CHAPTER II.—Order CROCODILIA.

CROCODILES, ALLIGATORS, GAVIALS.

Of the numerous and various kinds of Reptiles, the fossil remains of which have been discovered in the tertiary and secondary strata of Great Britain, many are found to have their nearest representatives, amongst the actual members of the class, in the present order; and here more particularly in the long and narrow-snouted genus called, through a corrupt latinization of its native name, Gavialis, which is now represented by the Gavial or, more properly, Garrhial, of the river Ganges.

In the interpretation of the fossil remains of Reptiles, no skeleton has more frequently to be referred to than that of the Gavial or Crocodile, or has thrown more light on the nature of those singularly-modified forms of the class which have long since passed away.

It is accordingly requisite for the palaeontologist who would describe the fossil remains of reptiles, to make himself, in the first place, thoroughly conversant with the osteology of the recent Crocodilia. This knowledge can be gained only by assiduous study of the skeletons themselves, with the aid of the best descriptions, or the guide of a competent teacher. But to enable the reader to follow or comprehend the description of the fossil Saurians, some elementary account of the Crocodilian skeleton is at least necessary, accompanied with illustrations of the parts which, in the sequel, will have to be frequently referred to under special or technical names.

In Pl. 1 (Crocodilia) is given a reduced or miniature side view of the skeleton of a Gavial which was twenty-five feet in length—dimensions which are rarely found to be surpassed in the present day. Beneath it is a restoration of the skeleton of the Telcosaur, or extinct Gavial of the Triassic or Oolitic period, showing how closely the general type of conformation has been adhered to, the modifications of the more ancient form of Crocodile evidently adapting it for moving with greater speed and facility through the water, and indicating it to have been more strictly aquatic, and probably marine.

The particular nature of these modifications will be explained when I come to describe the Crocodiles of the secondary strata. I propose at present to give a preliminary sketch of the osteology of the recent Crocodilia.

A glance at a natural or well-articulated skeleton of one of these reptiles, such as
is figured in Pl. 1, will show that it consists mainly of a series of segments, more or less alike. From the back of the head to the end of the tail, the chief part of each segment consists of a cylindrical portion or 'body,' differing only in its proportions, and diminishing as it recedes from the trunk. Every segment sends a plate of bone upwards from its upper or dorsal surface, which plate or 'spine' is supported by an arch of bone, except in the diminishing segments at the end of the tail.

Other plates of bone, of more variable forms and dimensions, project from each side of the segments of the trunk and basal part of the tail. In a less proportion, but still in a great number of the segments, an arch of bone is formed below, or on the ventral side of the cylindrical body; but this lower arch is more variable in its proportions and mode of composition than the upper arch: it is open or incomplete in the neck. Under all these variations, however, there is plainly manifested a fundamental unity of plan in the composition of the different segments, which have accordingly received the common appellation of 'vertebra.'

For the convenience of description, the vertebrae are divided, though somewhat arbitrarily, into groups bearing special or specific names. Those next the head, with the inferior arch incomplete below, are called 'cervical vertebrae;' they are usually nine in number: those that follow with the inferior arch closed below, or which have the laterally projecting parts slender and freely moveable, are called 'dorsal vertebrae;' the other vertebrae of the trunk that have no lateral moveable appendages, are called 'lumbar vertebrae;' the last vertebrae of the trunk, always two in number in the Crocodilia, the inferior arches of which coalesce to support and be supported by the hind limbs, are the 'sacral vertebrae;' the segments of the tail are the 'coccygeal,' or 'caudal vertebrae,' whether they possess or not an inferior arch, or whatever other modifications they may offer.

These names, 'cervical,' 'dorsal,' 'lumbar,' 'sacral,' 'coccygeal,' were originally applied to corresponding segments or vertebrae in the human skeleton, from the study of which the nomenclature of osteology takes its date: it may well be supposed, therefore, that a classification and designation of vertebrae based upon knowledge limited to their characters in a single example of the vertebrated series, and that example one in which the common type has been most departed from, to adapt it to the peculiar attitude and powers of the human species, would fall far short of what is required to express the general ideas derived from a comparison of all the leading modifications of the vertebrate skeleton; and accordingly the anatomist who passes from a previous acquaintance with human osteology only, to the study of those of the lower Vertebrata, finds that he has to rectify, in the first place, the erroneous notions which anthropotomy has taught him of the nature of the primary segment of his own and other vertebrated skeletons, and to acquire true ideas, with the concomitant nomenclature, of the essential constituents or anatomical elements of such segment.

In human anatomy, for example, the costal elements are only recognised when they
retain throughout life that distinctness, or moveable union with the rest of their segment, which they manifest at their first appearance; and they are then classified as distinct bones from the rest of their segment, to which the term 'vertebra' is restricted, and which is equally regarded as a single bone; as, e. g., in the dorsal region of the skeleton. In the cervical region the whole segment is called 'vertebra,' and is recognised as the equivalent bone to a dorsal vertebra, although it includes the costal elements, because these have coalesced with the rest of their segment, which ankylosis is misinterpreted as a mere modification of a transverse process; and the 'cervical vertebra' is distinguished by having that process 'perforated,' and not entire as in the other vertebrae.

But, in the Crocodile, the embryonic condition of the cervical ribs in Man is retained throughout life; and, therefore, if we were to be guided by the characters laid down by the recognised authorities in anthropotomy for the classification of its vertebrae, we should seek in vain for any vertebrae with "transverse processes perforated for the transmission of vertebral arteries," whilst we should find all the vertebrae from the head to the loins, "with articular surfaces, either on their sides or their transverse processes, where they join with ribs," and should accordingly have to reckon these as "dorsal vertebrae."

These and many similar instances which might be adduced, have compelled me to premise a few brief explanations of the principles and nomenclature by which I shall describe the fossil remains of the Reptilia, and illustrate their nature by reference to the skeletons of their existing representatives, in the present Work.

The primary segment of the skeleton of all Vertebrata is a natural group of bones, which may be severally recognised and defined under all the modifications to which such segment may have been subjected in subservient adaptation to the habits and exigencies of a particular species.

A view of such a segment, as it exists in the thorax of the crocodile, the tortoise, and the bird, is given at p. 5.

The part marked e is the 'centrum,' or body of the vertebral segment; it is always developed originally as a separate element, and retains its character of individuality in the tortoise and crocodile. The bony arch above the centrum was formed originally by two distinct side-plates,—the 'neurapophyses,' n, which coalesce with one another at their summits and thence develope a median plate or process of bone called the 'neural spine' ns. Other bony processes which shoot out from the neurapophyses are more variable, and will be afterwards noticed. The arch so formed coalesces with the centrum in the bird, and constitutes an apparently single bone, to which, in anthropotomy, the name 'vertebra' would be restricted. But it would be as reasonable to confine it to the central element (e) in the tortoise and crocodile; for the parts of the inferior arch are not less essentially parts of the same natural segment, than the neurapophyses which have formed the upper arch. The next pair of elements,
then, which we have to notice, is marked in figs. 4, 5, and 6, pl., signifying 'pleurapophysis,' the name of these elements. In the segments figured they retain their primitive distinctness, and acquire unusual length, in order to aid in encompassing the dilated canal or cavity for the heart and lungs; so modified, these elements are commonly called 'ribs,' or 'vertebral ribs.'

The elements more constantly employed to protect the vascular or 'haemal' axis, in other words, to form the inferior or haemal canal, are those marked k in figs. 4 and 6; they are the 'haemapophyses,' which are usually articulated, like the neurapophyses, with the centrum, but are displaced by the great centres of the vascular system in the thorax, where they have got the special name of 'sternal ribs,' and also that of 'costal cartilages,' or 'cartilages of the ribs,' when they do not become ossified. The haemal arch in the thorax is usually completed by a median element (ks), called a 'haemal spine,' but which itself becomes vastly expanded in the bird (fig. 4); it is, nevertheless, the part in the haemal arch which repeats below, or answers to the part (ns) in the upper arch. In the segments of the trunk and tail, the element (ns) retains its normal size and form as a 'neural spine'; but where the central axis of the nervous system becomes unusually developed, as in the head, e. g., analogous to the development of the vascular centres in the chest, the neural canal is correspondingly expanded, and the cavity acquires a special name, and is called 'cranium,' just as the analogously expanded haemal canal is called 'thorax.' Into the formation of the wall of the cranium other vertebral elements enter besides the neurapophyses, those e. g. which are numbered 8 and 12 in figs. 10 and 11; the neural spine (7 and 11 in the same figures) retains its primitive distinctness, is expanded horizontally, and, like the 'sternum' in the thorax of the bird (ks, fig. 4, p. 5), it receives a special name, e. g. 'parietal' in fig. 10, and 'frontal' in fig. 11. The elements aa (figs. 4 and 6) form a symmetrical pair of bones or cartilages, attached at one end to the haemal arch, and projecting outwards and backwards. These are the 'prosartemata,' or appendages; they are, of all the elements of the vertebral segment, those that are least constant in regard to their presence, and, when present, are subject to the greatest amount of development and metamorphosis: they become, e. g., the opercular bones in the frontal segment of the fish; the branchiostegial rays in the parietal segment; and the pectoral fins in the occipital segment, and they are developed into the fore limbs and hind limbs, the arms, wings, and legs of other Vertebrata.*

As the nervous and vascular centres become reduced in size, the bony canals or arches protecting them are simplified and contracted, and the vertebra assumes a symmetrical character. In the Crocodile, the haemal arch, in the tail, e. g., is formed by the haemapophyses, which ascend and articulate directly with the centrum; the pleurapophyses are shortened, directed outwards, and become anchylosed to

* The facts and arguments in support of this conclusion, are detailed in my works 'On the Nature of Limbs,' and 'On the Archetype of the Vertebrate Skeleton,' 8vo (Van Voorst).
form ‘transverse processes;’ but such a vertebra, when analysed as it is developed, resolves itself very nearly into the ideal type given in the subjoined diagrammatic cut (fig. 7); \( n \) is the neural axis, called ‘myelon,’ or ‘spinal marrow;’ \( h \) is the \( \text{hæmal} \) axis, the chief trunk of which is called ‘aorta,’ and ‘caudal artery.’ The names of the vertebral elements which, being usually developed from distinct centres, are called ‘autogenous,’ are printed in Roman type; the italics denote the ‘exogenous’ parts, more properly called ‘processes,’ which shoot out from the preceding elements.

On comparing this form of the primary segment with that figured in Cut 4, p. 5, it will be seen that they differ by altered proportions with some change of position of certain elements; but every modification resulting in the various forms of the parts of the skeleton figured in Pl. 1, has its seat in one or other of the segmental or ‘vertebral’ elements above defined; and the same principle I believe that I have established with regard to the internal skeleton in all vertebrate animals.

With this preliminary explanation, the nature and relations to the typical vertebra of the parts of the Crocodilian vertebrae, figured in Plates 1, 2, will be, it is hoped, readily appreciated. In Plate 1, in which are figured some of the most perfectly-preserved fossil reptilian vertebrae which have hitherto been discovered, the elements and processes are indicated by the initial letter of their names. Figs. 1 and 2 give a side view and a back view of a cervical vertebra, apparently the fourth, of the Crocodilus Hastingsiae, from the Eocene deposits at Hordwell; \( c \) is the centrum, \( n \) the neural canal formed by the neurapophyses, which have coalesced superiorly with each other, and with the neural spine (\( ns \)). Inferiorly they articulate by a suture (which is shown by the wavy line on each side of the process \( d \) in fig. 1) with the centrum; \( pl \) is the pleurapophysis, which articulates by two parts, the lower one called the ‘head’ to the process from the centrum, the upper one called the ‘tubercle’ to the process from the neurapophysis; beyond the union of the head and tubercle, the pleurapophysis projects freely outwards and downwards, but instead of being elongated in that direction, it becomes expanded in the direction of the axis of the body, i.e. forwards and backwards, and so acquires a shape which has given rise to the name ‘hatchet bone’ or ‘hatchet-shaped process,’ * applied to this element in the Plesiosaurus.

* “To compensate for the weakness that would have attended this great elongation of the neck, the Plesiosaurus had an addition of a series of hatchet-shaped processes on each side of the lower part of the cervical vertebra.” (Buckland, Bridgewater Treatise, vol. i, p. 206, and vol. ii, p. 30, 1836.)

Cuvier recognised in these lateral bones, “en forme de hache,” the homologues of the “petites côtes cervicales” of the Crocodile. (Ossemens Fossiles, 4to, tom. v, pt. ii, p. 479, 1824.) And Conybeare had
The purport of this modification is the same in the *Crocodilia* as that which seems to be more called for in the *Plesiosaurus*, viz. to augment the strength of the cervical region of the skeleton; and this is so effectually done by the overlapping of the hatchet-shaped ribs of this region in the *Crocodilia*, as shown in Plate 1, that the flexibility of the neck is much restricted, although the joint of the head allows that part to be bent from side to side at nearly right angles with the neck. When, however, the head is held firmly forwards by its powerful muscles, the imbricated vertebrae of the neck transmit with great effect the impulse which the strong and long tail gives to the rest of the body in the act of swimming.

In fig. 3 the cervical vertebra is represented minus its pleurapophyses, and it answers accordingly to that portion of the natural segment to which the term ‘vertebra’ is usually restricted in the dorsal region of the trunk. The exogenous processes shown in this view of the vertebra are, $p$, the ‘parapophysis’ or inferior transverse process, developed from the centrum; $d$, the ‘diapophysis’ or upper transverse process developed, as in most cases it is, from the neurapophysis; $z, z'$, are the ‘zygapophyses’ or ‘oblique processes,’ which, from their function in articulating together contiguous vertebrae, are also called ‘articular processes.’ In most of the cervical, and in some of the dorsal, vertebrae of the Crocodile, an exogenous process is developed from the under surface of the centrum, called ‘hypapophysis;’ it is indicated by the letters $hy$ in fig. 2. In some species it is double,* and beneath the atlas it becomes ‘autogenous’ or is developed as a separate element, $ca, ex$, fig. 8, in which condition the part is found beneath the centra of two or three of the anterior cervical vertebrae in the Ichthyosaurus.†

The first and second vertebrae of the neck are peculiarly modified in most air-breathing Vertebrata, and have accordingly received the special names, the one of ‘atlas,’ the other of ‘axis.’ In Comparative Anatomy these become arbitrary terms, the properties being soon lost which suggested those names to the human anatomist; the ‘atlas’ e.g. has no power of rotation upon the ‘axis’ in the Crocodile, and it is only in the upright skeleton of man that the large globular head is sustained upon the shoulder-like processes of the ‘atlas.’ In the Crocodile, these vertebrae are concealed by the peculiarly prolonged angle of the lower jaw in the side view of the skeleton in Plate 1, and a woodcut of the two vertebrae is therefore subjoined. The pleurapophyses are previously extended the same homology to the “particularly prominent wing-like appendages to the transverse processes in many of the long-necked quadrupeds, and the long styloid processes of the cervical vertebra of birds.” (See his admirable Memoir of June 14th, 1822, in the Geol. Trans., 2d series, vol. i, p. 384.)

* In *Crocodilus banifissus*, e.g., see the Quarterly Journal of the Geological Society, November 1849, p. 381, pl. x, fig. 2.

† This interesting discovery was communicated by its author, Sir Philip de M. Grey Egerton, Bart., to the Geological Society of London, in 1836, and is published in the fifth volume of the second series of their Transactions, p. 187, pl. 14.
retained in both segments, as in all the other vertebrae of the trunk. That of the atlas, fig. 8, pl. a, is a simple slender style, articulated by the head only, to the independently developed inferior part of the centrum, or 'hypapophysis' (ca, ex). The neurapophyses (na) of the atlas retain their primitive distinctness; each rests in part upon the proper body of the atlas (ca), in part upon the hypapophysis. The neural spine (ns, a) is also here an independent part, and rests upon the upper extremities of the neurapophyses. It is broad and flat, and prepares us for the further metamorphosis of the corresponding element in the cranial vertebrae.

The centrum of the atlas (ca), called the odontoid process of the axis in Human Anatomy, here supports the abnormally-advanced rib of the axis vertebra, which in some Crocodilia is articulated by a bifurcate extremity, like the ribs of the succeeding cervical vertebrae; but it is not expanded or hatchet-shaped at the free extremity. The proper centrum of the axis vertebra (cx) is the only one in the cervical series which does not support a rib; it articulates by suture with its neurapophyses (nx), and is characterised by having its anterior surface flat, and its posterior one convex.

With the exception of the two sacral vertebrae, the bodies of which have one articular surface flat and the other concave, and of the first caudal vertebra, the body of which has both articular surfaces convex, the bodies of all the vertebrae beyond the axis have the anterior articular surface concave, and the posterior one convex, and articulate with one another by ball-and-socket joints. This type of vertebra, which I have termed 'procoelian,'* characterises all the existing genera and species of the family Crocodilia, with all the extinct species of the tertiary periods, and also two extinct species of the Greensand formation in New Jersey.† Here, so far as our present knowledge extends, the type was lost, and other dispositions of the articular surfaces of the centrum occur in the vertebrae of the Crocodilia of the older secondary formations. The only known Crocodilian genus of the periods antecedent to the Chalk and Greensand deposits with vertebrae articulated together by ball-and-socket joints, have the position of the cup and the ball the reverse of that in the modern Crocodiles, and the genus, thus characterised by vertebrae of the 'opisthocoelian' type, has accordingly been termed Streptospondylus, signifying 'vertebrae reversed.' The aspects of the zygapophyses are, however, more constant; the anterior ones, pl. 1 D, fig. 3 z, look obliquely inwards; the posterior ones, ib. z', obliquely outwards. In a vertical section, therefore, of a Crocodilian vertebra, such as is figured in pl. 4, fig. 3, the smooth, flattened inner surface of the anterior zygapophysis is turned towards the observer, and the convex outer surface of the posterior zygapophysis. Thus the anterior and posterior extremity of the vertebra being determined by observation of the aspect and direction of the zygapophyses, it is at once seen whether the body has the procoelian structure, as in pl. 4, fig. 3, or the opisthocoelian structure, as in fig. 4. But the most prevalent type

* Πρός, before; κολός, concave.
† Quarterly Journal of the Geological Society, November 1849.
of vertebra amongst the Crocodilia of the secondary periods was that in which both articular surfaces of the centrum were concave, but in a less degree than in the single concave surface of the vertebrae united by ball and socket. A section of a vertebra of this 'amphicoelian' type, such as existed in the Teleosaurus and Stenocerasaurus, is figured in Pl. 4, fig. 6. In the Ichthyosaurus, the concave surfaces are usually deepened to the extent and in the form shown in fig. 7. Some of the most gigantic of the Crocodilia of the secondary strata had one end of the vertebral centrum flattened, and the other (hinder) end concave; this 'platycoelian' type we find in the dorsal and caudal vertebrae of the gigantic Cetiosaurus (Pl. 4, fig. 5).

