal extremity. But while in the caudal segments the arches degenerate before the centra, in the cranium the centra degenerate very soon. It is in harmony with this that the chorda dorsalis is one of the first elements to disappear in the cranial segments; while the division of the basis cranii into trabeculæ is to be accounted for in the way above shown‖.

* In this respect longitudinal and intersegmental fissures resemble one another. The parts of the embryo which are developed in immediate contact with the cavity of the ovum, and in which the great systems are fully represented, viz. the thorax and abdomen, are those in which the various tissues, the osseous, muscular, nervous, and vascular, ultimately exhibit the most complete segmentation; but it is only in the head and neck—an extremity of the embryo in which the systems are not typically developed, (and there it is only in the visceral walls, which have in the head and neck the most rudimentary development,)—that segments are for a time partially separated by fissures of the blastema. These intersegmental fissures are directly connected with the rudimentary condition of the parts which they separate, and disappear as the latter become more fully developed; and I have wished in the text to indicate that that also is the case with longitudinal fissures.

† At least that part of the intermaxillary which, as above shown, is in osseous fishes combined with the nasal.

‡ The foramen in the basioccipital of *Phoca vitulina* is doubtless a phenomenon of the same description.

§ *Op. cit.* p. 52.

‖ In justification of the plan pursued in this communication, in which the main argument is drawn from comparative anatomy and then shown to be in accordance with development, I shall here state why I cannot go so far as to concur in Professor HUXLEY's doctrine (*op. cit.* p. 5), that "the study of the gradations of structure presented by a series of living beings may have the utmost value in suggesting homologies, but the study of development alone can finally demonstrate them." Were that doctrine true, it

Conceiving, then, the development of the anterior part of the cranium to take place in the manner above stated, I consider that the nasals have the same relation to the segment to which they belong as the frontal has to its segment, inasmuch as they are continuous in position with the frontal, except in those lower vertebrata in which the prefrontals complete a well-developed intervening arch. They are more closely connected with the corresponding elements behind them than with the remaining elements of their own segment, as a natural consequence of the fission of segments. And now it will be understood how it is that the nasals are often so far sundered from the intermaxillaries: it is, that the preceding segment having a very elongated centrum (the vomer) and a very imperfect neural arch (the lateral masses of the ethmoid), the intermaxillaries are projected forwards in front of the vomer, while the nasals cling behind to the frontals.

With respect to the expanded form of the nasals in many reptiles, in birds, and in mammals, I apprehend that they are not to be considered as spreading downwards to form an imperfect arch of the neural series, but as spreading outwards to protect two intersegmental passages; for it is the nostrils, and not, in any sense, a continuation of the cranial cavity, which they protect. This will be best understood by looking at the Frog's skull, in which the osseous cranial cavity is closed-in at the fore part of the prefrontals, and the neural arch of the segment in front is reduced to zero, the position where it exists in certain fishes being represented in the Frog by the line of junction of the nasals with one another and with the mesial cartilage below; while the expansions of the nasals over the nostrils are like the projections outwards of two transverse processes, and are strictly similar to those elongated projections of the frontals which roof-in

would be impossible finally to demonstrate the correspondence of any two structures in different animals, since we do not see one developed out of the other. But, on the contrary, there is a vast number of such correspondences so plainly obvious as to need no demonstration. That which makes these correspondences so evident is simply the comparison of the bones; and it is the business of the anatomist, in cases of correspondence less obvious, to submit the structures which he compares to a careful scrutiny, until, by minute examination of their relations, and determining what is constant and what is variable, he is able to give a certain judgment upon points which appear to the uninitiated eye obscure. But if the prosecution of such researches renders certain the correspondence of a number of elements in different animals, will not the light thrown by the varied relations of these elements upon the laws which regulate their arrangement furnish as certain and secure data on which to build as can be obtained from the use of any scientific instrument whatever? It has not been the instruments used, but the manner in which they have been handled, that has led to the discrepancies of morphological theories. I have an interest to insist on this matter, because it is impossible that the questions discussed in the present communication can be settled by embryological evidence, for these reasons: viz. the maximum segmentation of the cranium is found, not in the embryo, but at the period of most characteristic development of the bones composing it; and the whole history of the sclerotomes to whose elucidation this communication is devoted is not given in any single species; but, on the contrary, were we to search in the mammal for the stages illustrated in the structure of fishes, we should find that at the period at which these stages would fall due to be represented, there is as yet no differentiation of tissues, and the osseous system whose history we seek to trace has not begun to appear.

