

1. Contribution to the Skeletal Anatomy of the *Mesosuchia* based on Fossil Remains from the Clays near Peterborough in the Collection of A. Leeds, Esq. By J. W. HULKE, F.Z.S.

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(Plates XVIII. & XIX.)

The primary divisions of the Order Crocodilia laid down by Cuvier (1), and extended by R. Owen (2) and by T. Huxley (3), are so true to nature that they have been substantially adopted by all subsequent writers and have proved insusceptible of material modification. However, within these great divisions the classification of the Crocodilia has, as Strauch truly remarks with reference to its extant members, ever constituted one of the more difficult tasks of the systematic herpetologist (4). This he rightly attributes principally to the small amount of material available for an exhaustive study of the entire skeleton of the several Crocodilian species preserved in our Museums, and in some measure to the mutable nature of those parts from which the systematic herpetologist has mainly taken the distinctive characters he employs, viz.—the skull, in which the proportions of the proper cranial and the facial region notably alter with the age of the individual in all species; and the integument, the scutes of which exhibit, within limits, differences as regards their shape and their arrangement in the same species. Even now, after an interval of more than twenty years since the publication of Strauch's admirable synopsis (5), no public osteological collection in this metropolis, so far as I can ascertain, possesses a series illustrating the changes of form which the Crocodilian skeleton undergoes in its growth from the young to the mature individual in any one species. Indeed as regards one—*Gavialis*, and this not the least important, I find that neither the British Museum nor that of the Royal College of Surgeons contains a single entire skeleton. The latter, however, possesses a few detached bones of this genus (crania are well represented in both collections). Exact and comprehensive anatomical knowledge not limited to external features, but extended to the whole skeleton and to the soft parts, must form the only safe basis of any enduring classification. As regards the extinct members of the Order, the difficulties are for very obvious reasons greatly increased. Highly instructive as are the magnificent skeletons bedded in slabs of rock that adorn our galleries, these often fail to afford information respecting forms and structural details which yet may be of first-rate importance. Obviously many such details can only be apprehended by the study of detached bones that can be separately handled, and be viewed in turn from every side. It is the facility for such study that gives a high value to a large collection of Crocodilian remains from pits opened in

the Oxford Clay¹, near Peterborough, obtained by A. Leeds, Esq., to whom I tender my warm thanks for most courteously affording me an opportunity of studying them at leisure during the past winter. They are easily freed from the clay by washing, after which many of the bones, except for some crushing by earth-pressure, are nearly as complete as freshly macerated osteological specimens. The mode of their occurrence in the rock, their facies, and their relative proportions concur in affording a high degree of probability to Mr. A. Leeds's conviction that each of his series represents one individual, and is not derived from several skeletons. An impression that they help to clear up some points in the skeletal structure of the earlier Crocodilians hitherto obscure and requiring confirmation is my apology for offering an account of these remains. Mr. Leeds's collection contains remains referable to both the primary groups into which Messrs. E. and E. E. Deslongchamps in their classical 'Memoirs' (6) divide the family *Teleosauria*; their genus *Teleosaurus* is exemplified by a member of the subgenus *Steneosaurus*, and their genus *Metriorhynchus* by probably more than one species. Mr. Leeds tells me that *Steneosaurian* remains occur sparingly and they are restricted to the upper beds, whereas those of *Metriorhynchus* are plentiful, and they are distributed throughout the whole series of the beds, from the uppermost to the lowest exposed in the pits.

The cranial characters distinctive of the two genera laid down by Messrs. Deslongchamps (7) are plainly recognizable in the skulls in Mr. Leeds's collection. As, however, these are much crushed and otherwise imperfect, I do not offer any description of them.

METRIORHYNCHUS.

Vertebræ.—All, except the first two and the two sacral, have both terminal surfaces of the centrum more or less concave, the character which stamps the *Protosuchii* of R. Owen (8), the *Mesosuchia* of T. Huxley (9), and distinguishes these from all the more recent Crocodilians, including those of Tertiary age and also the extant members which together compose Huxley's suborder *Eusuchia* (10).

Atlas.—This vertebra (Plate XVIII. fig. 1) is composed of the same elements as in extant Crocodiles, viz.—of an azygos ventral piece ("basilar Stück," Stannius) (11); of a pair of lateral pieces which, in conjunction with the basilar piece, constitute an incomplete ring; of a *pars odontoidea*; and of an upper piece ("pièce supérieure," Cuvier; oberes Schlussstück of German zootomists). The existence of this last element may not be doubted, although it is not preserved in any atlas in the collection, since its presence has been demonstrated in the earlier Crocodilians of the Lias (12), in those of contemporary rocks in Normandy (13), in those of Tertiary rocks (notwithstanding Ludwig's opinion that it is absent from the Crocodilians of the Mayence basin (14)—an idea founded on a misapprehension), as it is also in all extant Crocodilians.

¹ Through misapprehension of information given me respecting these pits, I was formerly under the impression that they were in the Kimmeridge Clay.

In immature individuals all the component elements of the atlas are distinct, but in mature individuals they are often synostosed, as are also the atlas and epistropheus.

Basilar piece (Stannius).—In its form and its connections this part agrees closely with that of extant Crocodilians. Its anterior or cranial surface contributes nearly the lower or ventral half of the articular cup for the reception of the occipital condyle. Its inferior surface is convex transversely; whilst its superior is slightly concave in this direction, and it is adapted to the corresponding surface of the *pars odontoidea*. Its supero-lateral margins unite with the “lateral pieces.” Its posterior margin, thin, has at its junction with the lateral margin, on each side, a large articular facet for the first pair of ribs.