With a few exceptions, all the modern Reptiles of the order Lacertilia have the same procoelian type of vertebrae as the modern Crocodilia, and the same structure prevailed as far back as the period of the Mosasaurus, and in some smaller members of the Lacertilian order in the Cretaceous and Wealden epochs.

Resuming the special description of the osteology of the modern Crocodilia, we find the procoelian type of centrum established in the third cervical, which is shorter but broader than the second; a parapophysis is developed from the side of the centrum, and a diapophysis from the base of the neural arch; the pleurapophysis is shorter, its fixed extremity is bifid, articulating to the two above-named processes; its free extremity expands, and its anterior angle is directed forwards to abut against the inner surface of the extremity of the rib of both the axis and atlas, whilst its posterior prolongation overlaps the rib of the fourth vertebra.

The same general characters and imbricated coadaptation of the ribs characterise the succeeding cervical vertebrae to the seventh inclusive, the hypapophysis (hy, fig. 2, Pl. 1 D) progressively though slightly increasing in size. In the eighth cervical the rib becomes elongated and slender; the anterior angle is almost or quite suppressed, and the posterior one more developed and produced more downwards, so as to form the body of the rib, which terminates, however, in a free point. In the ninth cervical the rib is increased in length, but is still what would be termed a 'false' or 'floating rib' in anthropotomy.

In the succeeding vertebrae the pleurapophysis articulates with a hæmapophysis, and the hæmal arch is completed by a hæmal spine; and by this completion of the typical segment we distinguish the commencement of the series of dorsal vertebrae. With regard to the so-called 'perforation of the transverse process,' this equally exists in the present vertebra, as in the cervicals, as may be seen by comparing fig. 6, p. 5, with fig. 2, Pl. 1 D; in both, the foramen is the vacuity intercepted between the bifurcate extremity of the rib and the rest of the vertebra with which that rib articulates; and, on the other hand, the cervical vertebrae equally show surfaces for the articulation of ribs. Cuvier, in including the proximal portions of the ribs with the rest of the vertebra, in his figure of a dorsal vertebra of a Crocodile,* so far follows nature, and produces a parallel to

* Ossemens Fossiles, 4to, tom. v, pt. ii, pl. iv, fig. 4.
his figure of a cervical vertebra; but the entire natural vertebra or segment includes the parts delineated in outline in Cut 6, p. 5. In that figure is shown the semiossified bar $h'$ which is interposed between the pleurapophysis $pl$ and hæmapophysis $h$ in the Crocodilia and some existing Lizards. The typical characters of the segment due to the completion of both neural and hæmal arches, is continued in some species of Crocodilia to the sixteenth, in some (Crocodilus acutus) to the eighteenth vertebra. In the Crocodilus acutus and the Alligator lucius, the hæmapophysis of the eighth dorsal rib (seventeenth segment from the head) joins that of the antecedent vertebra. The pleurapophyses project freely outwards, and become 'floating ribs' in the eighteenth, nineteenth, and twentieth vertebrae, in which they become rapidly shorter, and in the last appear as mere appendages to the end of the long and broad diapophyses: but the hæmapophyses by no means disappear after the solution of their union with their pleurapophyses; they are essentially independent elements of the segment, and they are continued, therefore, in pairs along the ventral surface of the abdomen of the Crocodilia, as far as their modified homotypes the pubic bones. They are more or less ossified, and are generally divided into two or three pieces.

Another character afforded by the hæmal arch is the more important in reference to palæontology, as it affects the centrum and neural arch of the vertebra as well as the pleurapophysis; and thus aids in the determination of the vertebra. The parapophysis progressively ascends upon the side of the centrum in the two anterior dorsal vertebrae, and disappears in the third, or, passing upon its neurapophysis, blends with the base of the diapophysis. In this segment, therefore, the proximal end of the rib ceases to be bifurcate, but is simply notched, the curtailed head being applied to the end of the thickened anterior part of the transverse process, and the tubercle abutting against its extremity; in the five following dorsals the head and tubercle of the rib progressively approximate and blend together, or the head disappears in the tenth dorsal, in which the rib is simply attached to the end of the diapophysis. The hypapophysis ceases to be developed after the third or fourth dorsal vertebrae. The zygapophyses become gradually more horizontal, the anterior ones looking more directly upwards, the posterior ones downwards.

The 'lumbar vertebrae' are those in which the diapophyses cease to support moveable pleurapophyses, although they are elongated by the coalesced rudiments of such which are distinct in the young Crocodilia. The development and persistent individuality of more or fewer of these rudimental ribs determines the number of the dorsal and lumbar vertebrae respectively, and exemplifies the purely artificial character of the distinction. The number of vertebrae or segments between the skull and the sacrum, in all the Crocodilia I have yet examined, is twenty-four. In the skeleton of a Gavial I have seen thirteen dorsal and two lumbar; in that of a Crocodilus cataphractus twelve dorsal and three lumbar; in those of a Crocodilus acutus, and Alligator lucius, eleven dorsal and four lumbar, and this is the most common number; but in
the skeleton of the Crocodile, I believe of the species called *Croc. biporcatus*, described by Cuvier, he gives five as the number of the lumbar vertebrae. But these varieties in the development or coalescence of the stunted pleurapophysis are of little essential moment; and only serve to show the artificial character of the 'dorsal' and 'lumbar' vertebrae. The coalescence of the rib with the diapophysis obliterates of course the character of the 'costal articular surfaces;' which we have seen to be common to both dorsal and cervical vertebrae. The lumbar zygapophyses have their articular surfaces almost horizontal, and the diapophyses, if not longer, have their antero-posterior extent somewhat increased; they are much depressed, or flattened horizontally.

The sacral vertebrae are very distinctly marked by the flatness of the coadapted ends of their centra; there are never more than two such vertebrae in the *Crocodilia* recent or extinct: in the first the anterior surface of the centrum is concave; in the second it is the posterior surface; the zygapophyses are not obliterated in either of these sacral vertebrae, so that the aspects of their articular surface—upwards in the anterior pair, downwards in the posterior pair—determines at once the corresponding extremity of a detached sacral vertebra. The thick and strong transverse processes form another characteristic of these vertebrae; for a long period the suture near their base remains to show how large a proportion is formed by the pleurapophysis. This element articulates more with the centrum than with the diapophysis developed from the neural arch; † it terminates by a rough, truncate, expanded extremity, which almost or quite joins that of the similarly but more expanded rib of the other sacral vertebrae. Against these extremities is applied a supplementary costal piece, serially homologous with the appendage to the proper pleurapophysis in the dorsal vertebrae, but here interposing itself between the pleurapophyses and hæmapophyses of both sacral vertebrae, not of one only. This intermediate pleurapophysial appendage is called the 'ilium'; it is short, thick, very broad, and subtriangular, the lower truncated apex forming with the connected extremities of the hæmapophysis an articular cavity for the diverging appendage, called the 'hind leg.' The hæmapophysis of the anterior sacral vertebra is called 'pubis'; it is moderately long and slender, but expanded and flattened at its lower extremity, which is directed forwards towards that of its fellow, and joined to it through the intermedium of a broad, cartilaginous, hæmal spine, completing the hæmal canal. The posterior hæmapophysis is broader, subdepressed, and subtriangular, expanding as it approaches its fellow to complete the second hæmal arch; it is termed 'ischium.' The great development of all the elements of these hæmal arches, and the peculiar and distinctive forms of those that have thereby acquired, from the earliest dawn of anatomical science, special names, relates phy-

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* Tom. cit., p. 95. It is to be observed that Cuvier begins to count the dorsal vertebrae when the rib has changed its hatchet-shape for a styloid shape.
† Cuvier, who well describes this structure, remarks, "aussi méritent-elles plutôt le nom des côtes que celui d'apophyses transverses." (Tom. cit., p. 98.)
siologically to the functions of the diverging appendage which is developed into a potent locomotive member. This limb appertains properly, as the proportion contributed by the ischium to the articular socket and the greater breadth of the pleurapophysis show, to the second sacral vertebra; to which the ilium chiefly belongs.

The first caudal vertebra, which presents a ball for articulating with a cup on the back part of the last sacral, retains, nevertheless, the typical position of the ball on the back part of the centrum; it is thus biconvex, and the only vertebra of the series which presents that structure. I have had this vertebra in three different species of extinct Eocene Crocodilia. In the Crocodilus toliapicus, Pl. 5, fig. 7; in the Croc. champsoïdes, Pl. 3 A, fig. 10; and in the Crocodilus Hastingsia, Pl. 1 D, fig. 7.

The advantage of possessing such definite characters for a particular vertebra is, that the homologous vertebra may be compared in different species, and may yield such distinctive characters as will be hereafter pointed out in those of the three species above cited.

The first caudal vertebra, moreover, is distinguished from the rest by having no articular surfaces for the hæmapophyses, which in the succeeding caudals form a hæmal arch, like the neurapophyses above, by articulating directly with the centrum. The arch so formed has its base not applied over the middle of a single centrum, but like the neural arch in the back of the tortoise and sacrum of the bird, across the interspace between two centra. The first hæmal arch of the tail belongs, however, to the second caudal vertebra, but it is displaced a little backwards from its typical position.

The detached centrum of a caudal vertebra, besides being more slender and compressed, is distinguished from those of the before-described vertebrae by the two articular surfaces at the posterior border of their under surface. The zygapophyses become vertical as far as the sixteenth or seventeenth, beyond which the two posterior zygapophyses coalesce in an oblique plane notched in the middle, which is received into a wider notch at the fore part of the neural arch of the succeeding vertebra. The sutures between the pleurapophyses and diapophyses are maintained during a long period of the animal's growth, and demonstrate the share which these two elements respectively take in the formation of the transverse process. So constituted, these processes progressively decrease in length to the fifteenth or sixteenth caudal vertebra, and then disappear. The neural spines progressively decrease in every dimension, save length, which is rather increased as far as the twenty-second or twenty-third vertebra, beyond which they begin again to shorten, and finally subside in the terminal vertebrae of the tail.

The caudal hæmapophyses coalesce at their lower or distal ends, from which a spinous process is prolonged downwards and backwards; this grows shorter towards the end of the tail, but is compressed and somewhat expanded antero-posteriorly. The hæmal arch so constituted has received the name of 'chevron bone.'

A side view of the body of a middle caudal vertebra of the Crocodilus toliapicus is
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given in Pl. 3, fig. 8, and an under view of the same in fig. 9, showing the two hyp-
apophysial ridges extending from the articular facets for the hæmapophyses at one end
to the other end of the centrum.

The segments of the endo-skeleton composing the skull are more modified than
those of the pelvis; but just as the vertebral pattern is best preserved in the neural
arches of the pelvis, which are called collectively 'sacrum,' so, also, is it in the same
arches of the skull, which are called collectively 'cranium.' The elements of these
cranial arches are composed preserve, moreover, their primitive or normal individuality
more completely than in any of the vertebrae of the trunk, except the atlas, and
consequently the archetypal character can be more completely demonstrated.

In fossil Crocodilia, and many other reptiles, the bones of the head are very liable
from this cause to a greater extent of dislocation and separation than happens to the
skull of the warm-blooded animal, in which a greater proportion of those primitive
bones coalesce with age. It not unfrequently happens that detached bones of the
skull of a reptile are found fossil, and the usually much modified form of these vertebral
elements renders their determination difficult. In order to diminish this difficulty, I
subjoin some figures of the individual bones from my work on the 'Archetype of the
Vertebrate Skeleton,' with such indication of their natural connexions, as is compatible
with a clear outline. A profile or side view of all the bones is offered in fig. 13, and
as those of the cranium are least familiar to the palæontologist in their detached state,
I have added a direct view of them nearly as they are arranged in the formation of the
successive neural arches of the skull. Such figures are the more necessary in the
present state of anatomy and palæontology, since the illustrations of the osteology of
the crocodile which have hitherto been prefixed to the descriptions of the fossil remains
of the Reptilian class, as, e. g., in the great work of Cuvier, include only figures of the
bones in question as they are naturally combined together in the entire skull.

If, after separating the atlas from the occiput, we proceed to detach the occipital
segment of the cranium from the next segment in advance, we find the detached segment presenting the
form of the neural arch, and it is easily and naturally divisible into the four bones figured in Cut. 9. The dotted
circle crosses the margins at which the bones were joined together, in order to encompass the hindmost segment
of the brain, called 'epencephalon,' whence this neural arch of the occiput is termed 'epencephalic arch.'
No. 1 is the base of the arch, and is the 'centrum' or body of the whole occipital vertebra: it presents, like
those of the trunk, a convexity or ball at its posterior articular surface, but its anterior one, like the hindmost centrum of the sacrum, unites with the next centrum in advance
by a flat rough 'sutural' or 'symphysial' surface. Like most of the centrums in the

![Fig. 9.](https://example.com/fig9)

Bones of the disarticulated epencephalic arch, viewed from behind (Crocodile).
neck and beginning of the back, that of the occiput develops a 'hypapophysis,' but this descending process is longer and larger, its base extending over the whole of the under surface of the centrum. It is a character whereby the occipital centrum of a Crocodilian reptile may be distinguished from that of a Lacertian one; for in the latter a pair of diverging hypapophyses project from the under surface, as is shown in most recent lizards and in the great extinct Mosasaurus.*

The upper and lateral parts of no. 1 present rough sutural surfaces, like those in the centrums of the trunk, for articulating with the 'neurapophyses,' nos 2, 2, which develope short, thick, obtuse, transverse processes (4, 4). The modified or specialized character of the elements of the cranial vertebrae has gained for them special names. The centrum (1) is called the 'basioccipital;' the neurapophyses (2, 2) are the 'exoccipitals;' the neural spine (3) is the 'superoccipital.' The transverse processes (4, 4), which may combine both diapophyses and parapophyses, but which, from the modifications of the transverse processes of the atlas, and the autogenous character of the parapophyses in some fishes, and of the processes in question in the Chelonian Reptiles, I believe to be best entitled to be regarded as the parapophyses, are called the 'paroccipitals;' they are never detached bones in the Crocodilia, as they are in the Chelonia and in most fishes.

The exoccipitals perform the usual functions of neurapophyses, and, like those of the atlas, meet above the neural canal; they are perforated to give exit to the vagal and hypoglossal nerves, and protect the sides of the medulla oblongata and cerebellum—the two divisions of the epencephalon. The superoccipital (3) is broad and flat, like the similarly detached neural spine of the atlas; it advances a little forwards, beyond its sustaining neurapophyses, to protect the upper surface of the cerebellum: it is traversed by tympanic air-cells, and assists with the exoccipitals (2, 2) in the formation of the chamber for the internal ear.

The chief modification of the occipital segment of the skull, as compared with that of the osseous fish, or with the typical vertebra, is the absence of an attached hæmal arch. We shall afterwards see that this arch is present in the Crocodile, although displaced; a profile of it is given, as restored to its typical position, in the side view of the bones of the skull, fig. 13.

Proceeding with the neural arches of the Crocodile's skull, if we dislocate the segment in advance of the occiput, we bring away in connexion with the long base-bone, 5 and 9, fig. 13, the bones which, in the same figure, are tied together by the double lines, N II, N III, and by the curved arrows, H II and H III. In fact, the centrums of two vertebrae have here coalesced, as we find to happen in the neck of the Siluroid fishes, and in the sacrum of birds and mammals. The two connate cranial centrums must be artificially divided, in order to obtain the segments distinct to which they belong. Fig. 10 gives a back view of the disarticulated bones of the neural

arch of the 'parietal vertebra,' as the segment is termed which is in advance of the occipital one. The hinder portion (5) of the great base-bone, which is the centrum of the parietal vertebra, is called 'basisphenoid.'

It supports that part of the 'mesencephalon,' which is formed by the lobe of the third ventricle, and its upper surface is excavated for the pituitary prolongation of that cavity. The basisphenoid develops from its under surface a 'hypapophysis,' which is suturally united with the fore part of that of the basioccipital, but extends further down, and is similarly united in front to the 'pterygoids' (24). These rough sutureal surfaces of the long descending process of the basisphenoid are very characteristic of that centrum, when detached in a fossil state. The neurapophyses of the parietal vertebra (6, 6) are called the 'alosphenoids;'* they protect the sides of the mesencephalon, and are notched at their anterior margin, for a conjugational foramen transmitting the trigeminal nerve. As accessory functions they contribute, like the corresponding bones in fishes, to the formation of the ear-chamber. They have, however, a little retrograded in position (see fig. 14, 6), resting below, in part upon the occipital centrum, and supporting more of the spine of that segment (3) than of their own (7). The spine of the parietal vertebra (fig. 10, 7) is a permanently distinct, single, depressed bone, like that of the occipital vertebra; it is called the 'parietal,' and completes the neural arch, as its crown or key-bone; it is partially excavated by the tympanic air-cells. The bones 8, 8 wedged between 6 and 7, manifest more of their parapophysial character than their homotypes (4, 4) do in the occipital segment, since they support modified ribs, are developed from independent centres, and preserve their individuality. They form no part of the inner walls of the cranium, but send outwards and backwards a strong transverse process for muscular attachment. They afford a ligamentous attachment to the hæmal arch (fig. 13, H ii) of their own segment, and articulate largely with the pleurapophysis (28) of the antecedent hæmal arch (H iii), whose more backward displacement, in comparison with its position in the fish's skull, is well illustrated in the metamorphosis of the toad and frog.