the orbits in Whales. In other animals the arrangement is perhaps not so distinct, and there may be a difficulty, especially in mammals, to determine if the nasals do not, in part, at least, form a continuation of the roof of the cranial cavity; for in them the neural arch of the ethmoidal sclerotome is, as we have seen, a continuation of that cavity, and is open in front. But, inasmuch as in the mammal the olfactory-sense capsules are withdrawn into the interior of the ethmoidal neural arch, the cranial cavity is closed in by soft parts at a point posterior to the nasals; and I therefore incline to think that the nasals, protecting in this, as in other cases, the nostrils, are, like those of the Frog, similar in nature to the orbital processes of the cetacean frontals.

NOTE.—Since writing the above, I have deemed that it would be advisable to add here some further details as to the morphological structure of the cranium in the mammal, even though it is impossible in this place to give the arguments on which these details are founded. The descending process of the occipital bone, the mastoid, the squamous, the external angular process of the frontal, and the lacrymal are serially corresponding structures, belonging respectively to the occipital, petrous, parietal, frontal, and ethmovomerine segments, and tending to project from their neural arches. There are no hæmal arches in connexion with the protective segments. Into the composition of the hæmal arch of the petrous segment enter the styloid processes, the stylohyoid ligaments, and the small cornua of the hyoid; while the great cornua of the hyoid belong not only to a segment behind, but to the true splanchnic skeleton; that is to say, to the series of sclerous structures internal to the primary vascular arches, and which are best developed in the branchial arches of fishes. The other hæmal arches are, as has been stated, the pterygoid, palatal, and maxillary, belonging respectively to the presphenoid, ethmovomerine, and facial segments. The maxillary arch, having assumed in the mammal as much as possible the aspect of a neural arch, as has been above explained, although in reality hæmal, has a bone radiating from it—the malar, which tends to form connexions with the bones radiating from the neural arches behind, viz. with the lacrymal, external angular process of the frontals, and the squamous. The lower jaw is not a hæmal arch at all; that is to say, it is not an arch belonging to a single segment and corresponding to the palate-bones, or to a pair of ribs, but is a limb-arch. For I hold that Professor GOODSIR has distinctly shown that the shoulder-girdle and pelvic girdle are not rib-arches, and that limbs do not belong merely to single segments; but seeing, on the other hand, that these girdles pursue an arched direction, I conceive that they are to be considered as arches external to the series of rib-arches, and supporting radiations, just as rib-arches sometimes do. Such a limb-arch is the lower jaw; but the visceral laminæ being very imperfect in the head, it is intimately connected with arches bounding the hæmal cavity. In the fish it supports extensive radiations, viz. the opercular apparatus, but in the mammal it bears no radiations. The quadrate jugal in the bird has every appearance of being a radiation homologous to the operculum; for not the quadrate jugal, but the bone called mastoid by Professor Owen, corresponds to the mammalian squamous. The quadrate bone of the bird has been abundantly proved to correspond to the incus of the mammal. The elements of the limb-arch are the incus, malleus, and lower jaw; and its superior member, the incus, is, throughout the vertebrate series, connected with the mastoid and squamous bones. As for the stapes, it is a radiation of the petrous sclerotome, and corresponds to the structure which supports the eye of the Shark, and to the ethmoidal turbinations in the presphenoidal and ethmovomerine sclerotomes. While, on the one hand, the rib-arches belong to the individual segments of the body, on the other there are three limb-arches, corresponding to the three great regions of the body: one for the head—the region in which the highest development of organs of animal life takes place; one for the cervical region—the region in which is the highest development of the vascular organs; and one for the abdomen—the region in which the greatest development is found of organs of vegetable life.

Explanation of the Plates.

PLATES IV. & V.

Fig. 1. Bones from specimen referred to in the text as No. 1.

A. The vomer, ethmoid, sphenoidal spongy bones, and left palate and maxillary bones, from the skull of an infant, slightly enlarged, and viewed from behind:—*a*, orbital plate of the ethmoid; *b*, posterior extremity of the vomer; *c*, sphenoidal process of the palate-bone; *d*, orbital surface of the palate-bone, and, immediately above it, the orbital portion of the sphenoidal spongy bone: between the two processes of the palate-bone is the spheno-palatine foramen, completed above by the inferior portion of the sphenoidal spongy bone: *e*, the superior portion of the sphenoidal spongy bone; *f*, inferior portion.