“*Lateral pieces.*”—These are composed of a thin, compressed, upper part which forms the side-wall of the neural canal, and of a stouter lower half. The division between these two parts is indicated on the median surface by a slight horizontal ridge which marks the former attachment of the “transverse ligament.” The anterior border of the stouter lower part is so wide that it deserves the term surface. Smooth, articular, forming a small segment of a circle, it contributes the upper lateral border of the occipital cup. The inferior border of the lateral piece unites with the supero-lateral border of the “basilar piece.” The posterior border, and the upper border of the upper part of the lateral piece, that part which bounds the neural canal, are thin; and at their junction they are produced backwards, and they form a rudimentary post-zygapophysis which articulates with a similarly dwarfed præ-zygapophysis on the epistropheus. The outer surface of the “lateral piece” is traversed obliquely by a ridge, which, starting from the angle formed by the junction of the anterior and superior margins of that part of the bone which bounds the neural canal, descends in a backward direction towards the postero-inferior angle, where it ends in a small projection or tubercle situated in the level of the diapophysis on the epistropheus. For reasons presently stated this little tubercle should rank as an upper atlantal transverse process or diapophysis. The median aspect of the stouter, lower part of the lateral piece rests on the *pars odontoidea*.

Pars odontoidea.—This has a slightly skewed cubic or pyramidal form, its inferior or ventral part being slightly smaller than the upper. The posterior surface, plane, is marked by horizontal ridges and furrows indicative of synchondrosis with the cranial, terminal surface of the centrum of the *epistropheus*. In aged individuals it is frequently synostosed with this. The outline of this (posterior) surface of the *pars odontoidea* is an inequilateral four-sided figure, in which the upper is longer than the lower side. Upon its upper surface may be discerned (1) a relatively wide, smooth, median tract—the floor of the neural canal; this is slightly encroached upon laterally by (2) a rough synchondrosial impression, marking the attachment of the neurapophysis, which also descends upon the lateral surface. The postero-lateral angles of the upper

surface of the *pars* are truncated by the abutments of the most anterior part of the neurapophysis of the epistropheus. Upon the anterior or cranial surface of the *pars* are discernible:—(1) a smooth upper tract of rhomboidal outline, of which the upper angle is truncated by the neural canal; this area contributes the upper, central, and deepest part of the occipital condylar cup; and (2) a lower, larger tract looking downwards and forwards, stamped by wrinkling denoting synchondrosial union with the “basilar piece.”

Epistropheus (Axis).—This bone (Plate XVIII. fig. 1) differs from all the vertebræ posterior to it, (1) in the great antero-posterior extent of its spinous process and of its neurapophysis, which latter, prolonged in advance of its proper centrum, abuts slightly upon the *pars*; and (2) in the flatness of the anterior terminal surface of its centrum, which in immature individuals bears the stamp of synchondrosis, and in aged individuals is often synostosed with the *pars*. The posterior terminal surface of the centrum is concave. In the level of the neurocentral suture, not quite equidistant from the two ends of the centrum, but rather nearer to the cranial, is a stout, upper, downward slanting, transverse process (diapophysis); its cross section is oval in outline, the major axis horizontal; and at the lower, anterior angle of the lateral surface, where this joins the under surface of the centrum, is an inconspicuous facet (parapophysis) for the *capitulum costæ*. Below the neural suture the middle of the centrum is compressed, and its sides here inclining inwards meet ventrally in a narrow edge or keel.

The morphology of some of the component parts of the atlas has been much discussed, nor have the last words been spoken. The correspondence of the *pars odontoidea* to the odontoid process of the epistropheus in higher Vertebrates was recognized by Cuvier (15). If the body of a vertebra be defined as that part of it which is traversed by the notochord, then, beyond doubt, embryology demonstrates that the *pars odontoidea* is a vertebral centrum, and also that it belongs to the atlas, since in an early embryonic stage the notochord may be seen piercing it, and it evidently, together with the pair of “lateral pieces” and the basilar piece, forms one undifferentiated “continuum.” These views of the morphology of the *pars* have been held by nearly all writers. E. Deslongchamps alone, I think, regarded the *pars* as representing the centrum, not of the atlas, but of a vertebra once ancestrally present between the atlas and the epistropheus, but now reduced to a rudiment. He appears to have been led to form this opinion by the occurrence of a notch in the free border of the spinous process of the epistropheus, and by the great antero-posterior extent of the neurapophysis of this latter. These facts appeared to him to hint that the neural arch of the epistropheus comprises two parts originally distinct,—one posterior, the proper arch of the epistropheus, the other anterior, the neural arch of a vertebra immediately anterior to the epistropheus which, its own centrum being reduced to a rudiment, has coalesced with that of the epistropheus (16). This conception of the *pars* is untenable.

That the pair of "lateral pieces" which, above, form the side-walls of the neural canal, below join the basilar piece, in front contribute to the supero-lateral part of the cup for the occipital condyle, which internally rest on the upper part of the antero-lateral aspect of the *pars*, encroaching slightly on the upper surface of this latter, are the morphological equivalents of the neurapophyses of other vertebræ is universally accepted. It is probable that they also comprise that part which in Mammalia, under the guise of the expanded root of the neurapophysis, contributes the dorso-antero-lateral portion of the body of the vertebra which P. Albrecht has named *hemi-centroid* (17). This part of the atlas retains its individuality throughout the vertebral column in some early reptiles, of which *Actinodon* is an example. Gaudry, who has given excellent figures of the vertebræ of this Saurian in his admirable 'Enchaînements,' very appropriately named this part *pleuro-centrum* (18); and this term has been adopted by E. D. Cope, who originally had designated the same part *centrum* in his accounts of *Trimerorhachidians* from homotaxic rocks in N. America (19).