On removing the neural arch of the parietal vertebra, after the section of its confluent centrum, the elements of the corresponding arch of the frontal vertebra, slightly disarticulated, present the arrangement shown in fig. 11. The compressed produced centrum (9) shown in natural connexion with the parietal centrum 5 in fig. 13.

* This bone is the 'rocher' or petrous portion of the temporal bone, according to Cuvier, in the Reptiles (Ossements Fossiles, v, pt. ii, 1824); but is the 'aile temporale du sphénoïde' in fishes (Histoire Naturelle des Poissons, tom. i, 1825), birds, and mammals.
and with the bone 10 in fig. 14, has its form modified like that of the vertebral centrums at the opposite extreme of the body in many birds; it is called the ‘presphenoid.’

The neurapophyses 10, 10, articulate with the upper part of 9; they are expanded and smoothly excavated on their inner surface to support the sides of the large prosencephalon; they dismiss the great optic nerves by the notch marked \( op \) in fig. 14, and the motor nerves of the eyeball by the notch \( s \). They show the same tendency to a retrograde change of position, as the neighbouring neurapophyses (6); for though they support a greater proportion of their proper spine (11), they also support part of the parietal spine (7), and rest, in part, below upon the parietal centrum (5): the neurapophyses (10, 10) are called ‘orbitosphenoids.’* The neural spine (11) of the frontal vertebra retains its “normal character as a single symmetrical bone, like the parietal spine which it partly overlaps; it also completes the neural arch of its own segment, but is remarkably extended longitudinally forwards, as is shown in figs. 13 and 14, 11, where it is much thickened, and assists in forming the cavities for the eyeballs (or, fig. 14): it is called the (frontal) bone.

In contemplating in the skull itself, or in such side views as are given in figs. 13 and 14, the relative position of the frontal (11), to the parietal (7), and of this to the superoccipital (3), which is overlapped by the parietal, just as itself overlaps the flattened spine of the atlas, we gain a conviction which cannot be shaken by any difference in their mode of ossification, by their median bipartition, or by their extreme expansion in other animals, that the above-named single, median, imbricated bones, each completing its neural arch, and permanently distinct from the piers of such arch, must repeat the same element in those successive arches, in other words, must be ‘homotypes,’ or serially homologous.† In like manner the serial homology of those piers, called ‘neurapophyses,’ viz. the laminae of the atlas (fig. 8 na), the exoccipitals (figs. 13 and 14, 2), the alisphenoids (6), and the orbitosphenoids (10), is equally unmistakable. Nor can we shut out of view the same serial relationship of the paroccipitals (4), as coalesced paraphyses of the occipital vertebra, with the mastoids (8), and the postfrontals (12), as permanently detached paraphyses of their respective vertebræ. All stand out from the sides of the cranium, as transverse processes for muscular attachment, all are alike autogenous in the Chelonians, and all of them, in fishes, offer articular surfaces

* According to Cuvier, this bone is the ‘aile temporaire du sphénoïde et une grande partie de l’aile orbitaire’ in Crocodiles. (Ossemens Fossiles, tom. v, pt. ii.)

† See my work ‘On the Archetype of the Vertebrate Skeleton,’ pp. 5-8, 8vo, Van Voorst, for the explanation of these terms.
for the ribs or hæmal arches of their respective vertebrae; and these characters are retained in the postfrontals as well as in the mastoids of the Crocodiles.

The frontal parapophysis (12, fig. 11) is wedged between the back part of the spine (11) and the neurapophysis (10); its outwardly projecting process extends also backwards and joins that of the succeeding parapophysis (8); but, notwithstanding the retrogradation of the inferior arch (fig. 13, H III), it still articulates with part of its own pleurapophysial element (28), which forms the proximal element of that arch.

There finally remain in the cranium* of the Crocodile, after the successive detachment of the foregoing arches, the bones intersected by the double line N iv, in fig. 13, which, as in fig. 14, are numbered 13, 14, and 15, and of which a foreshortened back view is represented in Cut. 12; but, notwithstanding the extreme degree of modification to which their extreme position subjects them, we can still trace in their arrangement a correspondence with the vertebrate type.

A long and slender symmetrical grooved bone (13, between 24, 24), like the ossified inferior half of the capsule of the notochord, is continued forwards from the inferior part of the centrum (9) of the frontal vertebra, and stands in the relation of a centrum to the vertical plates of bone (14), fig. 12, and fig. 14, which expand as they rise into a broad, thick, triangular plate, with an exposed horizontal superior surface. These bones, which are called 'prefrontals,' stand in the relation of 'neurapophyses' to the rhinencephalic prolongations of the brain, commonly but erroneously called 'olfactory nerves,' and they form the piers or haunches of a neural arch, which is completed above by a pair of symmetrical bones (15) called 'nasals,' which I regard as a divided or bifid neural spine.

The centrum of this arch is established by ossification in the expanded anterior prolongation of the fibrous capsule of the notochord, beyond the termination of its gelatinous axis. The

* The part called cranium in human anatomy is a quite artificial division of the skull; it includes the neurapophyses of the nasal vertebrae, coalesced with the capsules of the sense of smell, and excludes the centrum and neural arch of the same natural segment; it also includes one portion of the diverging appendage (27) of the maxillary arch, because it enters largely into the formation of the capacious cranial cavity of man, and another portion of the diverging appendage of the same arch (24), because it happens to coalesce with the basisphenoid. The capsule of the organ of hearing is included together with part of that of the olfactory organ, whilst the capsule of the organ of sight, and part of that of the organ of smell are excluded. None of these sense-capsules properly form any part of the cranium, but they are lodged in interspaces of its constituent arches. The cranial portion of the skull, as a natural division of that part of the endoskeleton, ought to consist exclusively of the neural arches and centra of the cranial vertebrae.
median portion above specified retains most of the formal characters of the centrum, but there is a pair of long, slender, symmetrical ossicles, which, from the seat of their original development, and their relative position to the neural arch, must be regarded as also parts of its centrum. And this ossification of the element in question from different centres will be no new or strange character to those who recollect that the vertebral body in man and mammalia is developed from three centres. The term 'vomer' is applied to the pair of bones 13, in fig. 12, because their special homology with the single median bone, so called in fishes and mammals, is indisputable; but a portion of the same element of the skull retains its single symmetrical character in the Crocodile, and is connate with the enormous pterygoids (24), between which it is wedged. In some Alligators (All. niger) the divided anterior vomer extends far forwards, expands anteriorly, and appears upon the bony palate.

Almost all the other bones of the head of the Crocodile are adjusted so as to constitute four inverted arches, respectively completed or closed below at the points marked H IV, H III, H II, and H I, in fig. 13. These are the haemal arches of the four segments or vertebrae, of which the neural arches have been just described. But they have been the seat of much greater modifications, by which they are made subservient to a variety of functions unknown in the haemal arches of the rest of the body. Thus the two anterior haemal arches of the head perform the office of seizing and bruising the food; are armed for that purpose with teeth: and, whilst one arch is firmly fixed, the other works upon it like the hammer upon the anvil. The elements of the fixed arch (H IV), called 'maxillary arch,' have accordingly undergone the greatest amount of morphological change in order to adapt that arch to its share in mastication, as well as for forming part of the passage for the respiratory medium, which is perpetually traversing this haemal canal in its way to purify the blood. Almost the whole of the upper surface of the maxillary arch is firmly united to contiguous parts of the skull by rough or sutural surfaces, and its strength is increased by bony appendages, which diverge from it to abut against other parts of the skull. Comparative anatomy teaches that, of the numerous places of attachment, the one which connects the maxillary arch by its element (20) with the centrum (13) and the descending plates of the neurapophyses (14) of the nasal segment, is the normal or the most constant point of its suspension, the bone (20) being the pleurapophysial element of the maxillary arch: it is called the 'palatine,' because the under surface, shown in Pl. 4, 2, and Pl. 1 B, at 20, forms a portion of the bony roof of the mouth called the 'palate.'

It is articulated at its fore part with the bone (21) in the same plates, which bone is the haemapophysial element of the maxillary arch. It is called the 'maxillary,' and is greatly developed both in length and breadth; it is connected not only with 20 behind, and 22 in front, which are parts of the same arch (see fig. 13), and with the diverging appendages of the arch, viz. (26) the malar bone, and (24) the pterygoid, but also with the nasals (15) and the lachrymal (16), as well as with its fellow of the
opposite side of the arch. The smooth expanded horizontal plate which effects the latter junction, shown in Pl. 1 B, and Pl. A 2, at 21, is called the palatal plate of the maxillary; the thickened external border, where this plate meets the external rough surface of the bone, and which is perforated for the lodgement of the teeth, is the 'alveolar border' or 'process' of the maxillary. The hæmal spine or key-bone of the arch (22) is bifid, and the arch is completed by the symphysial junction of the two symmetrical halves at H 4v, fig. 13; these halves are called 'premaxillary bones;'

Disarticulated bones of the Skull of an Alligator, N 1 to 4v the neural arches; H 1 to 4v the hæmal arches and appendages.

these bones, like the maxillaries, have a rough facial plate, Pl. 1 A, 22 and a smooth palatal plate Pl. 1 B, 22, with the connecting alveolar border. The median symphysis is perforated vertically through both plates; the outer or upper hole being the external nostril, the under or palatal one being the prepalatal or naso-palatal aperture; this is completely inclosed by the premaxillary bone, as shown in Pl. 1 B, fig. 2, 22, and Pl. 1 C, 22, np; whilst, in all known existing Crocodiles and Alligators, the tips of the nasal bones, as at 15, fig. 1, Pl. A 2, enter into the back part of the circumference of the nasal aperture. In the Gavials, as may be seen in Pl. 1, fig. 1 a, the nasal aperture is wholly surrounded by the premaxillaries, i; and one of the fossil Eocene Crocodiles,
presently to be described, Pl. 1 A, fig. 1, differs from all the modern species, in the exclusion of the nasal bones (13) from the nasal aperture.

Both the palatine (fig. 13, 20) and the maxillary (ib. 21) send outwards and backwards, parts or processes which diverge from the line of the hæmal arch of which they are the chief elements; and these parts give attachment to distinct bones which form the 'diverging appendages' of the arch, and serve to attach it, as do the diverging appendages of the thoracic hæmal arches in the bird, to the succeeding arch.

The appendage (24) called 'pterygoid' effects a more extensive attachment, and is peculiarly developed in the Crocodilia. As it extends backwards it expands, unites with its fellow, below the nasal canal, and encompassing that canal, coalesces above it with the vomer, and is firmly attached by suture to the presphenoid and basisphenoid: it surrounds the hinder or palatal nostril, and, extending outwards, as shown in Pl. 1 A, fig. 3 (24), it gives attachment to a second bone (25), called 'ectopterygoid,' which is firmly connected with the maxillary (25), the malar (26), and the post-frontal (12). The second diverging ray is of great strength; it extends from the maxillary (21) ('hæmapophysis' of the maxillary arch) to the tympanic (28) ('pleurapophyses' of the mandibular arch), and is divided into two pieces, the malar (26), and the squamosal (27). Such are the chief Crocodilian modifications of the hæmal arch and appendages of the anterior or nasal vertebra of the skull.

The hæmal arch of the frontal vertebra is somewhat less metamorphosed, and has no diverging appendage. It is slightly displaced backwards, and is articulated by only a small proportion of its pleurapophysis (28), to the parapophysis (12) of its own segment; the major part of that short and strong rib articulating with the parapophysis (8) of the succeeding segment. The bone (28) called 'tympanic,' because it serves to support the 'drum of the ear,' in air-breathing vertebrates, is short, strong, and immovably wedged, in the Crocodilia, between the paroccipital (4), mastoid (8), post-frontal (12), and squamosal (27); and the conditions of this fixation of the pleurapophysis are exemplified in the great development of the hæmapophysis (mandible), which is here unusually long, supports numerous teeth, and requires, therefore, a firm point of suspension, in the violent actions to which the jaws are put in retaining and overcoming the struggles of a powerful living prey. The moveable articulation between the pleurapophysis (28) and the rest of the hæmal arch is analogous to that which we find between the thoracic pleurapophysis and hæmapophysis in the Ostrich and many other birds. But the hæmapophysis of the mandibular arch in the Crocodiles is subdivided into several pieces, in order to combine the greatest elasticity and strength with a not excessive weight of bone. The different pieces of this purposely subdivided element have received definite names. That numbered 29, which offers the articular concavity to the convex condyle of the tympanic (28), is called the 'articular' piece; that beneath it (30), which develops the angle of the jaw, when this projects, is the 'angular' piece; the piece above (29') is the 'surangular'; the thin, broad, flat
piece (31), applied, like a splint, to the inner side of the other parts of the mandible, is the 'splenial;' the small accessory ossicle (31') is the 'coronoid,' because it develops the process so called, in lizards; the anterior piece (32), which supports the teeth, is called the 'dentary.' This latter is the homotype of the premaxillary, or it represents that bone in the mandibular arch, of which it may be regarded as the hæmal spine; the other pieces are subdivisions of the hæmapophysial element. The purport of this subdivision of the lower jaw-bone has been well explained by Conybeare* and Buckland,† by the analogy of its structure to that adopted in binding together several parallel plates of elastic wood or steel to make a crossbow, and also in setting together thin plates of steel in the springs of carriages. Dr. Buckland adds, "those who have witnessed the shock given to the head of a Crocodile by the act of snapping together its thin long jaws, must have seen how liable to fracture the lower jaw would be, were it composed of one bone only on each side." The same reasoning applies to the composite structure of the long tympanic pedicle in fishes. In each case the splicing and bracing together of thin flat bones of unequal length and of varying thickness, affords compensation for the weakness and risk of fracture that would otherwise have attended the elongation of the parts. In the abdomen of the Crocodile the analogous subdivision of the hæmapophyses, there called abdominal ribs, allows of a slight change of their length, in the expansion and contraction of the walls of that cavity; and since amphibious reptiles, when on land, rest the whole weight of the abdomen directly upon the ground, the necessity of the modification for diminished liability to fracture further appears. These analogies are important, as demonstrating that the general homology of the elements of a natural segment of the skeleton is not affected or obscured by their subdivision for a special end. Now this purposive modification of the hæmapophyses of the frontal vertebra is but a repetition of that which affects the same elements in the abdominal vertebrae.

Passing next to the hæmal arch of the parietal vertebra (fig. 13, H III), we are first struck by its small relative size; its restricted functions have not required it to grow in proportion with the other arches, and it consequently retains much of its embryonic dimensions. It consists of a ligamentous 'stylohyal'—its pleurapophysis, retaining the same primitive histological condition which obstructs the ordinary recognition of the same elements of the lumbar hæmal arches. A cartilaginous 'epiphyal' (39) intervenes between this and the ossified 'hæmapophysis' (40), which bears the special name of ceratohyal. The hæmal spine (41) retains its cartilaginous state, like its homotypes in the abdomen: there they get the special name of 'abdominal sternum,' here of 'basi-hyal.' The basihyal has, however, coalesced with the thyrohyals, to form a broad cartilaginous plate, the anterior border rising like a valve to close the fauces, and the posterior angles extending beyond and sustaining the thyroid and other parts of the

* Geol. Trans., 1821, p. 565.
† Bridgewater Treatise, 1836, vol. i, p. 176.
larynx. The long bony 'ceratohyal' (fig. 13, 40), and the commonly cartilaginous 'epihyal' (ib. 39), are suspended by the ligamentous 'stylohyal' to the paroccipital process; the whole arch having, like the mandibular one, retrograded from the connexion it presents in fishes.

This retrogradation is still more considerable in the succeeding hæmal arch. In comparing the occipital segment of the crocodile's skeleton with that of the fish, the chief modification that distinguishes that segment in the crocodile is the apparent absence of its hæmal arch. We recognise, however, the special homologues of the constituents of that arch of the fishes' skeleton in the bones 51 and 52 of the crocodile's skeleton (fig. 13); but the upper or suprascapular piece (50) retains, in connexion with the loss of its proximal or cranial articulations, its cartilaginous state: the scapula (51) is ossified, as is likewise the coracoid (52), the lower end of which is separated from its fellow by the interposition of a median, symmetrical, partially ossified piece called 'episternum' (H 1). The power of recognising the special homologies of 50, 51, and 52 in the crocodile, with the similarly numbered constituents of the same arch in fishes*, though masked, not only by modifications of form and proportion, but even of very substance, as in the case of 50, depends upon the circumstance of these bones constituting the same essential element of the archetypal skeleton: for although in the present instance there is superadded to the adaptive modifications above cited, the rarer one of altered connexions, Cuvier does not hesitate to give the same names, 'suprascapulaire' to 50 and 'scapulaire' to 51, in both fish and crocodile: but he did not perceive or admit that the narrower relations of special homology were a result of, and necessarily included in, the wider law of general homology. According to the latter, we discern in 50 and 51 a teleologically compound 'pleurapophysis,' in 52 a 'hæmapophysis,' and in 50 the 'hæmal spine,' completing the hæmal arch.