B. Another view taken from the same specimen:—*a*, *b*, *c*, the parts of the inferior margin of the vomer which articulate with the palate, maxillary, and intermaxillary bones respectively; *d*, inferior aspect of the sphenoidal spongy bone; *e*, orbital plate of the ethmoid, seen in perspective; *f*, inferior turbinated process of the ethmoid.

Fig. 2. Bones from specimen referred to in the text as No. 2.

A. Ethmoid, with sphenoidal spongy bones attached:—*a*, cribriform plate; *b*, os planum; *c*, superior portions of the sphenoidal spongy bones, with space between them for the body of the presphenoid; *e*, *e*, orbital portions; *f*, *f*, inferior portions.

B. Sphenoid:—*a*, body of postsphenoid; *b*, body of presphenoid.

Fig. 3. Bones from specimen referred to in the text as No. 3.

A:—*a*, part of the orbital plate of the frontal; *b*, os planum; *c*, presphenoid;

d, external pterygoid plate; *e*, palate-bone; *f*, orbital surface of sphenoidal spongy bone; *g*, the space between the orbital and sphenoidal processes of the palate-bone, bridged over by the sphenoidal spongy bone.

B and C. Left sphenoidal spongy bone; viewed in B from its external, and in C from its superior aspect:—*a*, superior portion; *b*, orbital portion; *c*, inferior portion.

Fig. 4. A. Vomer, with the portions of the palate, maxillary, and intermaxillary bones with which it was articulated:—*a*, the process which rests upon the intermaxillaries; *b*, the process which descends behind the intermaxillaries.

B. Vomer from a fœtus:—*a*, *b*, *c*, the margins for articulation with the palate, maxillary, and intermaxillary bones respectively.

Fig. 5. Diagram of the vomer, ethmoid, and sphenoidal spongy bones of the human subject, with the vomer and ethmoid of the Sheep represented in dotted lines. The superior edge *a* of the human ethmoid corresponds to the edge a' of the Sheep's ethmoid; while *c* is the sphenoidal spongy bone rendered necessary in the human subject to fill up the space between b' and *b*.

Fig. 6. A. Posterior extremity of the vomer in the Orang.

B. The same in the Chimpanzee.

C. The same in the Gorilla.

Fig. 7. Bones from the Cat.

A. Vomer and ethmoid seen from below:—*a*, margin of vomer for articulation with the maxillaries; *b*, *b*, ethmovomerine laminæ.

B and C. Views of the presphenoid from the front and from behind.

D. Portion of base of skull of a new-born kitten:—*a*, intermaxillaries; *b*, vomer; *c*, presphenoidal centrum; *d*, postsphenoidal centrum; *e*, basioccipital; *f*, ethmoidal turbinations; *g*, pterygoid; *h*, tympanic.

Fig. 8. Vomer and ethmoid of the Fox:—*a*, ethmovomerine laminæ; *b*, margin of vomer for articulation with the maxillaries and palatals; *c*, margin for articulation with the intermaxillaries; *d*, groove corresponding to the upper part of the nasal foramen of the palate-bone.

Fig. 9. Intermaxillaries of *Ursus maritimus*.

A. Inferior aspect.

B. Superior aspect:—*a*, maxillary; *b*, mesial-palatine process of intermaxillary; *c*, incisive foramen; *d*, foramen peculiarly ursine; *e*, vomer.

Fig. 10. Vomer and ethmoid of *Phoca vitulina*:—*a*, vomerine groove; *b*, lateral mass of the ethmoid; *c*, central plate; *d*, expanded superior margin of central plate.

Fig. 11. Part of the skull of the Hedgehog:—*a*, frontal; *b*, nasals; *c*, left intermaxillary; *d*, vomer, with right ethmovomerine lamina removed; *e*, flat inferior margin of the central plate of the ethmoid; *f*, presphenoid; *g*, groove on the left ethmovomerine lamina corresponding to the nasal foramen of the palate-bone.

Fig. 12. The vomer and lateral masses of the ethmoid of the Lamb, seen from below:— *a*, the inferior margin of the vomer, rough posteriorly for articulation with the maxillaries, and smooth anteriorly where it comes in contact with the intermaxillaries; *b*, *b*, the grooves which complete the nasal foramina of the palate-bones. The spaces between these grooves and the margins of the vomer represent the ethmovomerine laminæ; and on the outer aspects of the grooves are the small orbital surfaces of the ethmoid.