No part of the atlas has been the subject of more discussion than the azygos "*basilar piece*" which inferiorly completes the ring. Cuvier regarded this as the body of the atlas (20). R. Owen considered it to be "the inferior part of the centrum of the atlas" (21). He also regarded it as homologous with the ventral spur or carina present in the cervical and in the foremost thoracic vertebræ in extant Crocodiles, from which it differs, he remarked, in being autogenous. Further, this author identified it with the foremost of the "subvertebral wedge-bones" which in *Ichthyosaurus* supplements inferiorly the atlantal cup for the occipital condyle (22). To the "subvertebral wedge-bones," to the ventral spur of the cervical vertebræ of extant Crocodilians, and to the Crocodilian atlantal basilar piece, R. Owen applies, alike to all, the term *hypapophysis*. But are all these morphologically equivalent structures, and is this term properly applicable to all? Apparently R. Owen himself has not invariably used the term *hypapophysis* in the same sense, since he evidently has applied it to a part which in one instance is a downward extension of the centrum, and in another instance he has connected it with a part having an autogenous origin distinct from the centrum. Now in embryos of extant Crocodilians it is easily demonstrable that the ventral spur of the cervical vertebræ is a downward production of the centrum, with the tissues of which it is always continuous (23). To this the term *hypapophysis* strictly applies. The cervical vertebræ in many extant lizards have a ventral spur of identic origin, but together with this there is frequently present another element, intercalated ventrally between the vertebral centra, originating independently of these, though later it not unusually coalesces with the genuine hypapophysis, commonly of the posterior of the pair of vertebræ between which the primitively separate piece lies. Instances of such intercalated pieces are common. They are shown in the two annexed sketches of cervical vertebræ of *Iguana* sp. and *Trachyosaurus*

rugosus. In the former the 'intercalary' or *intercentrum* only is present; in the latter lizard it coexists with a genuine *hypapophysis*. In any comparison of the Crocodilian atlantal basilar piece with the foremost of the "subvertebral wedge-bones" of *Ichthyosaurus*, the morphological significance of the pair of long, slender hypaxonic styles attached to the former may not be ignored. These styliform bones were regarded by Cuvier as "*apophyses transverses*" (24). Their separate ossification is unfavourable to this view, which is not now maintained by anyone. Their inferior position might seem to suggest their being a form of chevron. Is this a tenable supposition? The individual distinctness of each style, the absence of union of their ventral ends, is not sufficient, of itself, to refute this idea, since *Ichthyosaurus* and *Plesiosaurus* furnish familiar examples of the complete separateness of the two styles constituting their caudal chevrons. It is scarcely necessary to state that the reptilian caudal chevron originates in a downward extension of an intercentrum. This, as Dr. G. Baur has mentioned, is plainly demonstrable in *Sphenodon* (25). The development of the intercalated part seems often to be inversely proportioned to that of the freely ventrally dependent part that forms the chevron. The former may be reduced to a mere rudiment, or it may even disappear, whilst the latter may persist in its perfect form. I do not call to mind an example of the concurrence of an intercentrum and of a chevron, each being distinct, and both not forming a *continuum*. The pair of styles dependent from the posterior border of the basilar pieces do not, then, lend any support to the identification of the basilar piece of the Crocodilian atlas with an (Ichthyosaurian) intercentrum.

The obvious formal resemblance of the atlantal styles to the next posteriorly situated pair of similarly-shaped pieces, by all writers regarded as riblets, is a valid reason for regarding the styles also as riblets.

The chief and almost only difference is the simple form of their vertebral end, and their consequently *single* vertebral articulation. In estimating the value of this it should be borne in mind that the division of the vertebral end of the rib, which is so marked a feature in those of the other cervical vertebræ behind the epistropheus, is in *Eusuchia* usually indicated only by a shallow notch in the ribs of the vertebra just named. The ventral angle of the notch, which represents the *capitulum costæ*, is borne directly on a parapophysial facet or tubercle; whilst the upper angle of the notch, answering to the *tuberculum costæ*, is commonly only connected by ligament with the diapophysis. From the rudimentary condition of the costal tubercle in the second pair of riblets, it is easy to conceive that a slight further reduction of it might cause its complete suppression in the first pair, and this appears actually to have occurred as regards the atlantal styles in the *Eusuchia*. *Mesosuchia*, however, retain a trace of a costal tubercular articulation in the little process which projects from the outer surface of the atlantal neurapophysis (*cf.* Plate XVIII. fig. 1, *d*). The position of this little process in serial line with the upper transverse processes of the other cervical verte-

bræ speaks distinctly in favour of its diapophysial character. The common acceptance of the pair of atlantal styles as *riblets* seems, then, well founded.

The origin of the ribs in connection with the myocommata, their primitive independence of the permanent vertebræ, and their intervertebral position as regards the latter suggest the inquiry whether instances of ribs being borne on intercentra are known.

It has been thought that an affirmative answer to this is to be found in the vertebral column of *Rhachitomidæ* (E. D. Cope). In support of this Dr. G. Baur (26) cites Prof. E. D. Cope, who describes the capitellum of the furcate rib of a *Pelycosaurian*—*Embolophorus fritillus*—as being borne on an “*intercentrum*” (27). But the significance of this turns on the true morphology of the part here termed “*intercentrum*” by Cope. Now in stating the generic characters of *Trimerorhachis* this author writes:—“The centrum is represented by three cortical ossifications of the chorda sheath, a median inferior, and two lateral. The lateral pieces are quite distinct from one another, and are in contact with the neurapophyses above, and the posterior border of the median segment in front. The neural arch joins chiefly the lateral elements, but is in slight contact with the lateral summits of the inferior element.” “The median element I call *intercentrum*” (27). Again, referring to *Rhachitonus valens*, this author states: “Each vertebra consists of two segments, an *intercentrum* and a neural arch. The true centrum is wanting in the specimens at my disposal, and the *intercentrum* supports portions of two adjacent neural arches. With these it shares the intervertebral articular face usually borne by the centrum” (28). It is evident from these passages that Cope’s “*intercentrum*” (as is mentioned in an earlier part of his paper) is Gaudry’s “*hypocentrum*.” Again, in E. D. Cope’s definition of the *Ganocephala* the following statement occurs:—“Vertebræ consisting of centra and intercentra, the former not extending to the base of the vertebra, the latter not rising to the neural canal. The centrum consisting of two parts distinct from the superior neural arch, viz. a lateral piece on each side” (29). Here *centrum* is used not as equivalent to *body*, for this latter term in its general application comprises also the inferior piece. It would appear that Cope’s application of the term *centrum* to the inferior piece was consequent on his interpretation of the pair of lateral pieces (Gaudry’s pleurocentra) as composing the centrum. I do not gather from any of his writings that Prof. Cope has, in any of the *Ganocephala* described by him, found intercalary pieces concurrently with vertebral bodies of the construction just mentioned, and the argument based on his observations in relation to this subject, viz. Gaudry’s *hypocentrum* is an *intercentrum*, is not, I submit, conclusive; and, this being so, the inference drawn from the supposed costal articulation with the *intercentrum* in *Trimerorhachis*, viz. that the atlantal basilar piece is really an *intercentrum*, appears to me to want confirmation. Lower in the vertebrate scale instances are known, of which *Spatularia* is an example, where, together with vertebræ consisting of a neural