The general relations of the scapulo-coracoid arch to a hæmal or costal one was early recognised by Oken. This philosopher, having observed the free cervical ribs in a specimen of the Lacerta apoda, Pallas (Pseudopus), deemed them representatives of the scapula, and this bone to be, in other animals, the coalesced homologues of the cervical pleurapophyses.† In no animal are the conditions for testing this question so favorable and obvious as in the crocodiles and gavials (Pl. 1): not only do cervical ribs coexist with the scapulo-coracoid arch, but they are of unusual length, and are developed from the atlas as well as from each succeeding cervical vertebra: we can also trace them beyond the thorax to the sacrum, and throughout a great part of the caudal region, as the sutures of the apparently long transverse processes of the

* See fig. 5, p. 18, and pl. ii, fig. 2, in 'The Archetype and Homologies of the Vertebrate Skeleton.'

† "Auch die Scapula nicht ein Knochen, sondern wenigstens eine aus fünf Halsrippen zusammengefasste Platte ist."—Programm über die Bedeutung der Schädelknochen, 4to, 1807, p. 16. He reproduces the same idea of the general homology of the scapula in the 'Lehrbuch der Natur-philosophie,' 1843, p. 331, ¶ 2381. Carus also regards the scapulo-coracoid arch as the reunion of several (at least three) proto-vertebral arches of the trunk-segments. (Urtheilen des Knochen und Schalen gerustes, fol., 1828.)
coccygeal vertebrae demonstrate in the young animal; the lumbar pleurapophyses being manifested at the same period as cartilaginous appendages to the ends of the long diapophyses.

The scapulo-coracoid arch, both elements (51, 52) of which retain the form of strong and thick vertebral and sternal ribs in the crocodile, is applied in the skeleton of that animal over the anterior thoracic hæmal arches. Viewed as a more robust hæmal arch, it is obviously out of place in reference to the rest of its vertebral segment. If we seek to determine that segment by the mode in which we restore to their centrums the less displaced neural arches of the antecedent vertebrae of the cranium or in the sacrum of the bird,* we proceed to examine the vertebrae before and behind the displaced arch, with the view to discover the one which needs it, in order to be made typically complete. Finding no centrum and neural arch without its pleurapophyses from the scapula to the pelvis, we give up our search in that direction; and in the opposite direction we find no vertebra without its ribs until we reach the occiput: there we have centrum and neural arch, with coalesced parapophyses—the elements answering to those included in the arch N r, fig. 13—but without the arch H r; which arch can only be supplied, without destroying the typical completeness of antecedent cranial segments, by a restoration of the bones 50—52, to the place which they naturally occupy in the skeleton of the fish. And since anatomists are generally agreed to regard the bones 50—52 in the crocodile (fig. 13) as specially homologous with those so numbered in the fish,† we must conclude that they are likewise homologous in a higher sense; that in the fish, the scapulo-coracoid arch is in its natural or typical position, whereas in the crocodile it has been displaced for a special purpose. Thus, agreeably with a general principle, we perceive that, as the lower vertebrate animal illustrates the closer adhesion to the archetype by the natural articulation of the scapulo-coracoid arch to the occiput, so the higher vertebrate manifests the superior influence of the antagonising power of adaptive modification by the removal of that arch from its proper segment.

The anthropotomist, by his mode of counting and defining the dorsal vertebrae and ribs, admits, unconsciously perhaps, the important principle in general homology which is here exemplified, and which, pursued to its legitimate consequences and further applied, demonstrates that the scapula is the modified rib of that centrum and neural arch which he calls the 'occipital bone,' and that the change of place which chiefly masks that relation (for a very elementary acquaintance with comparative anatomy shows how little mere form and proportion affect the homological characters of bones) differs only in extent and not in kind from the modification which makes a minor amount of comparative observation requisite, in order to determine the relation of the shifted dorsal rib to its proper centrum in the human skeleton.

* See 'On the Archetype and Homologies of the Vertebrate Skeleton,' p. 117, p. 159.
With reference, therefore, to the occipital vertebra of the crocodile, if the comparatively well-developed and permanently distinct ribs of all the cervical vertebrae prove the scapular arch to belong to none of those segments, and, if that hæmal arch be required to complete the occipital segment, which it actually does complete in fishes, then the same conclusion must apply to the same arch in other animals, and we must regard the occipital vertebra of the tortoise as completed below by its scapulo-coracoid arch and not, as Bojanus supposed, by its hyoidean arch.*

Having thus endeavoured to show what the scapular arch of the crocodile is, I proceed to point out the characteristic form of its chief elements. The upper and principal part of the scapula (51, fig. 13) is flattened, and gradually becomes narrower to the part called its neck, which is rounded, bent inwards, and then suddenly expanded to form a rough articular surface for the coracoid, and a portion of a smoother surface for the shoulder-joint. The contiguous end of the coracoid (52) presents a similar form, having not only the rough surface for its junction with the scapula, but contributing, also, one half of the cavity for the head of the humerus. It is perforated near the interspace between these two surfaces. As it recedes from them, it contracts, then expands and becomes flattened, terminating in a somewhat broader margin than the base of the scapula, which margin is morticed into a groove at the anterior border of the broad rhomboidal cartilage continued beyond the ossified part of the manubrium, which forms the key-bone of the scapular arch. The anterior locomotive extremity is the diverging appendage of the arch, under one of its numerous modes and grades of development.†

The proximal element of this appendage or that nearest the arch, is called the 'humerus' (53, fig. 13): its head is subcompressed and convex; its shaft bent in two directions, with a deltoid crest developed from its upper and fore part; its distal end is transversely extended, and divided anteriorly into two condyles. The shaft of this bone has a medullary cavity, but relatively smaller than in the mammalian humerus.

The second segment of the limb consists of two bones: the larger one (54) is called the 'ulna:' it articulates with the outer condyle of the humerus by an oval facet, the

* Anatome Testudinis Europaea, fol., 1819, p. 44. Geoffroy St. Hilaire selected the opercular and sub-opercular bones to form the inverted arch of his seventh (occipital) cranial vertebra, and took no account of the instructive natural connexions and relative position of the hyoidean and scapular arches in fishes. With regard to the scapular arch, he alludes to its articulation with the skull in the lowest of the vertebrate classes as an 'amalgame inattendue' (Anatomie Philosophique, p. 481): and elsewhere describes it as a "disposition véritablement très singulière, et que le manque absoluf du con et une combinaison des pièces du sternum avec celles de la tête pouvoient seules rendre possible."—Annales du Muséum, ix, p. 361. A due appreciation of the law of vegetative uniformity or repetition, and of the ratio of its prevalence and power to the grade of organization of the species, was, perhaps, essential in order to discern the true significat' of the connexion of the scapular arch in fishes.

† See my Discourse ' On the Nature of Limbs,' 8vo, Van Voorst, 1849, pp. 64-70.
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thick convex border of which swells a little out behind, and forms a kind of rudimental 'olecranon;' the shaft of the ulna is compressed transversely, and curves slightly outwards; the distal end is much less than the proximal one, and is most produced at the radial side.

The radius (55) has an oval head; its shaft is cylindrical; its distal end oblong and subcompressed.

The small bones (56) which intervene between these and the row of five longer bones, are called 'carpals:' they are four in number in the Crocodilia. One seems to be a continuation of the radius, another of the ulna; these two are the principal carpals; they are compressed in the middle and expanded at their two extremities; that on the radial side of the wrist is the largest. A third small ossicle projects slightly backwards from the proximal end of the ulnar metacarpal: it answers to the bone called 'pisiforme' in the human wrist. The fourth ossicle is interposed between the ulnar carpal and the metacarpals of the three ulnar digits.

These five terminal jointed rays of the appendage are counted from the radial to the ulnar side, and have received special names: the first is called 'pollex,' the second 'index,' the third 'medius,' the fourth 'annularis,' and the fifth 'minimus.' The first joint of each digit is called 'metacarpal:' the others are termed 'phalanx.' In the Crocodilia the pollex has two phalanges, the index three, the medius four, the annularis four, and the minimus three. The terminal phalanges, which are modified to support claws, are called 'ungual' phalanges.

As the above-described bones of the scapular extremity are developments of the appendage of the scapular arch, which is the hæmal arch of the occipital vertebra, it follows, that, like the branchiostegal rays and opercular bones in fishes, they are essentially bones of the head.

But the enumeration of the bones of the crocodile's skull is not completed by these: there is a bone anterior to the orbit, marked 73 in fig. 13, and in Pl. 1 A and A2; it is perforated at its orbital border by the duct of the lachrymal gland, whence it is termed the 'lachrymal bone,' and its facial part extends forwards between the bones marked 14, 15, 21, and 26. In many Crocodilia there is a bone at the upper border of the orbit, which extends into the substance of the upper eyelid; it is called 'superorbital.' In the Crocodylus palpebrosus there are two of these ossicles.

Both the lachrymal and superorbital bones answer to a series of bones found commonly in fishes, and called 'suborbitals' and 'superorbitals.' The lachrymal is the most anterior of the suborbital series, and is the largest in fishes; it is also the most constant in the vertebrate series, and is grooved or perforated by a mucous duct. These ossicles appertain to the dermal or muco-dermal system or 'exoskeleton;' not to the vertebral system or 'endoskeleton.'

The little slender bone, marked 16 in fig. 13, has one of its extremities in the form of a long, narrow, elliptic plate, which is applied to the 'fenestra ovalis' of the internal
ear; from this plate extends a long and slender bony stem, which grows somewhat cartilaginous, expands and bends down, as it approaches the tympanum or ear-drum, to which it is attached. The cartilaginous capsule of the labyrinth or internal ear is partially ossified by sinuous plates of bone connate with the neurapophyses (2 and 6), between which that organ is lodged; I apply the term ‘petrosal’ to the principal and most independent of those ossifications of the ear-capsule, to that, e. g., which retains some mobility after it has contracted a partial ankylosis to the exoccipital (2), and which appears upon the inner surface of the cranial walls at the part marked 16 in the subjoined Cut 14, between 2 and 6. It is the only independent bone on that surface of the cranium which, in my opinion, answers to the ‘pетrous portion of the temporal’ in human anatomy, and to which the term ‘rocher’ can be properly applied, in the language of the French comparative anatomists. Cuvier, however, restricts that name to the ‘alischpenoid’ (6, figs. 13, 14) in the Crocodiles.

The ossicles, (16 and 16'), together with the partial ossifications in the sclerotic capsule of the organ of sight, (17, fig. 13)—always more distinct in Chelonia than in Crocodilia—belong to that category of visceral bones to which the term ‘splanchno-skeleton’ has been given; they also are foreign to the true vertebrate system of the skeleton.

Thus the classification of the bones of the head of the Crocodiles, as of all other vertebrate animals, is primarily into those of

The Endo-skeleton,
The Splanchno-skeleton, and
The Exo-skeleton.

The bones of the endo-skeleton of the head form naturally four segments, called

Occipital vertebra, N I, H I;
Parietal vertebra, N II, H II;
Frontal vertebra, N III, H III;
Nasal vertebra, N IV, H IV.  

These segments are subdivided into the neural arches, called

Epencephalic arch (1 basioccipital, 2 exoccipital, 3 superoccipital, 4 connate paroccipital);
Mesencephalic arch (5 basisphenoid, 6 alisphenoid, 7 parietal, 8 mastoid);
Prosencephalic arch (9 presphenoid, 10 orbitosphenoid, 11 frontal, 12 postfrontal);
Rhinencephalic arch (13 vomer, 14 prefrontal, 15 nasal):
and into the hæmal arches and their appendages, called
Maxillary arch (20 palatine, 21 maxillary, 22 premaxillary) and appendages
(24 pterygoid, 24' ectopterygoid, 26 malar, 27 squamosal);
Mandibular arch (28 tympanic, 29—32 mandible);
Hyoidean arch (39 epihyal, 40 ceratohyal, 41 basihyal);
Scapular arch (50 suprascapula, 51 scapula, 52 coracoid) and appendages
(53—58 bones of fore-limb).
The bones of the splanchno-skeleton, are
The petrosal (16) and otosteals (16');
The sclerotals (17) which in most retain their primitive histological condition
as fibrous membrane.
The turbinals (18 and 19) and teeth.
The bones of the exo-skeleton, are
The lacrymals (73).
The superorbitals (present in Alligator sclerops).

There remains to complete this preliminary sketch of the osteology of the Crocodile
a brief notice of the bones composing the diverging appendage of the pelvic arch: these being a repetition of the same element as the appendage of the scapular arch modified and developed for a similar office, manifest a very close resemblance to it. The first bone, called the 'femur,' is longer than the humerus, and, like it, presents an enlargement of both extremities, with a double curvature of the intervening shaft, but the directions are the reverse of those of the humerus, as may be seen in Pl. 1, where the upper or proximal half of the femur is concave, and the distal half convex, anteriorly. The head of the femur is compressed from side to side, not from before backwards as in the humerus; a pyramidal protuberance from the inner surface of its upper fourth represents a 'trochanter;' the distal end is expanded transversely, and divided at its back part into two condyles.

The next segment of the hind-limb or 'leg,' includes, like the corresponding segment of the fore-limb called 'fore-arm,' two bones. The largest of these is the 'tibia,' and answers to the radius. It presents a large, triangular head to the femur; it terminates below by an oblique crescent with a convex surface.

The 'fibula' is much compressed above; its shaft is slender and cylindrical, its lower end is enlarged and triangular.

All these long bones have a narrow medullary cavity.

The group of small bones which succeed those of the leg, are the tarsals; they are four in number, and have each a special name. The 'astragalus' articulates with the tibia, and supports the first and part of the second toe. It is figured in Cuvier's
'Ossemens’s Fossiles,' tom. v, pt. ii, pl. iv, figs. 19 A, B, C, D. The ‘calcaneum’ intervenes between the fibula and the ossicle supporting the two outer toes; it has a short but strong posterior tuberosity.

The ossicle referred to represents the bone called ‘cuboid’ in the human tarsus. A smaller ossicle, wedged between the astralagus and the metatarsals of the second and third toes is the ‘ectocuneiform.’

Four toes only are normally developed in the hind-foot of the Crocodilia; the fifth is represented by a stunted rudiment of its metatarsal, which is articulated to the cuboid and to the base of the fourth metatarsal.

The four normal metatarsals are much longer than the corresponding metacarpals. That of the first or innermost toe is the shortest and strongest; it supports two phalanges. The other three metatarsals are of nearly equal length, but progressively diminish in thickness from the second to the fourth. The second metatarsal supports three phalanges; the third four; and the fourth also has four phalanges, but does not support a claw. The fifth digit is represented by a rudiment of its metatarsal in the form of a flattened triangular plate of bone, attached to the outer side of the cuboid, and slightly curved at its pointed and prominent end.

The teeth.—The most readily recognisable character by which the existing Crocodilians are classified and grouped in appropriate genera, are derived from modifications of the dental system.

In the Caimans (genus Alligator) the teeth vary in number from $\frac{18-18}{18-18}$ to $\frac{22-22}{22-22}$; the fourth tooth of the lower jaw is received into a cavity of the alveolar surface of the upper jaw, where it is concealed when the mouth is shut. In Pl. 1 C, fig. 2, these pits are shown behind the last premaxillary tooth e, in an eocene Alligator from Hordwell. In old individuals of the existing species of Alligator, the upper jaw is perforated by the large inferior teeth in question, and the fosse are converted into foramina.

In the Crocodiles (genus Crocodilus) the fourth tooth in the lower jaw is received into a notch excavated in the side of the alveolar border of the upper jaw, as in fig. 1, Pl. 1 C, behind the tooth e, and is visible externally when the mouth is closed, as in Pl. 1 B, fig. 1. In most Crocodiles, also, the first tooth in the lower jaw perforates the premaxillary bone when the mouth is closed, as in Pl. A 2, between the teeth marked a and b.

In the two preceding genera the alveolar borders of the jaw have an uneven or wavy contour, and the teeth are of an unequal size.

In the Gavials, (genus Gavialis) the teeth are nearly equal in size and similar in form in both jaws, and the first as well as the fourth tooth in the lower jaw, passes into a groove in the margin of the upper jaw when the mouth is closed, Pl. 1.

In the Alligators and Crocodiles the teeth are more unequal in size, and less regular
in arrangement, and more diversified in form than in the Gavials: witness the strong thick conical laniary teeth at the fore part of the jaw, as shown in Pl. 2 A, figs. 3 and 6, as contrasted with the blunt mammillate summits of the posterior teeth, as shown in Pl. 3 A, fig. 12. The teeth of the Gavial are subequal, most of them are long, slender, pointed, subcompressed from before backwards, with a trenchant edge on the right and left sides, between which a few faint longitudinal ridges traverse the basal part of the enamelled crown.

The teeth of both the existing and extinct Crocodilian reptiles consist of a body of compact dentine forming a crown covered by a coat of enamel, and a root invested by a moderately thick layer of cement. The root slightly enlarges, or maintains the same breadth to its base, which is deeply excavated by a conical pulp-cavity extending into the crown, and is commonly either perforated or notched at its concave or inner side.

The dentinal tubes in the crown of a fully-developed tooth form short curvatures at their commencement at the surface of the pulp-cavity, and then proceed nearly straight to the periphery of the crown; they very soon bifurcate, the divisions slightly diverging; then continuing their course with gentle parallel undulations, they subdivide near the enamel, and terminate in fine and irregular branches, which anastomose generally by the medium of cells. The dentinal tubes send off from both sides, throughout their progress, minute branches into the intervening substance, and terminate in the dentinal cells. These cells are subhexagonal, about \( \frac{1}{800} \) of an inch in diameter, and are traversed by from ten to fourteen of the dentinal tubes; they are usually arranged in planes parallel with the periphery of the crown, near which they are most conspicuous, and towards which their best defined outline is directed: they combine with the parallel curvatures of the dentinal tubes to form the striae, visible in sections of the teeth by the naked eye, which cause the stratified appearance of the dentine as if it were composed of a succession of superimposed cones. The diameter of the dentinal tube before the first bifurcation is \( \frac{1}{2000} \) of an inch, both the trunks and bifurcations of the tubes have interspaces equal to four of their respective diameters.