Fig. 13. Intermaxillaries of the Sheep:—*a*, *a*, incisive foramina; *b*, *b*, portions of the maxillaries; *c*, space for the anterior extremity of the septal cartilage.

Fig. 14. Intermaxillaries of the Alpaca. Letters as in fig. 13.

Fig. 15. Intermaxillaries of the Giraffe. Letters as in fig. 13.

Fig. 16. Part of the skull of the Horse:—*a*, vomer (the anterior half removed); *b*, part of the palate-bone; *c*, part of the pterygoid; *d*, ethmovomerine lamina; *e*, nasal foramen of the palate-bone.

Fig. 17. Section of the fore part of the skull of the Horse:—*a*, fore part of the vomer, resting on the maxillaries, and articulating in front with the intermaxillaries; *b*, incisive foramen; *c*, cul-de-sac for the anterior extremity of the septal cartilage.

Fig. 18. Vomer, &c. from the skull of the sucking Pig:—*a*, presphenoid; *b*, portion of the vomer which rests on the intermaxillaries; *c*, ethmovomerine lamina and part of the ethmoid; *d*, various distinct ossifications belonging to the ethmoid.

Fig. 19. Vomer, &c. of the young Elephant:—*a*, *b*, surfaces by which the intermaxillary and maxillary come in contact with their fellows of the opposite side; *c*, incisive foramen; *d*, *e*, processes of the vomer, by which its inferior and superior margins are made continuous with the corresponding margins of the intermaxillaries.

Fig. 20. Anterior nares of the Tapir:—*a*, vomer; *b*, maxillary; *c*, palate-plate of maxillary; *d*, intermaxillary; *e*, foramen corresponding to both incisive foramina and the space for the point of the septal cartilage in the Camel &c.; *f*, lateral mass of the ethmoid; *g*, expanded superior margin of the central plate of the ethmoid; *h*, united nasals.

Fig. 21. Part of the skull of *Cœlogenys*:—*a*, *b*, mesial borders of the maxillary and intermaxillary; *c*, vomer.

Fig. 22. View of the articulations of the vomer in the Rabbit. Above are the vomer and ethmoid forming one bone. Beneath are the bones of the upper jaw of the left side, and a portion of the intermaxillary of the right side adherent:— *a*, anterior extremity of the vomer grooved for the cartilaginous septum of the nose; *b*, the part of the vomer which articulates with *c*, the extremity of the expanded mesial processes of the intermaxillaries forming turbinations in connexion with JACOBSON'S organ.

Fig. 23. Part of the skull of the Kangaroo:—*a*, presphenoid; *b*, frontal; *c*, ethmovome-

rine lamina; *d*, nasals; *e*, central plate of the ethmoid; *f*, lateral ridge of the vomer peculiar to marsupiate animals.

Fig. 24. Part of the skull of the Dugong:—*a*, frontal; *b*, intermaxillary; *c*, vomer; *d*, maxillary; *e*, *e*, palatals; *f*, *f*, ethmovomerine laminæ and lateral masses of the ethmoid.

Fig. 25. Section of skull of *Delphinus orca*:—*a*, intermaxillary; *b*, maxillary; *c*, *c*, vomer; *d*, palatal; *e*, central plate of the ethmoid.

Fig. 26. Skull of *Delphinus globiceps* from above:—*a*, intermaxillary; *b*, *b*, maxillary; *c*, palatal; *d*, pterygoid; *e*, nasal foramen of palate-bone; *f*, central plate of the ethmoid; *g*, expansion of the ala of the vomer; *h*, the part of the frontal which would have been concealed by the nasal, had not that bone been removed.

Fig. 27. Diagram of the two most anterior segments of the mammalian skull, and of the neural arches of the other segments. The dotted part represents the extent of the septal cartilage. The centra are darkened. Two dotted lines and arrowheads show the direction of the anterior hæmal arches:—*a*, occipital segment; *b*, auditory segment; *c*, sphenoparietal segment; *d*, optic segment; *e*, frontal bone; *f*, central plate of the ethmoid; *g*, lateral mass of the ethmoid; *h*, vomer; *i*, palatal; *k*, nasal; *m*, intermaxillary; *n*, maxillary.

Fig. 28. Vomer and palatals of the Duck, viewed from above.