arch (the expanded root of which, descending laterally on the notochordal sheath, represents a pleurocentrum), and of an inferior or ventral ossicle lying vertically beneath it, and so representing Gaudry's *hypocentrum*, there are also present distinct inferior ossicles in the notochordal sheath, intercalated one between each pair of composite vertebral bodies, and thus intruded between the hypocentra. Similarly superior intercalaries occur between the neural arches. To such inferior "intercalaria" the term *intercentra* is strictly pertinent.

In the Ganoid *Amia calva* the cartilaginous tips of the transverse processes are structures having some correspondence to ribs. Now Dr. G. Baur mentions that in *Amia calva* the lateral (or transverse) process (Basalstumpf, Götte) at a certain point in the vertebral column, near the end of the body-cavity, passes from the centrum of a vertebra to the intercentrum next immediately following (30). In the only skeleton of *Amia calva* accessible to me (one prepared by Hyrtl preserved in the Museum of the Royal College of Surgeons), I find that behind the 6th vertebra following the body-cavity archless and arch-bearing centra alternate regularly; and, except for a slight difference of size, these two kinds of centra are barely distinguishable. The lateral or transverse process, which in that part of the vertebral column which corresponds to the body-cavity is borne by the arched centra, alone present there, is not, in this skeleton, in the region behind the body-cavity transferred from the arch-bearing to the here intercalated archless centra (or *intercentra*); but the transverse process continues to occur only on the arch-bearing centra, until at the caudal end of the column, through reduction of bulk and through crowding, the distinctness of the component pieces of the column is lost.

Ascending in the vertebrate scale, *Hatteria*, as shown by Dr. G. Baur, furnishes in its anterior vertebræ an example of the connection of a rib with a true intercentrum. Here the capitulum of the furcate rib, mostly represented by ligament, is ligamentously connected with the intercentrum, whilst the tuberculum rests on the centrum. I find this arrangement present in the three anterior pairs of ribs in two skeletons of *Hatteria* now before me. The secondary connection of the ribs with the permanent vertebræ, and the arrangement in *Hatteria* demonstrating the connection of the *capitulum costæ* and the *intercentrum*, would seem to favour the idea that the Crocodilian basilar piece is morphologically an intercentrum. The body of evidence, however, is I think, unfavourable to this conception; and this, together with the fact that in the early embryo the basilar piece is continuous with the *pars odontoidea* and with the neurapophysis (including the hemicentroids, Albrecht), gives very great probability to the hypothesis that the basilar piece is really that which R. Owen termed it—the inferior part of the centrum of the atlas. This is also C. K. Hoffmann's view of it (31).

The morphological equivalence of the Crocodilian basilar piece to the foremost of the subvertebral wedge-bones in *Ichthyosaurus* does not seem to me proven, but rather the contrary. Probably in the *Enaliosaur* the "body" of the atlas is the equivalent of the Croco-

dilian basilar piece + the two pleurocentra + the *pars odontoidea*. As bearing on this it is not without significance that the lateral surface of the atlas in *Ichthyosaurus* is impressed by a diapophysial and a parapophysial pit, for the double costal articulation, as occurs in the axis and the other vertebræ behind it.

There remains for discussion the inverted V-like piece that caps and superiorly closes the neural arch. As already said, this is missing in Mr. Leeds's specimens, but of its former presence no doubt may be entertained. What is its morphological import? Cuvier's view that it represents the *proc. spinosus* of other vertebræ was the doctrine generally accepted until about 10 years ago, when P. Albrecht advanced reasons for regarding it as a vestige of a vertebra ancestrally present between the atlas and the skull, but since suppressed. To this he attached the name *proatlas*. Albrecht's principal ground for this conception of the nature of the "*pièce supérieure*" appears to be the emergence of the first spinal nerve in front of the neural arch of the atlas, for which reason it is by some named suboccipital nerve, whereas all the other spinal nerves escape from the neural canal behind or through the neurapophysis of the vertebra to which they serially correspond. An approximately vertical plane laid through the point of emergence of a spinal nerve will divide the neurapophysis into an anterior part bearing the præzygapophysis, and a posterior portion supporting the postzygapophysis and the spinous process. The neurapophysis appears to have two roots, of which the posterior may be ligamentous, and the nerve passing out between these leaves the neural canal not, Albrecht says, intervertebrally as commonly taught, but vertebrally by piercing through the neurapophysis, which point of exit is morphologically intervertebrally situated. Now the vertebral complex called the atlas lies behind the first spinal nerve, and since the serial correspondence of the spinal nerves and vertebræ expressed in numerical order is not as 2:2 or 3:3, but as 2:(2-1), or 3:(3-1); or, to express the same circumstance another way, since the second and third spinal nerves correspond respectively to the vertebræ next in front of them, it follows that the first spinal or suboccipital nerve does not correspond to the atlas, but to a vertebra serially in advance of this. A vestige of such an anterior vertebra Albrecht discovers in Cuvier's *pièce supérieure*. This he regards as representing the neural arch of the ancestrally present, now suppressed, vertebra once interposed between the atlas and the occiput (31 a). This superior element was subsequently discovered by Albrecht in *Hatteria* (32). Dr. G. Baur has found it present in *Chameleo*, sp. (33). Prof. O. C. Marsh has observed its presence in *Morosaurus* and *Brontosaurus* (34). L. Dollo also has noticed it in *Iguanodon* (35). Its presence seems always associated with incomplete coalescence and synostosis of the two sides of the neural arch, and with the absence of a normal spinous process; and this is not without significance, for it hints that after all Cuvier's view respecting it may express the truth. The development of the "*pièce supérieure*" in two halves and its discontinuity from the atlantal neurapophyses are not irreconcilable with such

supposition, since instances of such plan of structure are common. Thus in Fish the spinous processes are built up by the apposition of a pair of flat styles primitively distinct, and this composite process is segmentally separate from the summit of the neural arch to which it is attached by the medium of soft tissue.