The enamel viewed in a transverse section of the crown presents some delicate striae parallel with its surface, whilst the appearance of fibres vertical to that surface is only to be detected, and these faintly, on the fractured edge. It is a very compact and dense substance; the dark brownish tint is strongly marked in the middle of the enamel when viewed by transmitted light.

The cells with which the fine tubes of the basal cement communicate, are oblong, about \( \frac{1}{800} \) of an inch across their long axis, which is transverse to that of the tooth; the inter-communicating tubes, which radiate from the cells, giving them a stellate figure. I have entered into these particulars of the microscopic texture of the teeth of the Crocodile because it will be seen in the sequel that important modifications of the dental tissues characterise some of the extinct Reptilia.
In the black Alligator of Guiana the first fourteen teeth of the lower jaw are implanted in distinct sockets, the remaining posterior teeth are lodged close together in a continuous groove, in which the divisions for sockets are faintly indicated by vertical ridges, as in the jaws of the Ichthysosaurs. A thin compact floor of bone separates this groove, and the sockets anterior to it, from the large cavity of the ramus of the jaw; it is pierced by blood-vessels for the supply of the pulps of the growing teeth and the vascular dentiparous membrane which lines the alveolar cavities.

The tooth-germ is developed from the membrane covering the angle between the floor and the inner wall of the socket. It becomes in this situation completely enveloped by its capsule, and an enamel-organ is formed at the inner surface of the capsule before the young tooth penetrates the interior of the pulp-cavity of its predecessor.

The matrix of the young growing tooth affects, by its pressure, the inner wall of the socket, and forms for itself a shallow recess; at the same time it attacks the side of the base of the contained tooth; then, gaining a more extensive attachment by its basis and increased size, it penetrates the large pulp-cavity of the previously formed tooth, either by a circular or semicircular perforation. The size of the calcified part of the tooth matrix which has produced the corresponding absorption of the previously formed tooth on the one side, and of the alveolar process on the other, is represented in the second exposed alveolus of the portion of jaw figured in Pl. 75, fig. 4, of my 'Odontography,' the tooth marked \( \alpha \) in that figure, having been displaced and turned round to show the effects of the stimulus of the pressure. The size of the perforation in the tooth, and of the depression in the jaw, proves them to have been, in great part, caused by the soft matrix, exciting dissolution and absorbent action, and not by mere mechanical force. The resistance of the wall of the pulp-cavity having been thus overcome, the growing tooth and its matrix recede from the temporary alveolar depression, and sink into the substance of the pulp contained in the cavity of the fully-formed tooth. As the new tooth grows, the pulp of the old one is removed; the old tooth itself is next attacked, and the crown being undermined by the absorption of the inner surface of its base, may be broken off by a slight external force, when the point of the new tooth is exposed.

The new tooth disembarrasses itself of the cylindrical base of its predecessor, with which it is sheathed, by maintaining the excitement of the absorbent process so long as the cement of the old fang retains any vital connexion with the periosteum of the socket; but the frail remains of the old cylinder, thus reduced, are sometimes lifted off the socket upon the crown of the new tooth, when they are speedily removed by the action of the jaws. This is, however, the only part of the process which is immediately produced by mechanical force: an attentive observation of the more important previous stages of growth, teaches that the pressure of the growing tooth operates upon the one to be displaced only through the medium of the vital dissolvent and absorbent action which it has excited.
Most of the stages in the development and succession of the teeth of the Crocodiles are described by Cuvier* with his wonted clearness and accuracy; but the mechanical explanation of the expulsion of the old tooth, which Cuvier adopts from M. Tenon, is opposed by the disproportion of the hard part of the new tooth to the vacuity in the walls of the old one, and by the fact that the matter impressing—viz. the uncalcified part of the tooth-matrix—is less dense than the part impressed.

No sooner has the young tooth penetrated the interior of the old one, than another germ begins to be developed from the angle between the base of the young tooth and the inner alveolar process, or in the same relative position as that in which its immediate predecessor began to rise, and the processes of succession and displacement are carried on, uninterruptedly, throughout the long life of these cold-blooded carnivorous reptiles.

From the period of exclusion from the egg, the teeth of the crocodile succeed each other in the vertical direction; none are added from behind forwards, like the true molars in Mammalia. It follows, therefore, that the number of the teeth of the crocodile is as great when it first sees the light as when it has acquired its full size; and, owing to the rapidity of the succession, the cavity at the base of the fully-formed tooth is never consolidated.

The fossil jaws of the extinct Crocodilians demonstrate that the same law regulated the succession of the teeth, at the ancient epochs when those highly organized reptiles prevailed in greatest numbers, and under the most varied generic and specific modifications, as at the present period, when they are reduced to a single family, composed of so few and slightly varied species, as to have constituted in the Systema Naturae of Linnaeus, a small fraction of the genus Lacerta.

Having completed the analysis of the constituent parts of the framework of the Crocodilia, which are petrifiable or conservable in a fossil state, and from the study and comparison of which we have to gain our insight into the nature and affinities of the extinct Reptiles, there remains only to be made a few observations on the characteristic mode in which the bones are associated together in certain parts of the skeleton in the present order, and especially in the skull.

With regard to the trunk, the Crocodilia are distinguished from the Lacertilia and from all other existing orders of Reptiles, by the articulation of the vertebral ribs (pleurapophyses) in the cervical and anterior part of the dorsal segments by a head and tubercle to a parapophysis and diapophysis. As this double joint is associated with a double ventricle of the heart, and as the single articulation of every rib in other Reptiles is associated with a single ventricle of the heart, we may infer a like difference in the structure of the central organ of circulation in the extinct reptiles, manifesting the above-defined modifications in the proximal joints of the ribs.

The sacrum consists of two vertebrae only, in Crocodilia as in Lacertilia: they are modified in the present order, as before described, p. 89.

The skull consists, as we have also seen, of four segments. The hinder or occipital surface of the skull presents, in the Crocodilia as in the Lacertilia, a single convex occipital condyle, formed principally by the basioccipital, and not showing the trefoil character which it bears in the Chelonia (Pl. 11, fig. 4), in which the exoccipitals contribute equal shares to its formation. In the Batrachia, the exoccipitals exclusively form the joint with the atlas, and there are accordingly two condyles. The occipital region of the crocodilian skull is remarkable for its solidity and complete ossification, and for the great extent of the surface which descends below the condyle. (Pl. 1 A, fig. 2.) In the Lacertilia, a wide vacuity is left between the mastoid, exoccipital, and paroccipital; but in the Crocodilia this is reduced to the small depressions or foramina near 3, fig. 2, Pl. 1 A. The tympanic pedicles (28) extend outwards and downwards, firmly wedged between the paroccipital, mastoid, and squamosal; in the Lacertians these pedicles are suspended vertically from the point of union of the mastoid and paroccipital.

The chief foramen in the occipital region is that called ‘foramen magnum’ (between 2 and 2, in fig. 2), through which the nervous axis is continued from the skull. On each side of the foramen magnum is a small hole, called ‘precondyloid foramen,’ for the exit of the hypoglossal nerve. External to this is a larger foramen, marked n in fig. 2, for the transmission of the nervus vagus and a vein. Below this is the ‘carotid foramen’ c. All these are perforated in the exoccipital. Below the condyle there is usually a foramen, and sometimes two, for the transmission of blood-vessels. Lower down, at the suture between the basioccipital and basisphenoid, is a larger and more constant median foramen, indicated by the dotted line from e t; it is the bony outlet of a median system of eustachian tubes, peculiar to the Crocodilia. On each side of the median eustachian foramen, and in the same suture, is a smaller foramen, which is the bony orifice of the ordinary lateral eustachian tube. The membranous continuations of the lateral eustachian tubes unite with the shorter continuation from the median tube, and all three terminate by a common valvular aperture, upon the middle line of the faucial palate, behind the posterior or palatal nostril. The large, bony aperture of this nostril is formed by the pterygoids (24 in fig. 2). The carotid canal, c, opens by a short bony tube into the tympanic cavity, and is described as the ‘eustachian canal’ in the ‘Leçons d’Anatomie comparée’ of Cuvier. The artery crosses the tympanic cavity, and enters a bony canal at its fore part, which conducts to the ‘sella turcica’ in the interior of the cranium.

The median eustachian foramen is described by Cuvier as the ‘arterial foramen,’* the canal from which divides and terminates in the ‘sella turcica.’† By MM. Bronn,

* Ossemens Fossiles, tom. v, pt. ii, p. 133.
† Tbid. p. 78.
Kaup, and De Blainville, the median Eustachian foramen is contended to be the bony aperture of the posterior nostrils.*

The results of the dissections and injections of recent Crocodiles and Alligators, by which I have been able to rectify the discrepant opinions regarding the carotid, eustachian, and naso-palatal foramina, and which have led to the discovery of a third median eustachian canal, or rather system of canals, between the tympanic cavities and fauces, peculiar to the Crocodilian Reptiles, are given in detail in the ‘Philosophical Transactions’ for 1850. The complexity of the superadded system has doubtless chiefly contributed to mislead the justly-esteemedit authorities who have believed that they saw in it characters of the carotid canals or of the posterior nasal passages. The eustachian apparatus in the Crocodilia may be briefly described as follows: From the floor of each tympanic cavity two air-passages are continued; the canal from the fore part of the cavity extends downwards, backwards, and inwards, in the basisphenoid, which unites with its fellow from the opposite tympanum, to form a short median canal, which descends backwards to the suture between the basisphenoid and the basioccipital, where it joins the median canal formed by the union of the two air-passages from the back part of the floor of the tympanum, which traverse the basioccipital. The common canal formed by the junction of the two median canals descends along the suture to the median foramen e&t, fig. 2, Pl. 1A. The air-passage from the back part of the tympanum, which traverses the basioccipital, swells out into a rhomboidal sinus in its convergent course towards its fellow, and from this sinus is continued the normal lateral eustachian canal, which, on each side, terminates below in the small aperture, external to the median eustachian foramen.

That part of the outer surface of the skull which is covered by the common integument is more or less sculptured with wrinkles and pits in the Crocodilia: the modifications of this pattern are shown in Pl. A 2, fig. 1, in the nilotic Crocodile, and in Pl. 1A, in the eocene Crocodile from Hordwell. The flat platform of the upper surface of the cranium is perforated by two large apertures, surrounded by the bones numbered 7, 8, 11, 12; these apertures are the upper outlets of the temporal fossæ, divided from the lower and lateral outlets by the conjoined prolongations of the mastoid 8 and postfrontal 12: if ossification were continued thence to the parietal 7, the temporal fossæ would be roofed over by bone, as in the Chelones. In old Crocodiles and Alligators there is an approximation to this structure, and the upper temporal apertures are much diminished in size. In the Gavials (Pl. 1, fig. 1a) they remain more widely open, and, in the fossil Gavials of the secondary strata, they are still wider, as seen in fig. 2a; by which the structure of the cranium approaches more nearly to that of the Lacertian reptiles, where the temporal fossa is either not divided into an upper and lateral outlet, or is bridged over by a very slender longitudinal bar from the postfrontal to the mastoid. The lateral outlets of the temporal fossæ (Pl. 1A.

* Abhandlungen über die Gavialärtigen Reptilien der Lias-formation, folio, 1841, pp. 12, 16, 44.
fig. 1) are divided from the orbits by a bar of bone developed from the postfrontal (12) and malar (26), and against the inner side of the base of which the ectopterygoid abuts; the posterior boundary of the fossa is made by the tympanic (28) and squamosal (27). The orbits, having the postfronto-malar bar (12, 26) behind, are surrounded in the rest of their circumference by the frontal (11), the prefrontal (14), the lachrymal (73), and the malar (26). The supraorbital or palpebral ossicle is rarely preserved in fossil specimens.

The facial or rostral part of the skull anterior to the orbit, is of great extent, broad and flat in the Alligators and some Crocodiles, narrower, rounder, and longer in other Crocodiles, always most narrow, cylindrical, and elongated in the Gavials. The anterior or external nostril is single, and is perforated in the middle of the anterior terminal expansion of the upper jaw. This expansion is least marked in the broad-headed species (compare Pl. 1 A, fig. 1, with Pl. 2 A, fig. 1); in existing Crocodiles and Alligators the points of the nasal bones penetrate its hind border, as at 15, fig. 1, Pl. A 2. In the Gavials (Pl. 1, fig. 1 a) the nasals (n) terminate a long way from the nostril. The Crocodilia resemble the Chelonia in the single median nostril.* In the Lacertilia there is a pair of nostrils, one on each side the median plane, which is occupied by a bridge of bone extending from the usually single premaxillary to the nasals. The plane of the single nostril is almost horizontal in all existing and tertiary Crocodilia.

On the inferior or palatal surface of the skull (Pl. 1 B, fig. 2), the most anterior aperture is the circular prepalatal foramen surrounded by the premaxillaries 22; then follows an extensive smooth, horizontal, bony plate, formed by the premaxillaries (22), the maxillaries (21), and the palatines (20). The postpalatal apertures are always large in the Crocodilia, and are bounded by the palatines (20), maxillaries (21), pterygoids (24), and ectopterygoids (25). The posterior aperture of the nostril is formed wholly by the pterygoids; it is shown in Pl. 1 a, fig. 3, between the bones marked 24. Behind it is the median and lateral eustachian foramen already described, as belonging rather to the posterior region of the head.

**Crocodilus toliapicus, Owen.** Pl. 2, 2, B, fig. 1.

Synt. **Crocodile de Sheppy (?), Cuvier.** Ossemens Fossiles, 4to, tom. v, pt. ii, p. 165.


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Owen. Reports of the British Association, 1841, p. 65.

In proceeding to the comparison, and preparing for the description of the British fossil Crocodilia, I endeavoured, in the first place, to obtain the bones of the species

* In a skeleton of the Alligator lucius in the Museum of the Royal College of Surgeons, a slender bar of bone is continued from the nasals to the premaxillary, across the median nasal aperture, as it is in the skull of the same species figured in the 'Ossemens Fossiles,' tom. v, pt. ii, pl. i, fig. 8.
which now exists in a locality nearest to Great Britain, and also of an individual of that same species which had lived at a remote period; and I have been favoured by the kindness of my esteemed friend Philip Duncan, Esq., Fellow of New College, Oxford, and Conservator of the Ashmolean Museum, with the opportunity of examining the bones of a mummified Crocodile from a sarcophagus at Thebes, in that collection at Oxford. Two views of the skull of this old Egyptian Crocodile are given in Pl. A 2. The total length of the skull from the bone marked 28 to the end of 22, is twice the breadth of the back part of the skull. The upper apertures of the temporal fossa are subcircular; the point of the squamosal (27) projects into the lateral aperture. The breadth of the back part of the sculptured cranial platform (8, 8), is less by one fourth than the breadth of the skull anterior to the orbits. The breadth of the interorbital space is nearly equal to the transverse diameter of the orbit. The points of the nasals (15) project into the external nostril. The postpalatal apertures reach as far forwards as the seventh tooth, counting from the hindmost; there are nineteen alveoli on each side of the upper jaw, the five anterior teeth being lodged in the premaxillary, which is perforated by the first tooth of the lower jaw.

Geoffroy St. Hilaire has applied the old Egyptian name Σοῦχος to the mummified Crocodiles of that country; but there is no good specific character which distinguishes them from the modern Crocodiles of the Nile, to which Cuvier has given the name of Crocodylus vulgaris.

Cuvier appears to have first called the attention of palæontologists to the remains of Crocodylia in the Eocene clay forming the Isle of Sheppy, in the last volume of the second edition of his great work on the ' Ossemens Fossiles,' p. 165, 1824. He there specifies a third cervical vertebra, which was obtained by M. G. A. Deluc, at Sheppy, and of which Cuvier made a drawing at Geneva; he says it much resembles the corresponding vertebra in one of our living Crocodiles, and might have come from an individual about five feet in length. "M. Deluc," he adds, "found very near it a much smaller vertebra, which I recognised as belonging to a monitor or some allied genus."*

Our knowledge of the Eocene Crocodiles of Sheppy received a remarkable accession at the publication of the highly interesting and instructive 'Bridgewater Treatise' of Dr. Buckland, in which he states that "true Crocodiles, with a short and broad snout, like that of the Caiman and the Alligator, appear, for the first time, in strata of the tertiary periods, in which the remains of mammalia abound. . . . One of these," he adds, "found by Mr. Spencer in the London Clay of the Isle of Sheppy, is engraved Pl. 25', fig. 1," and the name 'Crocodylus Spenceri' is appended to that figure.

* Could this have been a vertebra of the large serpent, which I have subsequently described under the name of Palaeophis? I have not as yet met with a single lacertian vertebra from Sheppy. If the collection of M. Deluc be still preserved at Geneva, the vertebra in question might be compared with the figures of the Palaeophis toliapicus, 'Ophidia,' Pl. 1.
In preparing my ‘Report on British Fossil Reptiles’ for the British Association in 1841, I examined the original specimen figured by Dr. Buckland, in which unfortunately the end of the snout with the intermaxillaries and an indeterminate proportion of the maxillaries having been broken off and lost, no exact idea could be formed of the proportions of the facial or rostral part of the skull.

In a larger specimen of the fossil skull of a Crocodile from Sheppy, in the British Museum, the whole of the upper, as well as the lower jaw, were preserved, and as the proportions of the snout agreed with those of some true Crocodiles, and differed in an equal degree with those species from the Gavial; and as, like the Crocodiles and Caimans, it presented the more important distinction of a different composition of that part of the skull, I retained for the specimen in that ‘Report’ the name of Crocodilus Spenceri, proposed by the author of the Bridgewater Treatise for the Sheppy Crocodile, so differing from the Gavial.