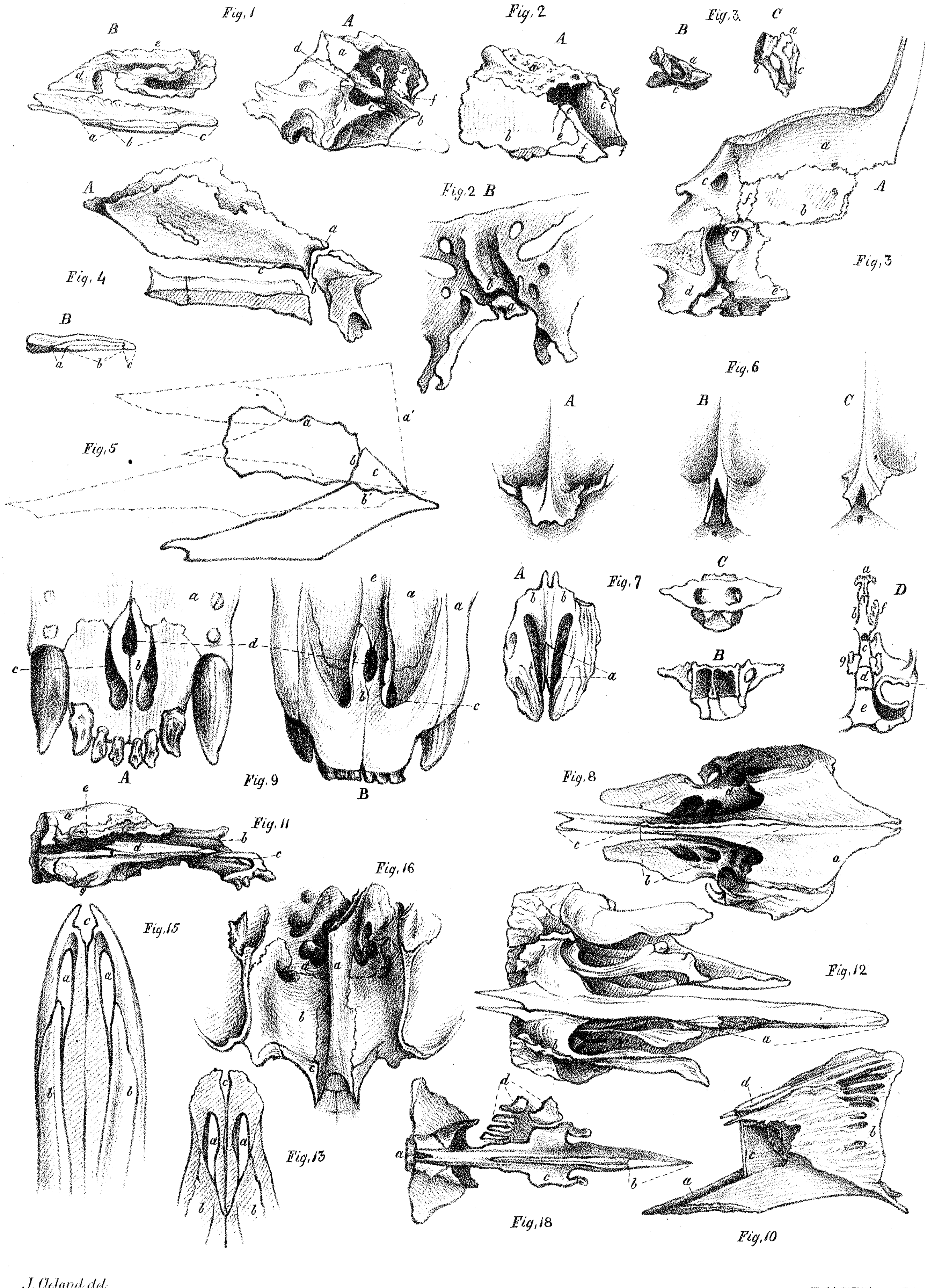
Fig. 29. A. Section of the skull of the Cod. The cranial cavity is represented dark; the cut surfaces of bones are marked with oblique lines, and the cartilages are left white, while the interorbital septum is dotted:—*a*, intermaxillary; *b*, vomer; *c*, basisphenoid; *d*, basioccipital; *e*, nasal; *f*, frontal; *g*, supra-occipital.

B. A similar section through the nasal and vomer, after the cartilage has been removed:—*b*, vomer; *e*, nasal; *h*, prefrontal.

Fig. 30. A. Intermaxillary and vomer of *Python*:—*a*, intermaxillary; *b*, vomer.