The Crocodilian atlas is not to be regarded as a degraded vertebra, but as one retaining the plan of construction common in the earliest reptiles and their progenitors. *Actinodon* needs but the addition of an internal ossification enclosing the axial part of the notochord to furnish a close parallel.

Remaining Cervical Vertebrae (Plate XVIII. fig. 2).—All behind the two foremost possess an upper and a lower transverse process, the former borne upon the arch, the latter upon the centrum. The former (*diapophysis*) is always longer than the lower, and projected outwards and downwards. Its root is in or slightly above the level of the neuro-central suture, and it is nearly equidistant from both ends of the centrum. The *parapophyses*, shorter and stouter, approach closely the anterior terminal surface of the centrum. In vertebrae closely following the *epistropheus*, the parapophyses occur at the junction of the lateral with the inferior surface of the centrum, thus augmenting the breadth of this. Between the parapophyses, anteriorly, the ventral surface is depressed, whilst posteriorly, in the same direction (transversely), the surface presents a low keel. Both terminal surfaces of the centrum have a roughly circular outline; the anterior is nearly plane, and the posterior is distinctly concave. As the trunk is approached the parapophysis ascends on the side of the centrum, and the diapophysis rises on the neural arch. The antero-posterior extent of the sutural attachment of the neuropophysis to the centrum nearly equals that of the latter. The spinous process is compressed, its outline square. The zygapophyses spread considerably, and the articular surfaces of the anterior have an upward slant.

Trunk Vertebrae (Plate XVIII. fig. 3).—In the front of the thoracic region of the vertebral column the parapophysis leaves the centrum, and the capitular costal facet appears on the anterior border of the upper transverse process, just external to the præzygapophysis, as in now living Crocodiles. The transverse process is long, it is directed nearly horizontally outwards, and it bears at its free extremity the costal tubercular joint. The figure of the centrum is cylindroid, its middle is constricted. Towards the loins the parapophysial or, as it may be preferably named, the capitular costal articulation moves outwards towards the free end of the transverse process, where it finally coalesces with the tubercular facet, both forming there one single costal articulation.

Sacrum (Plate XVIII. fig. 4).—There are two sacral vertebrae. These may be distinguished from all others by their greater massiveness, also by the stoutness and length of their transverse processes. These latter are composed (1) chiefly of an inferior element which ossifies independently of the centrum (with which it is united by a suture that long continues distinct), and in virtue of this claims to

rank as a rib; and (2) of a much smaller component which, descending from the neural arch upon the upper surface of the sacral rib, thins out on this, and ends at a short distance from the base of this. The long sacral ribs have a strong downward slant. Their distal end is dilated, thus increasing the extent of the iliac articulation. In a cross section through the middle of a sacral rib, the vertical exceeds the horizontal diameter. The rib of the first sacral vertebra is attached by a large base to the lateral surface of the centrum close to its anterior end, but it does not contribute any portion to the anterior, terminal, articular surface of the centrum. The neurapophysis encroaches slightly on this surface. The anterior terminal surface of the first and the posterior terminal surface of the second sacral vertebra are distinctly concave. Their dimensions exceed those of the applied surfaces of the vertebræ, which are nearly plane, with a slight central depression. The rib of the second sacral vertebra is attached to the side of the centrum nearly equidistantly between the two ends, and no part of the costal suture approaches either terminal surface of the centrum. The spinous processes are tall, their antero-posterior extent is less than in the thoracic vertebræ.

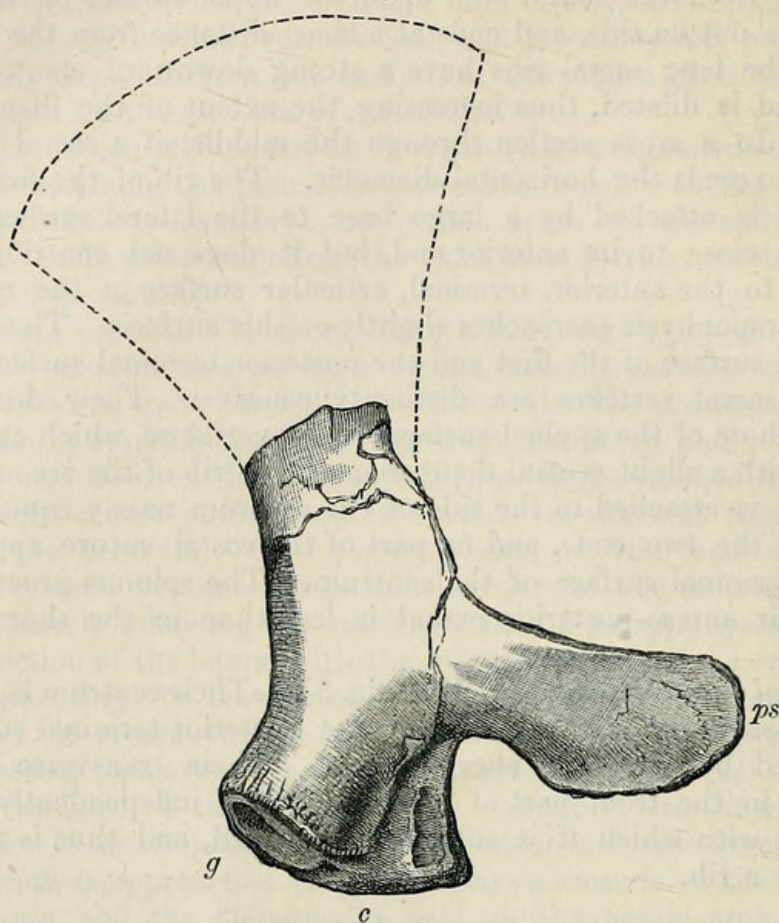
Caudal Vertebræ (Plate XVIII. fig. 5).—Their centrum is laterally compressed. The lower border of the posterior terminal surface is truncated by a double chevron facet. Their transverse process, present in the front part of the tail, ossifies independently of the centrum with which it is suturally connected, and thus is morphologically a rib.