The able keeper of the Mineralogical Department of the British Museum, Charles König, K.H., F.R.S., to whom I am indebted for every facility in describing and figuring this specimen, has suggested that the name by which Baron Cuvier first indicated the existence of a true Crocodile in the Eocene clay of Sheppy, should have the priority, and I adopt, therefore, the name Crocodilus tolaiacus, which he has attached to the specimen in question, and with the more readiness since I have now reason to doubt whether the mutilated cranium, figured in the ‘Bridgewater Treatise,’ belongs to the same species.

The more entire fossil skull in question presents the following dimensions:

<table>
<thead>
<tr>
<th>Description</th>
<th>Feet</th>
<th>Inches</th>
<th>Lines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length from the hindmost part of the lower jaw</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Breadth between the articular ends of the tympanics</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Do. across the orbits</td>
<td>0</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Do. of the intertemporal space</td>
<td>0</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Do. of the interorbital space</td>
<td>0</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>From the articular end of the tympanic to the orbit</td>
<td>0</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>From the occipital condyle to the orbit</td>
<td>0</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>From the orbit to the external nostril</td>
<td>0</td>
<td>14</td>
<td>0</td>
</tr>
<tr>
<td>Breadth of the cranium five inches in advance of the orbits</td>
<td>0</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Do. across the external nostril</td>
<td>0</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Depth of the lower jaw at the vacuity between the angular and surangular</td>
<td>0</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Length of that vacuity</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Breadth of the base of one of the larger maxillary teeth</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
</tbody>
</table>

This remarkably fine fossil skull, which is figured one third of its natural size in Pl. 2, and Pl. 2 D, fig 1, presents proportions which come nearest to those of the Crocodilus acutus, being longer in proportion to its basal breadth than in the Crocodilus Suchus, in which the diameter between the articular ends of the tympanis (28) is just half the length of the entire skull. The interorbital space in the Crocodilus tolaiacus is relatively
narrower and flatter than in the *Crocod. acutus* or *Crocod. Suchus*, and the facial part of the skull becomes narrower before the expansion of the upper jaw, at the figure 15, than it does in either of those species. The narrow elongated nasals on which the figure 15 is placed, extend forwards to the external nostril (22), as in the true Crocodiles, and the alveolar border is festooned as is shown in the side view in Pl. 2. The teeth are \( \frac{22-22}{20-20} \) in number: they are more uniform in size, and more regularly spaced than in the recent species above cited, and resemble in this respect the teeth of the *Crocodilus Schlegelii* of S. Müller, which is from Borneo. The extent of the symphysis of the lower jaw is greater in the *Crocodilus toliapicus* than in the *Crocod. acutus*, and the Sheppy species in this respect more nearly resembles the living species from Borneo above cited.

**Crocodilus champsoides**, *Owen*. Plates 2A, 2B, fig. 2.'

**Syn.** *Crocodile de Sheppy (?), Cuvier*. Loc. cit.


The fossil skull already described establishes the fact of the existence of a true Crocodile in the London Clay at Sheppy, but not of a species with a short and broad snout; the present specimen equally demonstrates the presence at the earliest period of the Tertiary geological epoch of *Crocodilia* with those modifications of the cranial and dental structure on which the characters of the restricted genus *Crocodilus* of modern Zoology are founded, but they are associated with a general form of the head which approaches more nearly to the Gavials than does that of the *Crocodilus toliapicus*, and which are most nearly paralleled amongst the known existing true Crocodiles by the *Crocodilus Schlegelii*. This Bornean species was, in fact, originally described as a new species of *Gavial*, but the nasal bones, as in the fossil from Sheppy figured in Pl. 2A, 15, extend to the hind border of the external nostril.

The fine subject of Plate 2A, forms part of the collection of J. S. Bowerbank, Esq. F.R.S., which is well known for its rich and varied illustrations of the fossils of the Isle of Sheppy.

The following are some of its admeasurements:

<table>
<thead>
<tr>
<th>Description</th>
<th>Feet</th>
<th>Inches</th>
<th>Lines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length from the occipital condyle to the end of the premaxillaries</td>
<td>1</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Breadth across the hinder angles of the supracranial platform</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Do. across the orbits</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Do. of the intertemporal space</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Do. of the interorbital space</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Do. across the external nostril</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>From the occipital condyle to the orbit</td>
<td>0</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>From the orbit to the external nostril</td>
<td>3</td>
<td>10</td>
<td>0</td>
</tr>
</tbody>
</table>
The skull yielding the above dimensions is much smaller than that of the *Crocodilus toliapicus*, Pl. 2 B; but it cannot have belonged to a younger individual of the same species, because, in existing Crocodiles, the part of the skull anterior to the orbits is proportionally shorter in the young than in the old individuals, as may be seen by comparing the figures which Cuvier has given of the skulls of three individuals of different ages of the *Crocodilus biporcatus*, in figures 4, 18, and 19, of plate 1 of the last volume of the 'Ossemens Fossiles'; whereas the part of the skull anterior to the orbits is relatively longer and more slender in the smaller fossil skull now described than in the larger one on which the species *Croc. toliapicus* is founded. We have, therefore, satisfactory proof that two species of true Crocodile existed during the deposition of the Eocene Clay at the actual mouth of the Thames, and have left their remains in that locality.

Their specific distinction is further illustrated by the different forms and proportions of particular parts of the skull. The alveolar border is more nearly straight; the transverse expansion of the maxillaries (21) is less, whilst that of the premaxillaries (22) is greater; the interorbital space is broader and more concave. The teeth are more uniform in size, are more regularly spaced, and are wider apart: they are, likewise, upon the whole, larger in proportion to the size of the jaw. Figure 5, Pl. 2 A, shows the crown of a new tooth just emerging from the second socket of the maxillary bone of the natural size; figure 6 is the fourth tooth of the premaxillary, fully formed; fig. 7 is the displaced tooth which is cemented by the matrix to the palatal surface of the premaxillary in fig. 2. The enamelled crown shows the fine raised longitudinal ridges better developed than one usually sees them in modern Crocodiles. There are twenty-one alveoli on each side of the upper jaw.

In all the particulars in which the skull under description differs from that of the *Crocodilus toliapicus*, it departs further from the nilotic crocodile, and resembles more the Gavial-like Crocodile of Borneo; and as one of the old Egyptian names of the Crocodile, *Champsia*, has been applied generically to the Gavials by some recent Erpetologists, I have adopted the term 'Champsoides' to signify the resemblance of the present extinct species of Eocene Crocodile to the Gavials.

The basioccipital condyle, together with the condyloid processes of the exoccipital, project backwards in the *Croc. champsoides* farther than in any modern Crocodile; and the supraoccipital 3, fig. 4, Pl. 2 A, descends nearer to the foramen magnum.

The upper jaw is more depressed, and the suborbital part of the maxillary bone is much less inclined to the vertical in the present skull than in the original of Dr. Buckland's figure of the *Crocodilus Spenceri*, which in other respects more nearly resembles the *Croc. champsoides* than the *Croc. toliapicus*; the difference above specified seems to be greater than can be accounted for by any accidental pressure to which the fossil skull figured in Pl. 2 A can have been subjected. The mutilated skull to which the term *Croc. Spenceri* was originally applied, is defective, as I have said, in the
CROCODILIA.

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facial or maxillary portion which is requisite for its unequivocal determination to either of the two species which the more perfect specimens since acquired have proved to have existed at the Eocene tertiary period. The form of the mutilated portion of skull, and the figure of it given in Pl. 25 of the 'Bridgewater Treatise,' might well appear to indicate a short and broad snouted species of true Crocodile; but if it be not distinct from the two better represented species above described, I should be more inclined to refer it to that which has the longest and narrowest snout, from the conformity of the characters of the part of the skull which is preserved. A view of the palatal surface of the specimen in question is given in Pl. 2 B, fig. 2.

Crocodilian vertebrae referable to the two foregoing species of Sheppy Crocodiles.

Not more than two species of Crocodile are indicated by the detached vertebrae from Sheppy; but the different proportions of the homologous cervical vertebrae, figs. 3 and 7, Pl. 3 A, and of the characteristic biconvex caudal vertebra, fig. 7, Pl. 3, and fig. 10, Plate 3 A, would have determined the fact of there being two distinct species, had their cranial characters, which are so satisfactorily demonstrated in Plates 2 and 2 A, remained unknown. I refer, provisionally, the shorter and thicker vertebrae to the Crocodilus toliapicus with the shorter and thicker snout, and the longer and thinner vertebrae to the Croc. champsoiides with the snout of similar proportions.

Vertebrae of the Crocodilus toliapicus, Plate 3 and Plate 3 A, figs. 1, 2, 3, 5, 6.

The vertebra, figs. 1, 2, Pl. 3 A, is the fourth cervical; it differs from that of the Crocodilus acutus, Croc. Suchus, and Croc. biporcatus, in the greater breadth and squareness of the base of the hypapophysis (fig. 2 h), which extends almost to the bases of the parapophyses p; the vertical diameter of the parapophyses is greater in comparison with their antero-posterior extent in the fossil than in the above-cited recent Crocodiles; the neurapophyses are thicker, and terminate in a more rounded border both before and behind; their bases extend inwards, and meet above the centrum, whilst a narrow groove divides them in the recent Crocodiles above cited; the length of the centrum is greater in proportion to the height and breadth in the fossil vertebra. In other respects the correspondence is very close, and the modern crocodilian characters are closely repeated. Traces of the suture between the centrum and neurapophysis remain, as shown at n, n, fig. 1. The diapophysis d, and the upper portion of the neural arch, with the zygaphyses and neural spine, have been broken away; the borders of the articular ends of the centrum have been worn away.

The vertebra (fig. 3, Pl. 3 A) is the sixth cervical: in this specimen the base of the hypapophysis is contracted laterally and extended antero-posteriorly; the side of the centrum above the parapophysis (p) has become less concave; the vertebra has increased
more in thickness than in length; in these changes it corresponds with the modern Crocodiles; it has been mutilated and worn in almost the same manner and degree as the fourth cervical.

The vertebra (figs. 1, 2, Pl. 3) is a seventh cervical of a smaller individual of the *Crocodilus toliapicus*. The hypapophysis has become more compressed and more extended antero-posteriorly; the parapophysis has become shortened antero-posteriorly, and increased in vertical diameter. The anterior concave surface of the centrum (fig. 1) is more circular, less extended transversely, than in the corresponding vertebra of the recent Crocodiles compared with the fossil.

Figures 3, 4, Pl. 3, are two views of the eighth cervical of an individual of about the same size as that to which the fourth and sixth cervicals in Pl. 3 A belong. Fig. 4, exemplifies the same difference which fig. 1 presents in regard to the more circular contour of the anterior concave surface of the centrum as compared with recent Crocodiles; the bases of the neurapophyses are thicker and more rounded anteriorly; the neural canal is rather more contracted; the base of the hypapophysis more extended in the axis of the vertebra (see fig. 3) than in the recent Crocodiles compared. The parapophyses have now risen, as in those Crocodiles, to the suture of the neurapophysis, and the diapophysis springs out at some distance above that suture.

Fig. 6, Pl. 3, shows the under surface of a dorsal vertebra, in which the hypapophysis ceases to be developed (probably the fourth or fifth).

Fig. 5, Pl. 30, gives the same view of one of the lumbar vertebrae, showing the elongation of the centrum, and the broad bases of the depressed diapophyses; there is an indication of two longitudinal risings towards the back part of the under surface of the centrum.

Figs. 5 and 6, Pl. 3 A, give two views of the anterior sacral vertebra of the *Crocodilus toliapicus*; it is concave and much expanded transversely at its fore part (fig. 5), flattened and contracted behind. Traces of the suture remain to show the proportion of the anterior articular surface which is formed by the base of the pleurapophysis p; and fig. 6 shows the extension of that base from the side of the centrum upon the diapophysis or overhanging base of the neurapophysis; the under surface of the centrum of this vertebra has a slight median longitudinal rising.

Fig. 7, Pl. 3, gives a side view of the characteristic, biconvex, anterior caudal vertebra of the *Crocodilus toliapicus*.

Figs. 8, 9, Pl. 3, give two views of a middle caudal vertebra: in fig. 9 are shown the characteristic hypapophysial ridges extending from the articular surfaces for the haemapophyses at the hind part of that aspect of the centrum: in fig. 8 the processes of the neural arch are restored in outline; a thick and low ridge extends from the middle of the side of the centrum to the base of the transverse process which it strengthens, like an underpropping buttress.
Vertebrae of the Crocodilus champsoïdes.

Figures 7 and 8, Pl. 3 A, give two views of the third cervical vertebra of the above-named gavial-like Crocodile, which vertebra, besides its longer and more slender proportions, differs in the smaller size of its hypapophysis from the corresponding vertebra in any existing species of Crocodile or Gavial: the process in question being in the form of a low crescentic ridge, as shown at figure 8, between the bases of the parapophyses (p).

Both parapophyses terminate by a convex surface, which appears to have been a natural one. Between the parapophysis (p) and diapophysis (d), fig. 7, the side of the centrum is more deeply excavated than in the Crocodilus toliapicus. The centrum contributes a small part to the base of the diapophysis, as in the third cervical vertebra of modern Crocodiles. The neurapophysis are thinner than in the Croc. toliapicus, and their bases do not join one another above the centrum. The longitudinal ridge extending from the anterior to the posterior zygapophysis is sharply defined.

Figure 4, Pl. 3 A, is the first dorsal vertebra of the Crocodilus champsoïdes, in which, as in existing Crocodiles, the parapophysis (p) has passed almost wholly from the centrum upon the neurapophysis, the diapophysis (d) having been subject to a corresponding ascent. The base of the compressed hypapophysis extends over the anterior third of the middle line of the under surface of the centrum. There is a remarkable transverse constriction at the base of the posterior ball of the centrum, as if a string had been tied round that part when it was soft, and there is no appearance of this groove having been produced by any erosion of the fossil, or being otherwise than natural.

The same character is repeated, though with less force, in the posterior dorsal vertebra, fig. 9, Pl. 3 A, and, together with the general proportions of the specimen, supports the reference of that vertebra to the Crocodilus champsoïdes. There is a slight longitudinal depression at the middle of the side of the centrum near the suture with the neurapophysis (n, n).

Figure 10 is a side view of the first caudal vertebra of the Crocodilus champsoïdes: besides being longer and more slender than that vertebra is in the Croc. toliapicus, the inferior surface of the centrum is less concave from before backwards.

The evidences of Crocodilian reptiles from the deposits at Sheppy less characteristic of particular species than those above described, are abundant. Mr. Bowerbank possesses numerous rolled and fractured vertebrae, condyloid extremities, and other portions of long bones; with fragments of jaws and teeth.

Mr. J. Whickham Flower, F.G.S., has transmitted to me some fragments of the skull of a Crocodile from Sheppy, including the articular end of the tympanic bone, equalling in size that of a Crocodilus biporcatus the skull of which measures two feet eight inches in length.

Mr. Leifchild, C.E., possesses a considerable portion of the lower jaw of a Crocodile
of at least equal dimensions, also from Sheppy, showing the angle of union of the rami of the lower jaw which corresponds with that in the *Crocodilus toliapicus*, Pl. 2.

In the museum of my esteemed and lamented friend, the late Frederic Dixon, Esq., F.G.S., at Worthing, is preserved a portion of the fossilized skeleton of a Crocodile, from the Eocene clay at Bognor, in Sussex; it consists of a chain of eight vertebrae, including the lumbar, sacral, and the biconvex first caudal, which are represented of their natural size in tab. xv, of Mr. Dixon's beautiful and valuable work on the 'Geology of Sussex.' A dorso-lateral bony scute adheres to the same mass of clay close to the vertebrae, and doubtless belonged to the same individual. The proportions of the vertebrae agree with those of the *Crocodilus toliapicus*. This fine specimen was discovered, and presented to Mr. Dixon, by the Rev. John Austin, M.A., Rector of Pulbrough, Sussex. Mr. Dixon had also obtained from the same locality a posterior cervical vertebra of a Crocodile, similar in its general characters to those above mentioned, but belonging to a larger individual. The length of the body of this vertebra is two inches and a half.

I have examined some remains of *Crocodilia* from the London Clay at Hackney; but as these also are not sufficiently perfect or characteristic for decided specific determination, no adequate advantage would be obtained by a particular description, or by figures of them.

The chief conclusion arrived at from the study of the Crocodilian fossils from the Island of Sheppy has been the proof, by the specimens selected for depiction in the present work, that at least two species of true *Crocodile* have left their remains in that locality; that neither of these had a short and broad snout like the Caimans, but that one of them—the *Croc. champsoïdes*—much more nearly resembled the Gavial of the Ganges in the proportion of that part of the skull; although, in its composition, especially as regards the length and connexions of the nasal bones, it is a true Crocodile.

Amongst the existing species of Crocodile the *Croc. acutus* of the West Indies offers the nearest approach to the *Croc. toliapicus*, and the *Croc. Schlegelii* of Borneo, most resembles the *Croc. champsoïdes*. But there are well-marked characters in both the skull and the vertebrae which specifically distinguish the two fossil Crocodiles of Sheppy from their above-cited nearest existing congener.

**Crocodilus Hastingsiæ**, Owen. Plates 1 A, 1 B, 1 C, fig. 1 and Pl. 1 E, figs. 2 and 5.

Reports of the British Association, 1847, p. 65.

That Crocodiles with proportions of the jaws assigned to the Eocene species noticed in Dr. Buckland's 'Bridgewater Treatise' and especially adapted for grappling with strong mammiferous animals, actually existed at that ancient tertiary epoch, and have left their remains in this island, is shown by the singularly perfect fossil skull figured in the above-cited plates. This specimen was discovered by the Marchioness of Hastings, in the Eocene fresh-water deposits of the Hordle Cliffs in Hampshire, which her
Ladyship has described in the volume of 'Reports of the British Association' above cited, (p. 63).