B. Nasal and vomer of *Malapterurus*:—*a*, nasal; *b*, vomer.

Fig. 31. Diagram of the two most anterior segments of the skull of the fish:—*a*, prefrontal; *b*, vomer; *c*, palatal; *d*, nasal; *e*, intermaxillary; *f*, maxillary; *g*, a dotted circle indicating the position of the nostril. The centra are darkened. The dotted lines and arrowheads show the direction of the hæmal arches.



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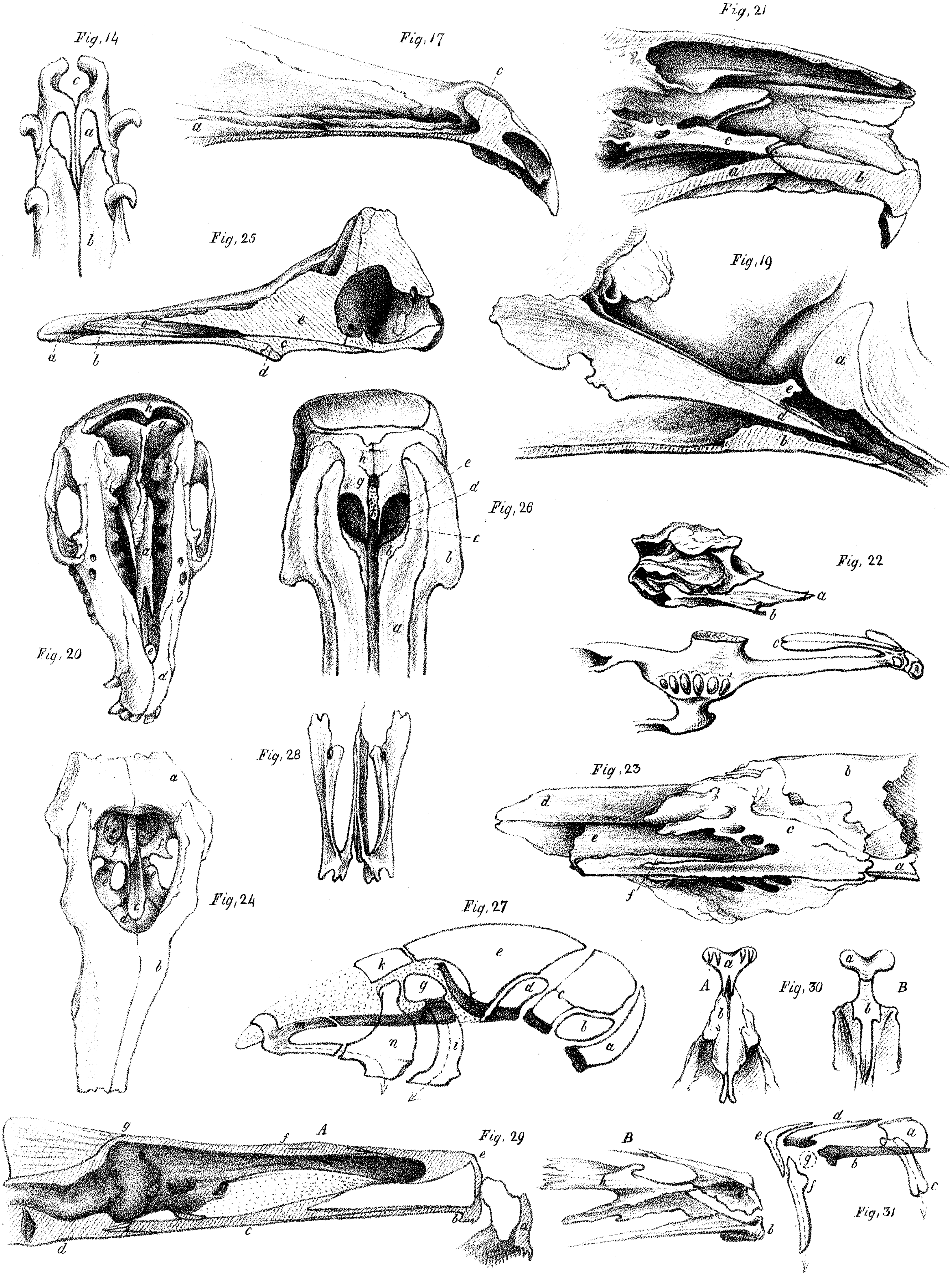

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