Pectoral Girdle.

The series of remains bearing the Cat. No. 30 comprises both coracoids and the right humerus. Both scapulæ are preserved in series No. 31. Unfortunately no series contains both the coracoid and the scapula.

Scapula (fig. 1, p. 428).—Of the right only the ventral half is preserved. The left comprises the whole bone, but both its ends are defective. Together they give the form of the entire bone. This is broader, shorter, stouter, and flatter than the scapula in extant Crocodiles. The shaft is short and contracted. Above this narrow part the antero-posterior dimension rapidly augments, chiefly by the backward inclination of the posterior border. The outline of the dorsal extremity is an arc of a large circle. The ventral end is deeply indented by a notch which separates off a stout posterior part (*gc*) from a thin flattened process (*ps*), which in the articulated skeleton appears to have been directed downwards and forwards. This latter appears to correspond to the process termed *acromial* on the anterior border of the scapula in some Anomodonts, and it suggests the presence of a precoracoid element in these Mesosuchia, of which the Eusuchia do not retain any trace. The stout process (*gc*) is subdivided into:—(*g*) a posterior subcircular, smooth, hollowed portion, obviously the scapular component of the glenoid fossa; and

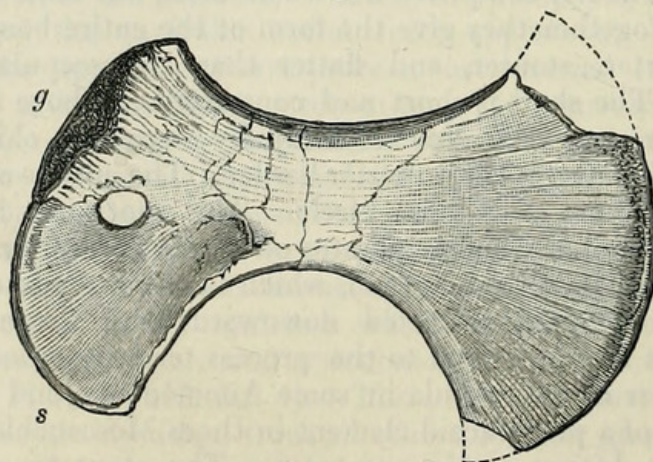
Fig. 1.

Scapula of *Metriorhynchus*.

g, glenoid articulation; *c*, coracoid border; *ps*, preapular process.

N.B.—The dotted outline is copied from the other scapula of the same individual.

Fig. 2

Coracoid of *Metriorhynchus*.

g, glenoid portion; *s*, scapular border.

(c) an anterior compressed portion, of which the edge is rough and suggestive of synchondrosial junction with the coracoid. This is separated by the notch from the præscapular or acromial process.

Coracoid (fig. 2, p. 428).—This is a flattened bone with a contracted middle and expanded crescent-shaped ends. The sternal end is undivided; its outline is an arc the chord of which is 40 mm. in the right and 42 mm. in the left scapula. The dorsal or scapular extremity exhibits posteriorly a stout subtriangular articular portion, the glenoid complement (*g*); and anteriorly a thin rough margin for union with the scapula (*s*). Opposite the junction of these two parts, the coracoid is perforated by a large submarginal foramen. The anterior and posterior borders of the coracoid are deeply concave, the former most so.

Humerus (Cat. No. 30).—The right humerus, although flattened and fractured by compression subsequently to death, shows very well the form of this bone. The proximal end bears a long oval articular surface, situated almost entirely behind the long axis of the shaft, convex in both directions from the dorsal or extensor to the ventral or flexor aspect, and also from the radial to the ulnar border. The radial border inclines forwards for a space of 22·5 mm., and beyond this it curves slightly inwards towards the axis of the bone, thus, by change of direction, forming a salient (deltoid?) crest; beyond this it passes in a nearly straight line nearly parallel to the posterior border to the distal end of the bone. The posterior or ulnar border is first concave near the proximal end, and thence nearly straight to the distal end. On the dorsal surface in its proximal half is a rough axial swelling, from which the surface declines towards the radial and ulnar borders. The ventral or under surface is sinuous, being gently convex in the direction of its long axis and concave in the preaxial portion, corresponding to the deltoid crest. The distal end shows the usual condylar division.

<i>Dimensions.</i>	millim.
Length.....	57
Proximal articular surface, long axis.....	16
" " " short axis.....	7
From proximal end to deltoid angle.....	23
Breadth at deltoid angle.....	21
Breadth midway between angle and distal end ..	13
Breadth at distal end.....	14

Pelvic Girdle (the sacrum is already described).

Ilium (Plate XIX. figs. 1, 2).—This is a flat roughly quadrilateral bone. The acetabular hollow (*a*) is shallow; its upper limit is indistinct. Its lower border presents two synchondrosial surfaces separated by a low prominence. Of these, the posterior (*p.i*) is stout and triangular; it projects at the junction of the inferior and the posterior border. The anterior of the two synchondrosial surfaces (*a.i*) is compressed and of oblong figure. Both articulated with the *ischium*, the posterior directly, the anterior doubtless by the interposition of

a cartilaginous band, as in extant Crocodilians. The posterior border of the *ilium* is short, and it is slightly encroached upon by the sutural pit for the attachment of the second sacral rib. The upper border widens anteriorly, and it ends in a short spur (*pa*) directed forwards. This overhangs the anterior border, which is long and straight. The median surface is indented, above, by two rough pits (*s*) for the attachment of the sacral ribs. The upper limits of these are slightly overhung by the inner lip of the upper border. Below these sutural impressions is a larger trihedral, relatively smooth area, corresponding to the acetabular hollow in the outer surface. No portion of the median surface lies above the level of the sacral articulations, a feature which sharply distinguishes the *ilium* of *Metriorhynchus* from that of *Steneosaurus*, and also from those of *Eusuchia*.