When the specimen was originally exposed, it was in the same extremely fragile and crumbling state as the beautiful carapaces of Trionyx obtained by Lady Hastings from the same locality, and described and figured in the chapter Chelonia; but thanks to the skill and care with which the noble and accomplished discoverer readjusted and cemented the numerous detached fragments of those specimens, the present unique fossil has been in like manner restored as nearly to its original state as is represented in the plates; and all the requisite characters for determining the nature and affinities of the species, can now be studied with the same facility as in the skulls of existing Crocodiles.

If the reader will compare the plates above cited with the section of Cuvier's 'Ossements Fossiles,' in which the distinctions between the Alligators and Crocodiles are specified,* he will see, (in fig. 1, Pl. 1 B) for example, that the fourth tooth or canine of the lower jaw is not received into a circumscribed cavity of the upper jaw, but is applied to a groove upon the side of the upper jaw, and is exposed. Fig. 1, Pl. 1 A, shows that the prefrontal (14) and lachrymal (73) bones, instead of descending much less upon the facial part of the skull, extend much more, and advance nearer to the end of the muzzle than in any Alligator, or even than in any actual species of broad-nosed Crocodile.

The vacuities left between the postfrontal (12), the parietal (7), and the mastoid (8) (Pl. 1 A, fig. 1, and Pl. 2 B, fig. 3), are as wide as in the skull of a Crocodilus biporcatus of equal size, and are larger than in the Alligator lucius or All. sclerops. Fig. 2, Pl. 1 B, shows that no part of the vomer is visible between the premaxillaries (22) and maxillaries (21), or elsewhere on the palate. But the palatine expansion of the vomer is not a constant character; it is wanting, for example, in the Alligator lucius of North America. The palatines (20) are not more advanced in the fossil in question than they are in the true Crocodiles, and their anterior portion does not expand to its anterior truncated termination. The posterior nostril, the entire contour of which is shown in the portion of the skull of the same species figured in Pl. 1 A, fig. 3, is longer than it is broad.

There is but one character in which the fossil skull in question differs from the true Crocodile, and agrees with most species of Alligator; it is in the reception of the two anterior teeth of the lower jaw into cavities of the premaxillaries, shown in

* "Les têtes des caïmans, outre le nombre des dents, et surtout la manière dont la quatrième d'en bas est reçue, outre les différences qui dépendent de la circonscription totale, se distinguent de celles des Crocodiles proprement dits, 1°, parce que le frontal antérieur et le lacrymal descendent beaucoup moins sur le museau; 2°, en ce que les trous percés à la face supérieure du crâne, entre le frontal postérieur, le pariétal et le mastoidien, y sont beaucoup plus petits, souvent même y disparaissent tout-à-fait, comme dans le caïman à paupières osseuses; 3°, en ce que l'on aperçoit une partie du vomer dans le palais, entre les intermaxillaires et les maxillaires; 4°, en ce que les palatins avancent plus dans ce même palais, et s'y élargissent en avant; 5°, en ce que les narines postérieures y sont plus larges que longues, etc." (tom. v, pt. ii, p. 105.)
fig. 2, Pl. 1 B, which are not perforated; so that there are no foramina anterior to the bony nostril, as in Pl. A 2, in the bone marked 22. These foramina are not, however, absent in all Alligators; the skull of the Alligator sclerops, figured by Cuvier (tom. cit., pl. i, fig. 7), shows them, as do all the species of true Crocodile the skulls of which are figured in the same plate. There is one character by which the Crocodilus Hastingsiae differs, from all known species of both Crocodile and Alligator: it is that afforded by the broad and short nasal bones (15, fig. 1, Pl. 1 A), which do not reach the external nostril; this being formed, as in the Gavials, exclusively by the premaxillaries 22.

In the general proportions, however, of the skull in question, especially the great breadth, shortness, and flatness of the obtusely-rounded snout, it resembles that of the Alligators more than that of any known species of true Crocodile, the length from the tympanic condyle to the end of the snout being to the breadth taken at the condyles as 16 to 9.

The following are dimensions of the fossil in question:

<table>
<thead>
<tr>
<th>Description</th>
<th>Feet</th>
<th>Inches</th>
<th>Lines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of skull from the angle of the lower jaw to the end of the snout</td>
<td>1</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Do. from the tympanic condyle to ditto.</td>
<td>1</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Do. do. to the orbit</td>
<td>0</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Do. from the orbit to the external nostril</td>
<td>0</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Breadth of the skull across the tympanic condyles</td>
<td>0</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Do. the orbits</td>
<td>0</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Do. the external nostril</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Longest diameter of upper temporal aperture</td>
<td>0</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Do. the post-palatal vacuities</td>
<td>0</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Depth of the lower jaw at the posterior vacuity</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Depth of the occipital region</td>
<td>0</td>
<td>4</td>
<td>3</td>
</tr>
</tbody>
</table>

The occipital region of the skull (Pl. 1 A, fig. 2), in the proportion of its breadth to the depth of the lateral parts formed by the conjoined paroccipitals (4) and mastoids (8), resembles that of the true Crocodiles rather than that of the Alligators, in which that region is proportionally deeper than in the Crocodiles; the vertical extent of the supraoccipital is less, and that of the conjoined parts of the exoccipitals above the foramen magnum is greater; the vertical extent of the descending part of the basioccipital is also greater in proportion to its breadth than in the Alligators. The proportion of the basisphenoid (5) and of the conjoined parts of the pterygoids (24) which appear in this view (fig. 2), is less than in the Alligators, but is greater than in most Crocodiles, thus presenting an intermediate character; but the entire exclusion of any part of the posterior nostril from this view is a character of the Alligators, and is due to the horizontal plane of that aperture in them, and to its position in advance of the posterior border of the pterygoids, from which it is partitioned off usually by a bony ridge. The posterior nostril has the same position and aspect in the Crocodilus Hastingsiae, and these characters of the posterior nostril are perhaps more distinctive between
Alligator and Crocodile than the shape of the aperture, in which the present fossil differs from both the Alligators and most of the Crocodiles with which I have compared it. The backward extension of the exoccipitals and of the basioccipital condyle, is such as to bring both parts into view in looking directly upon the middle of the upper surface of the skull, as in Pl. 1A, fig. 1. In this character the fossil resembles the Crocodiles more than the Alligators, but the projection is greater than in existing Crocodiles, and equals that in the Sheppy Crocodilus champsoides.

On the upper surface of the skull a distinctive character has been pointed out by Cuvier in the different proportions of the supra-temporal apertures in the Alligators and Crocodiles. The horizontal platform in which these apertures are perforated, is also square in the Alligators; the mastoidal angles being less produced outwards and backwards, and the postfrontal angles less rounded off; this difference is shown in the skulls figured in Cuvier's pl. i, tom. cit. The Croc. Hastingsiæ, both by the obtuseness of the postfrontal angles, and the acuteness and production of the mastoidal angles, resembles the Crocodiles, as well as by the size of the supra-temporal apertures; these are ovate with the small end turned forwards and a little outwards.

Another character may be noticed in the figures of the skulls of the three species of Alligators as compared with those of the three species of Crocodile in Cuvier's pl. i, viz. the larger proportional size of the orbits in the former, in which the orbit much exceeds in size the lateral temporal aperture. In the Alligator niger, also, I find the orbits enormous, and it is the encroachment of the narrow anterior part of the orbital cavity upon the nasal cavity of the prefrontal and lachrymal, that renders that part of those bones relatively shorter in the Alligators. In the Crocodilus Hastingsiæ the proportions of the lateral temporal apertures (Pl. 1A, fig. 1, 12, 26) and orbital (11, 14, 73) apertures, are like those in the species of Crocodile in which the orbits are smallest. The extent of the facial part of the prefrontal (14) and lachrymal (73) is greater in the Croc. Hastingsiæ than in any existing species of true Crocodile. Another characteristic of the present fossil presented by the upper surface of the skull, is the shortness as well as breadth of the nasal bones, and their almost truncate anterior termination at nearly one inch from the external nostril. In all the Alligators' skulls that I have examined or seen figured, the nasal bones are broadest at their posterior third part, and converge to a point anteriorly, where in the Alligator lucius, e.g., they extend across the nasal aperture.

The interorbital space is slightly concave in the Crocodilus Hastingsiæ; two broad and slightly elevated longitudinal tracts are continued forwards upon the face from the fore part of the orbits; but they are not developed into ridges, as in the Croc. biporcatus. The maxillaries swell out a little in advance of the middle of the nasals, and then contract to the crocodilian constriction at the suture with the premaxillaries, where the tips of the lower canines appear in the upper view (fig. 1, Pl. 1A), and their whole crown is exposed in the side view (fig. 1, Pl. 1B). The conjoined parts of the premaxillaries send a short pointed projection into the back part of the external nostril.
On the under or palatal surface of the skull (Pl. 1 B, fig. 2) the maxillo-premaxillary suture runs almost transversely across, as in the *Crocodilus rhombifer*, figured by Cuvier in pl. iii, fig. 2, of the volume above cited. There is no appearance of the vomer upon the palate. The palatal bones (20), though somewhat broader anteriorly, and more abruptly truncate than in any existing Crocodile that I have seen, are more like those bones in the true Crocodiles than in the Alligators. The portion between the post-palatal vacuities is longer and narrower; the posterior end of the palatines is narrower, and the part of the bone anterior to the notch receiving the posterior angle of the palatal plate of the maxillary does not expand in advancing forwards, as it does in the Alligators: in the *Alligator niger* this expansion is greater than in the *All. lucius*, and the posterior ends of the palatines are also remarkably expanded, and applied to the anterior borders of the pterygoids almost as far as their articulation with the ectopterygoids, the postpalatal vacuities not at all encroaching on the pterygoids, as they are seen to do at 24, Pl. 1 B, fig. 2, and also in the figure of the *Crocodilus rhombifer* above cited, and in other true Crocodiles. The form of the pterygoids (24, Pl. 1 B, fig. 2) is peculiar in the *Crocodilus Hastingsiæ*: they are contracted anteriorly, and send forwards a short truncated process to meet the narrow posterior ends of the palatines (20); and the same character being repeated in another skull of the same species, from Hordle, also in the collection of Lady Hastings, in which this part of the bony palate (Pl. 1 A, fig. 3) is more perfect than in the subject of Pl. 1 B, fig. 2, it may be regarded with some confidence as specific. In the *Crocodilus champsoïdes* of Sheppy it will be seen, by fig. 2, Pl. 2 B, that the pterygoids (24, 24) are not produced where they join the palatines (20). In the Alligators, the posterior border of the conjoined pterygoids is deeply notched behind the posterior nostrils, the angles of the notch being slightly extended backwards: in most Crocodiles, the sides of the notch are so developed that it does not sink deeper than the line of the posterior border of the pterygoids; and this modification is exaggerated in the *Crocodilus Hastingsiæ* (Pl. 1 A, fig. 3) in which the notch in question is merely the interval between two slender diverging processes from the middle of the back part of the pterygoids. 24. The posterior aperture of the nasal passages is wholly surrounded in the *Crocodilus Hastingsiæ* by the horizontal plate of the pterygoids, and has the same position and aspect as in the Alligators; but its form is heart-shaped, with the apex directed backwards, and the antero-posterior diameter exceeding the transverse one. I have not met with this form of the posterior nostril in any other species of Crocodilian; but it is repeated in two individuals of the *Croc. Hastingsiæ*, and may be regarded as a specific character.

The ectopterygoid, 25, Pl. 1 A, fig. 3, Pl. 1 B, fig. 2 (d, fig. 2, pl. iii, 'Ossemens Fossiles,' t. v, pt. ii) articulates with a larger proportion of the outer surface of the pterygoids (24) in the Crocodiles than in the Alligators: it agrees with the Crocodiles in the extent of this articulation in the *Croc. Hastingsiæ*.

The number of teeth in this species is $\frac{22-22}{20-20} = 84$. 

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In the upper jaw the fourth, ninth, and tenth are the largest; and the fifteenth and sixteenth exceed in size those immediately before and behind them. The alveolar border of the jaw increases in depth to form the sockets requisite for firmly lodging these larger teeth, and gives rise to the festooned outline of the jaw, which is found in all Crocodiles and Alligators in proportion as the teeth are unequal in size.

The lower jaw presents the same compound structure as that in the Crocodilia, with the general form characteristic of that in the Alligators and in most of the true Crocodiles: the symphysis, e. g. is as short as Crocodilus biporcatus and the Alligator niger, in which it extends as far back as the interval between the fourth and fifth socket. This is the relative position of the back end of the symphysis in a fine and perfect under jaw of the Crocodilus Hastingsiae in the collection of the Marchioness of Hastings. In a portion of the under jaw of apparently the same species of Crocodile, from the same locality, in the collection of Searles Wood, Esq., F. G. S., the symphysis terminates opposite the interval between the third and fourth tooth.

The chief distinction observable between the modern Crocodiles and Alligators in the lower jaw is the greater relative size of the vacuity between the angular (30) and surangular (29) pieces, and the greater relative depth of the ramus at that part, in the Alligators. In these characters the lower jaw of the present species more resembles that of the true Crocodiles; although, as the vacuity in question is somewhat larger, a slight affinity to the Alligator might be inferred from that circumstance. The comparative figures of the hinder third of the mandibular ramus in Plate 1 E, figs. 4, 5, 6, will exemplify the difference in question, and the degree of proximity to the crocodilian and alligatorial characters respectively.

With regard to another character deducible from the relation of the backwardly-produced angle of the jaw to the articular surface, the Crocodilus Hastingsiae more decidedly resembles the Alligator: I allude to the depth of the excavation between the articular cavity (29) and the end of the angle (30), and to the lower or higher level of the angle itself: the fossil jaw (fig. 5) resembles the Alligator (fig. 6) in this respect more than the Crocodile (fig. 4). The alveoli are twenty in number in each ramus of the Crocodilus Hastingsiae: the third and fourth are large, of equal size, and close together; behind these the eleventh, twelfth, and thirteenth are the largest, and the alveolar ridge is raised to support them; after the seventeenth the summits of the crowns of the teeth become obtuse, and the crowns mammilloid, and divided by a constriction or neck from the fang; they each, however, have a separate socket, as in the Crocodiles, the septa not being incomplete at the hinder termination of the dental series, as in the Alligator niger figured in my 'Odontography.'*

Fig. 3, Pl. 2 B, gives a representation, of the natural size, of the cranial platform of a young Crocodilus Hastingsiae in the collection of Searles Wood, Esq.; the hemispheric depressions in the surface of the bone are more regular, distinct, and relatively

* Tom. ii, pl. lxxv, fig. 3.
larger, and the interorbital part of the frontal is narrower, concomitantly with the larger proportional eyeballs and orbits of the young animal. The relatively larger supratemporal apertures form another character of nonage; but there is no ground for deducing a specific distinction from any of the differences observable between this part of the young crocodile’s cranium and the corresponding part of that of the more mature specimen (Pl. 1 A).

**Alligator Hantoniensis**, Wood. Plate 1 C, fig. 2.

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On reviewing the characters of the skull of the *Crocodilus Hastingsiæ* we perceive that they combine to a certain extent those which have been attributed to the genus *Crocodilus* and the genus *Alligator*; in general form it resembles most the latter, but agrees with the former in some of the particulars that have been regarded by Cuvier and other palæontologists as characteristic of the true Crocodiles. I allude more particularly to the exposed position of the inferior canines when the mouth is shut. Respecting which, however, I am disposed to ask, whether this be truly a distinctive character of importance? One sees that it needs but a slight extension of ossification from the outer border of the groove to convert it into a pit; yet the character has never been found to fail as discriminative of the several species of existing Crocodiles and Alligators hitherto determined. It constitutes, however, the only difference between the skulls of the *Crocodilus Hastingsiæ* in the collection of the Marchioness of Hastings and that fine portion of skull now, by the kindness of Mr. Searles Wood, before me, on which he has founded the species named at the head of the present section. So closely, in fact, do those specimens from the same rich locality correspond, that any other comparative view than that given in Pl. 1 C appeared superfluous. In both the broad nasal bones terminate at the same distance from the external nostril, which is accordingly formed exclusively by the premaxillaries; in both, the palate-bones present the same narrow, truncate posterior ends, and the same equal breadth of their anterior portions included between the maxillaries; only these terminate rather more obliquely in Mr. Wood’s specimen, their anterior ends forming together a very obtuse angle directed forwards. But this is comparatively an unimportant difference, and I regard as equally insignificant the slight interruption of the transverse line of the maxillo-premaxillary suture, at the middle part, which will be seen by comparing fig. 2 with fig. 1, in Pl. 1 C. The teeth are the same in number, arrangement, and proportion in the *Alligator Hantoniensis* as in the *Crocodilus Hastingsiæ*, and the alveolar border of the jaws describes the same sinuous course.

Had the complete fossil skull first submitted to my inspection at the meeting of the British Association at Oxford presented the same fossæ for the reception of the lower canines which exist in fig. 2, Pl. 1 C, I should have referred it to the Alligators,
notwithstanding the crocodilian characters of the small orbits, the long facial plates of the prefrontal and lachrymal, the wide supratemporal apertures, the non-expansion of the fore part of the palatines, and the non-appearance of the vomer on the palate, with other minor marks of the like affinity. For all these characters arise out of secondary modifications, and are presented in different degrees in the different species of Crocodile, and are rather of a specific than a generic value. They determine the judgment by the extent of their concurrence rather than by their individual intrinsic worth, and for that reason, therefore, the exposed position of the lower canine in the lateral groove of the upper jaw inclined the balance in favour of a reference of the previously-described fossil to the true Crocodiles. One cannot, indeed, attach any real generic importance to the modification of the upper jaw in relation to the lower canines. In three examples, however, in the collection of the Marchioness of Hastings, the crocodilian modification of this character is repeated, as it is shown in Pl. 1 B, fig. 1; and we have to choose, therefore, between the conclusion that Mr. Wood’s specimen (Pl. 1 C, fig. 2) presents an accidental variety in this respect, or to view the fossæ in the upper jaw as indicative of not only a different species but a distinct genus from the Crocodilus Hastingsiæ. I should be glad to have more evidence on this point, and especially the opportunity of comparing the posterior nostrils, the orbits, the supratemporal apertures, and the occipital part of the skull of a specimen from Hordle, repeating the alligatorial character of the fossæ in the upper jaw for the lower canines. I am disposed to regard this character, notwithstanding its constancy in the living species of Alligator, as a mere variety in the Hordle fossil; but pending the acquisition of further evidence, it seems best to record this fossil under the title proposed for it by the able geologist by whom it was discovered.