Ischium.—This is a large, flat, triangular bone. The median border (*m*), which met that of the other side as a ventral symphysis, and the posterior border are almost straight. The anterior border (*a*), shorter, has a concave outline. The anterior median angle is acute, the posterior is rounded off. The outer angle, bearing the coxal articulation, is the stoutest part. It is subdivided by a notch into (1) a wide oval posterior portion, and (2) a narrow anterior salient process, corresponding to the two divisions of the iliac component of the joint.

Os Pubis (Plate XX. fig. 6).—This bone is long, flat, spatulate or paddle-shaped, being very similar in form to that in extant Crocodiles.

The acetabulum in these Mesosuchia was composed, as in Eusuchia, by the *ilium* and *ischium* alone, to the exclusion of the *os pubis*, which presumably was connected only with the ischiatic process and the cartilage intercalated between this and the *ilium*.

The morphology of these three components of the pelvic girdle has occasioned almost as much discussion as that of the component parts of the atlas.

As an excellent summary of it has lately appeared in Bronn's *Klassen*, Rept. S. 53 u. f., by C. K. Hoffmann, and as now there is a general agreement that the *ilium* and the *ischium* in Crocodilia are respectively simply the equivalents of the bones so named in higher Vertebrates, it is unnecessary here to review the opinions which different writers have formerly expressed of the essential nature of these two bones. But the morphology of the part here named *pubis* requires consideration because very recently proof has been offered by Prof. H. G. Seeley that it cannot properly be identified with the *os pubis* of higher Vertebrata, and that it must be regarded as "a distinct element of the skeleton, which is connected with the pubic portion of what I (Prof. H. G. S.) term *ischio-pubic*¹ bone and is in the position of the *præ-pubic bone*" (37). Here Prof. H. G. Seeley apparently adopts Fürbringer's views respecting the dual composition of the bone, by most writers considered to be the *ischium* only. He also, in the paper from which the above quotation is taken, cites with approval Hoffmann's (*earlier*) interpretation of the *pubis*

¹ Italics are mine.—J. W. H.

as *præpubis*. Further, Prof. H. G. Seeley homologizes this *præpubis* with a bone having similar relations to the other elements of the pelvic girdle thought to be present in *Ornithosauria*. But C. K. Hoffmann has abandoned his earlier interpretation of the bone, and he, in a more recent publication, says that he now considers as *pubis* the bone which once he regarded as *præpubis* (36). Prof. H. G. Seeley finds that the bone commonly accepted as the Crocodilian *pubis* is much more slender, and it is much less expanded at the anterior end in all the species from the Lias and Lower Oolite rocks; and he refers to "some undescribed types in the collection of A. Leeds, Esq., in which it is reduced to a mere bony style without expansion at either end, comparable in form and substance to a lucifer match" (37).

It is manifest that the bone here described by Prof. H. G. Seeley in the above quotation cannot be identified with that bone which, from its constant association with the other pelvic bones, and from its close resemblance to the Eusuchian *pubis*, I have described and figured as the *os pubis* of these Peterborough Mesosuchians. Although I have some knowledge of Mr. Leeds's collection, I have not seen in it such *pubic* (*præbubic*, S.) bones with undilated ends; and Mr. Leeds assures me that he has not any such as those to which Prof. Seeley refers. The only bones in the collection at all corresponding to Prof. Seeley's description, I have ventured to interpret as the detached styliform atlantal riblets. R. Owen, referring to a Liassic Teleosaur preserved in the Whitby Museum, writes, "Both *ischium* and *pubis* are relatively more expanded than in the Gavial" (38).

In the Liassic Crocodilians, so far as these are known to me, the *ossa pubis* are similar in form, they have similar connections, and they are essentially identical with the *ossa pubis* of the Eusuchia. As regards the pelvic element in *Ornithosauria*, by some authors termed *præpubis*, with which Prof. H. G. Seeley (in this matter following Quenstedt) homologizes this Crocodilian bone, I have for some time had doubts of its existence as a separate, distinct element. In illustration of the view he adopts concerning it, Prof. Seeley reproduces Quenstedt's representation of the bones in question, as displayed in Quenstedt's plate of *Pterodactylus* (*Cycnorhamphus*) *suevicus* (39). But these parts are, I suggest, susceptible of another reading; the paddle- or fan-like bone as H. v. Meyer described it, with narrow short shaft and expanded opposite end, is not, I submit, a bone complete in itself, but merely the ventral symphyseal portion of an *os pubis* constructed and associated with the other pelvic elements after the common Lacertilian plan. Quenstedt's figure represents the two paddle-like pieces detached from their connections, flatly extended, as he conceived their natural position beneath the abdomen, in advance of the acetabulum (43). My first suspicions of the inaccuracy of this arrangement were aroused by observing that in those figures of *Pterodactyles* given by H. v. Meyer in his 'Rept. a. d. lith. Schiefer,' in which both *ossa pubis* (*præpubis*) are displayed in side or oblique view, the right or left bone (as the case