**Crocodilus Hastingsiæ. Plate 1 D.**

*Vertebrae referable to the Crocodilus Hastingsiæ.*

The fossil crocodilian vertebrae obtained from the Eocene sand at Hordle, notwithstanding the comparatively limited extent of the researches in that interesting formation, are at least as abundant as those which have been discovered at Sheppy, but they do not, as at that locality, indicate two distinct species; all that have, hitherto, been found belong to one and the same kind of Crocodile, and from their robust proportions, would seem to have come from a species with a short and broad muzzle, like that of the Crocodile or Alligator, the fossil skulls of which have been described.

Perhaps the most perfect fossil reptilian vertebra that has hitherto been discovered is the one figured, of the natural size, in Pl. 1 D, figs. 1, 2, and 3. It is the fifth cervical vertebra. As compared with that of the *Crocodilus toliapicus* (Pl. 3 A, figs. 1, 2), which it resembles in size, the hypapophysis, *hy* (fig. 2, Pl. 1 D), is much more compressed, and the under part of the centrum is more extensively and deeply exca-
vated between it and the parapophyses (p); it is also excavated on each side behind the base of the hypapophysis, from which a progressively widening smooth ridge is continued to near the posterior surface of the centrum. The interspace at the side of the vertebra, between the parapophysis and diapophysis, is smaller but deeper in the *Crocodilus Hastingsiae*. The neurapophyses meet above the centrum in both; but in the *Crocodilus Hastingsiae* they are thicker anteriorly and thinner at their posterior border, and the neural canal (fig. 2, n) is more contracted than in the *Crocodilus toliapicus*.

As compared with the cervical vertebra of the *Crocodilus champsoïdes* from Sheppy, the present vertebra differs in the form of the hypapophysis in a greater degree than from the *Crocodilus toliapicus*. Fig. 8, Pl. 3 A, shows as little as does fig. 2 in the same plate, the median ridge and lateral excavations of the under part of the centrum which characterise the present vertebra of the *Crocodilus Hastingsiae*. The *Crocodilus champsoïdes* resembles the *Crocodilus Hastingsiae* in the character of the proportion and depression of that part of the side of the centrum forming the interspace between the parapophysis and diapophysis; but the antero-posterior extent of the parapophysis is relatively less in that Sheppy species. The outer surfaces of the neurapophyses in the *Crocodilus Hastingsiae* slope or converge towards each other from before backwards, in a much greater degree than in either of the Sheppy species. I have not observed in any recent Crocodile or Alligator the median ridge, continued backwards from the hypapophysis and the lateral depressions, so strongly developed, as in the *Crocodilus Hastingsiae*. The fore part of the neurapophyses is relatively thicker in this than in the recent species. The pleurapophyses pl, (figs. 1, 2), are well developed both forwards and backwards, and the latter productions are expanded and excavated above for the reception of the fore part of the succeeding cervical rib. The zygapophyses (x) are thicker at their base, especially the hinder pair, where the base fills up the entire interval between the articular surface and the base of the spine (see fig. 2). There is the usual deep excavation at the fore and back part of the base of the spine (ns) for the insertion of the interspinal ligaments. The neural spine is compressed, moderately long, straight and truncate at its summit.

Although the hypapophysis maintains its characteristic form with much constancy in the homologous vertebrae of the same species of Crocodile, it varies in different cervical vertebrae of the same individual in certain existing species. It is, for example, shorter and thicker in the third and fourth vertebrae than in the succeeding ones in the *Crocodilus acutus*; whilst in the *Crocodilus biporcatu* the hypapophysis of the third cervical is more compressed than that of the sixth. The greatest difference is, however, presented, as far as I have yet made the comparison, by the cervical vertebrae of the *Alligator lucius*, in respect of the hypapophysis, which is broad and short in the third and fourth cervicals, but becomes long and slender in the succeeding cervicals. The small vertebral centrum (fig. 4, Pl. 1 D) resembles, in its broad and stunted
hypapophysis, that of the third cervical vertebra of the Alligator, but with an indication of a median rising and lateral depressions, behind that process, like those which are more decisively shown in the fifth cervical vertebra of the larger individual of the Crocodilus Hastingsiæ, to which species I believe the specimen fig. 4 to belong. It is the homologous vertebra with fig. 8, Pl. 3 A, and well illustrates the different proportions of the bones in different species of Crocodile.

Fig. 6 gives a view of the anterior surface of the first sacral vertebra of the Crocodilus Hastingsiæ: the under surface of the centrum has ceased to develope the median ridge; the short and thick ribs (pl) have completely coalesced with both the centrum and neural arch. The anterior concavity has a fuller and more exact elliptical form than that of the Crocodilus toliapicus (fig. 5, Pl. 3 A); the anterior zygapophyses do not project over the rim of that concavity; but, like those of the Alligator and Crocodile, they are more transversely extended than in the Gavial.

The general proportions of the first caudal vertebra (fig. 7, Pl. 1 D) are intermediate between those of the Crocodilus toliapicus (fig. 7, Pl. 3) and of the Crocodilus champsoïdes (fig. 10, Pl. 3 A): the under surface of the centrum is flat, not concave, lengthwise, as in both the Sheppy Crocodiles; the side of the centrum is irregularly tuberculate, not smooth, and concave lengthwise; the broad and high neural spine is deeply grooved at its fore part: a smaller proportion of the hinder end of the centrum (fig. 5) is occupied by the articular ball than we find in the antecedent vertebrae.

As none of the other numerous vertebrae and portions of vertebrae give any indications of a different species from the Crocodilus Hastingsiæ, or add any material characters to those of that species which have been deduced from the parts of the skeleton already described, I refrain from trespassing on the reader’s attention or occupying further space by their description or figures.

Genus—Gavialis, Oppel.

Gavialis Dixoni, Owen. Plate 3 B.

The characters of the genus Gavialis are much more strongly marked than are those which distinguish the Alligators from the Crocodiles, and leave no ambiguity in the conclusions that may be deduced from them. The present interesting addition to the catalogue of British Fossil Reptiles, is due to the discovery in the Eocene deposits at Bracklesham, by my lamented friend the late Frederic Dixon, Esq., F.G.S., of the remains figured in Pl. 3 B. The portions of the lower jaw demonstrate, by the slender proportions of the mandibular rami (figs. 1, 5), the extent of the symphysis, the uniform level of the alveolar series, and the nearly equal distance of the sockets of the comparatively small, slender, and equal-sized teeth, the former existence in England, during the early tertiary periods, of a Crocodilian with the maxillary and dental
characters of the genus Gavialis. These characters are, however, participated in by some of the extinct Crocodilians of the secondary strata (see Pl. 1, fig. 2'); but in them they coexist with a different type of vertebra from that of the recent and known tertiary Crocodilian genera: it became necessary, therefore, to ascertain what form of vertebra might be so associated with the fossil Gavial-like jaws and teeth in the Bracklesham Eocene deposits, as to justify the conclusion that such vertebrae had belonged to the same species as the jaws. Now, the only Crocodilian vertebrae that have yet been found at Bracklesham, so far as I can ascertain, present the procoelian type of articular surfaces of the body (Pl. 3 B), like that in Mr. Dixon's collection fig. 8. This vertebra answers to the fifth cervical vertebra in the existing Crocodilians, and accords in its proportions with that in the Gangetic Gavial. There are a few indications of specific distinction; the parapophysis (p) or lower transverse process articulating with the head of the rib, is relatively shorter antero-posteriorly. The broad, rough, neurapophysial sutures (n) meet upon the middle of the upper part of the centrum; the elsewhere intervening narrow neural tract sinks deeper into the centrum than in the modern Gavial, but is perforated, as in that species, by the two approximated vertical vascular fissures. The hypapophysis (hs) or process from the inferior surface of the centrum, has been broken off in the fossil, but it accords in its place and extent of origin with that in the fifth and following cervical vertebrae of the Gavial. Assuming the fossil procoelian vertebrae from Bracklesham, and the above-described vertebra in particular, to have belonged to the same individual or species as the portions of fossil jaw (figs. 1, 5), then these mandibular and dental fossils must be referred to the genus Gavialis, or to the long-, slender-, and subcylindrical-snouted Crocodilia with procoelian vertebrae.

This genus is now represented by one or two species peculiar to the great rivers of India, more especially the Ganges; and the fossil differs from both the Gavialis gangeticus, Auct., and from the (perhaps nominal) Gavialis tenuirostris, Cuv., in the form and relative size of the teeth. The crown (figs. 6, 7) is less slender in the fossil than in the existing Gavials, and less compressed, its transverse section being nearly circular. There are two opposite principal ridges, but they are less marked than in the existing Gavials; and are placed more obliquely to the axis of the jaw, i.e., the internal ridge is more forward, and the external one more backward, when the tooth is in its place in the jaw. In the modern Gavial, the opposite ridges, besides being more trenchant, are nearly in the same transverse line. The other longitudinal ridges on the enamel of the fossil teeth, are more numerous, more prominent, and better defined, than in the existing Gavials: the intermediate tracts of enamel present the same fine wrinkles in the fossil as in the existing Gavials' teeth.

The two chief portions of jaw (fig. 1, and figs. 4, 5) belong to two individuals of different ages; indicated by the difference in the breadth and depth of the ramus: both specimens being from the corresponding part of the jaw, viz. where it forms the
long symphysis characteristic of the Gavials. The specimen (figs. 4, 5) includes a larger proportion of the jaw than the fragment delineated in fig. 1.

On comparing the latter fragment of the fossil lower jaw with a specimen of a lower jaw of the Gavialis gangeticus of the same breadth across the symphysial part, at the intervals of the sockets, which breadth is 3 centimeters (1 inch 3 lines), I find that the longitudinal extent of 10 centimeters (near 4 inches) of a ramus of the fossil jaw includes five sockets; but in the recent Gavial the same extent of jaw includes seven sockets, showing that the teeth are fewer as well as larger in the fossil Gavial, in proportion to the breadth of the jaws.

The second portion of the jaw (fig. 2) is from the part where the rami diverge posteriorly from the symphysis, and near the posterior termination of the dentary series. Here the teeth become shorter in proportion to their thickness, and somewhat closer placed together: there is a shallow depression (c) in each interspace of the teeth, for the reception of the crowns of the opposite teeth when the mouth is shut. These depressions are longer, deeper, and better defined in the fossil than in the recent Gavial of the same size.

The fragments of jaw and teeth of the fossil Gavial of Bracklesham show examples of young teeth penetrating the base of the old ones, according to the law of succession and shedding of the teeth, which characterises the existing Crocodilia: fig. 2 shows the apex of one of the successional teeth at d; and fig. 3 d the hollow base of the same incompletely formed tooth seen from below.

Besides the fossil jaws, teeth, and vertebrae of the extinct Gavial, a nearly entire femur (fig. 9) of a Crocodilian has been discovered in the Eocene deposits at Bracklesham, which in its proportions, agrees with that bone in the Gavial of the Ganges. Cuvier, in his comparison of the bones of the Gavial with those of the Alligators and true Crocodiles, merely observes, "La forme des os du Gavial ressemble aussi prodigieusement à celle des os du Crocodile, seulement les apophyses épineuses des vertèbres sont plus carrées."

With regard to the femur, this bone is more slender in proportion to its length in the Gangetic Gavial, than in the Crocodilus biporatus or the Alligator lucius, and the anterior convex bend of the shaft commences nearer the head of the bone; and in these characters the fossil femur from Bracklesham corresponds with the modern Gavial, and differs from the Crocodiles and Alligators, and also from the Crocodilus Hastingsiae, of which species specimens of the fossil femur have been kindly submitted to me by the Marchioness of Hastings and Alexander Pytts Falconer, Esq. The fossil femur of the Gavial from Bracklesham (fig. 9) may therefore be referred, with the utmost probability, to the same species as the portions of jaw, teeth, and vertebrae above described; and as these clearly demonstrate a species distinct from any known Gavial, I propose to call the extinct species of the Eocene deposits at Bracklesham, Gavialis Dixoni, after

* Osseens Fossiles, 4to, tom. v, pt. ii, p. 108.
my esteemed friend, by whose scientific and zealous investigations so much valuable additional knowledge has been obtained respecting the fossils of that rich, but, previously to his researches, little known locality.

The tooth represented of the natural size in fig. 10, Pl. 3 B, was also discovered at Bracklesham, and forms part of the collection of G. Coombe, Esq. It resembles, in its proportions and obtuse extremity, the teeth of the Crocodiles rather than those of the Gavials, and at first sight reminded me of those of the *Goniopholis* or amphicoelian Crocodile of the Wealden period. On comparing it closely with similar-sized teeth of that species, the enamel ridges were more numerous and decided in the *Goniopholis*; and the delicate reticular surface in the interspaces of the more widely separated and feebler longitudinal ridges in the Bracklesham tooth was wanting in the *Goniopholis*. The minute superficial characters of the enamel of the large and strong Crocodilian tooth from Bracklesham, closely agree with those of the *Gavialis Dissoni*. It is just possible that this may be a posterior tooth of a very large individual of that Gavial, as the teeth become at that part of the jaw shorter in proportion to their thickness in the modern Gavials. If it should not belong to that Gavial, it must be referred to a Crocodile distinct from those species of the secondary strata, or those existing Crocodiles which have teeth of a similar form; since they present a different superficial pattern of markings on the enamel.

On reviewing the information which we have derived from the study of the fossil remains of the procœlian *Crocodilia*, that have been discovered in the Eocene deposits of England, the great degree of climatal and geographical change, which this part of Europe must have undergone since the period when every known generic form of that group of reptiles flourished here, must be forcibly impressed upon the mind.

At the present day the conditions of earth, air, water, and warmth, which are indispensable to the existence and propagation of these most gigantic of living Saurians, concur only in the tropical or warmer temperate latitudes of the globe. Crocodiles, Gavials, and Alligators now require, in order to put forth in full vigour the powers of their cold-blooded constitution, the stimulus of a large amount of solar heat, with ample verge of watery space for the evolutions which they practise in the capture and disposal of their prey. Marshes with lakes, extensive estuaries, large rivers, such as the Gambia and Niger that traverse the pestilential tracts of Africa, or those that inundate the country through which they run, either periodically, as the Nile for example, or with less regularity, like the Ganges; or which bear a broader current of tepid water along boundless forests and savannahs, like those ploughed in ever-varying channels by the force of the mighty Amazon or Oronoko;—such form the theatres of the destructive existence of the carnivorous and predacious Crocodilian reptiles. And what, then, must have been the extent and configuration of the eocene continent which was drained by the rivers that deposited the masses of clay and sand, accumulated in some parts of
the London and Hampshire basins to the height of one thousand feet, and forming the graveyard of countless Crocodiles and Gavials? Whither trended that great stream, once the haunt of Alligators and the resort of tapir-like quadrupeds, the sandy bed of which is now exposed on the upheaved face of Hordwell Cliff?

Had any of the human kind existed and traversed the land where now the base of Britain rises from the ocean, he might have witnessed the Gavial cleaving the waters of its native river with the velocity of an arrow, and ever and anon rearing its long and slender snout above the waves, and making the banks re-echo with the loud and sharp snappings of its formidably-armed jaws. He might have watched the deadly struggle between the Crocodile and Palæotheræ, and have been himself warned by the hoarse and deep bellowings of the Alligator from the dangerous vicinity of its retreat. Our fossil evidences supply us with ample materials for this most strange picture of the animal life of ancient Britain, and what adds to the singularity and interest of the restored ‘tableau vivant,’ is the fact that it could not now be presented in any part of the world. The same forms of Crocodilian Reptile, it is true, still exist, but the habitats of the Gavial and the Alligator are wide asunder, thousands of miles of land and ocean intervening: one is peculiar to the tropical rivers of continental Asia, the other is restricted to the warmer latitudes of North and South America; both forms are excluded from Africa, in the rivers of which continent true Crocodiles alone are found. Not one representative of the Crocodilian order naturally exists in any part of Europe; yet every form of the order once flourished in close proximity to each other in a territory which now forms part of England.

Order—Lacertilia.

Pleurodont Lizard. Plate 3 (Ophidians), figs. 43, 44.

Although members of the present order, with the modern procoelian type of vertebrae, existed in England during the Wealden and Chalk periods, and the greater part of the actual class of Reptiles, in all parts of the world, is composed of the same order, yet but one solitary example of true Lacertian from the formations of the Eocene tertiary period has hitherto come under my observation—a fact which has often excited my surprise. Future researches may bring to light farther and better evidence of the class.

Among the fossils obtained by Mr. Colchester from the Eocene sand, underlyng the Red Crag at Kyson, or Kingston, in Suffolk, the existence of a Lizard, about the size of the Iguana, is indicated by a part of a lower jaw, armed with close-set, slender, subcylindrical, antero-posteriorly compressed teeth, attached to shallow alveoli, and with their bases protected by an external parapet of bone. The fragment of jaw is traversed by a longitudinal groove on the inside (fig. 44), and is perforated, as in most modern Lizards, by numerous vascular foramina along the outside (fig. 43). The teeth are hollow at their base.