may be) lies in a deeper plane in the slab of rock, it is more distant from the observer, as would naturally occur were the surfaces, and not the median edges only, inclined towards each other. Taf. i. fig. 2., Taf. iv. fig. 5 show this point. This hint receives confirmation from Zittel's very instructive plate of a specimen of *Pterodactylus suevicus* from Nusplingen (42). In this is displayed the left half of the pelvic girdle (seen in side view), showing the three pelvic bones still maintaining their normal relations, all contributing to form the acetabulum. The ilium and ischium are apparently entire, but the os pubis, in form of a narrow bar, ends abruptly, as if by fracture, at a short distance below the acetabulum. In front of the pubic piece is seen a paddle-like or fan-like piece, which is obviously the part regarded by some authors as *præpubis*. The close proximity of this to the part denoted to be pubis by its relation to the acetabulum and the correspondence of its stalk-like end to the apparently fractured end of this suggest that the paddle-like piece originally formed part of the pubic bone. The probability of this view finds strong confirmation in H. v. Meyer's figure of *Pterodactylus micronyx* (*op. cit.* Taf. iv. fig. 5), in which the two portions of the os pubis, as I incline to regard them, are shown in their normal connection, a slight apparent break of continuity in the pubic bar marking the point where the paddle-like portion usually becomes detached. Why should the separation of the two parts of the os pubis so commonly occur at this point? The form of the pubis in *Rhamphorhynchus* may elucidate this. The os pubis in this genus has the form of a flattened bar bent angularly near its middle; one limb of it passes from the acetabulum downwards and forwards in an approximately vertical plane, roughly parallel to that laid through the median axial plane of the pelvis; whilst the other limb, passing transversely to this axis, meets the corresponding limb of the os pubis of the other side, and unites with it in a median symphysis (42). It is manifest that such an angular bend in the direction of its long axis would be a weak point in the construction of the pubic bar, and would favour its fracture at this point, under stresses acting in any other direction than perpendicular to the plane which contains both the limbs.

In *Dimorphodon*, another genus, the evidence as yet available is not opposed to the idea that its pubis is constructed on a similar plan to that of *Rhamphorhynchus*, only the large foramen present in this latter between the pubis and the ischium is in *Dimorphodon* reduced to a narrow cleft. The larger of the two bones, marked 64 in R. Owen's figure of *Dimorphodon*, and identified by him as pubis (*præpubis*), may with probability be regarded as the right pubis detached from its normal connections and displaced, the left pubis lying in advance of the ischium, from which it is separated by a very narrow interval.

If, then, in Ornithosauria the bone frequently termed the *præpubis* is not such but only a detached part of a pubis of a common Lacertilian plan, no corroboration can be found in it that the Crocodilian bone in question is a *præpubis*.

The principal stumbling-block to the acceptance of the anterior of the two ventral bars in the Crocodilian pelvis as *os pubis* would seem to be its exclusion from the acetabulum. Should this constitute an insuperable difficulty? The *os pubis* is notably the more variable of the three components of the pelvic girdle. Its ossification is a later phylitic event than that of the ilium and ischium. Not to refer to Labyrinthodonts, in which fuller information about the pelvic girdle is still wanting, it is well known that in some extant Amphibia—for instance, in *Cryptobranchus japonicus* and in *Salamandra maculata*—the ischium is well ossified, whilst the pubis is still cartilaginous. This is so too in *Rana esculenta*; and in *Daty-lethra capensis* the osseous pubis is a small disk surrounded by cartilage, whereas the ischium is perfectly ossified. Even in higher Vertebrates differences in the degree of development of the *os pubis* occur, and this in nearly allied forms. Thus in the genus *Lepus*, in *L. timidus* the pubis enters into the formation of the acetabulum; but not in *L. cuniculus*, in which, by dominant growth of the ilium and ischium, the pubis is excluded from the acetabular cavity. Its exclusion from this may also result from the great development of a distinct ossicle ("*os acetabulare*"), which may become so large as not to leave space for the pubis in the acetabulum. Of this, *Talpa europæa* supplies an instance. Even in *Homo* an approach to this is exceptionally to be found. Thus, in the Osteological section of the Museum of the Royal College of Surgeons there is a skeleton of a youth (Cat. No. 54 a, Ost. Series) in which both acetabula contain, each, a large distinct ossicle of this kind, by which the area normally occupied by the *os pubis* is much reduced, the areas contributed by the ilium and ischium being much less encroached upon. Here we, as it were, seize the pubis in process of being excluded. Does its exclusion vitiate its claim to pubis? I submit that it has not this force; and, further, that the corresponding bone in Crocodilia, notwithstanding that it has no share in the acetabulum, is also pubis; and this identification is in harmony with the fact that in the embryo it forms with the ilium and ischium one continuous piece of cartilage.

STENEOSAURUS.

Vertebral Column.—The plan of this in *Steneosaurus* being the same as in *Metriorhynchus*, those details only will be noticed at length in which they differ.

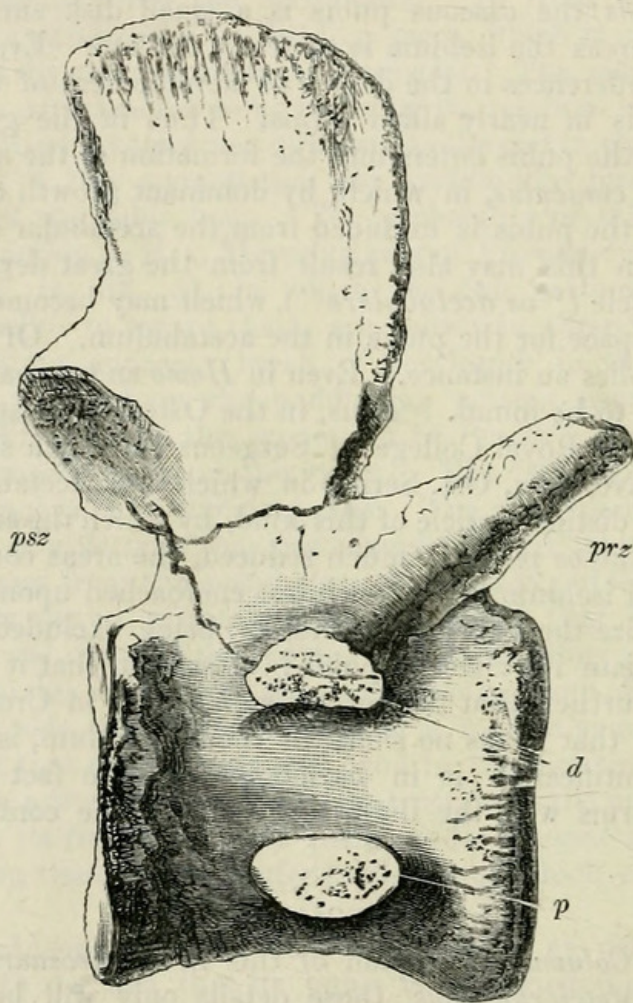
Atlas.—The same elements similarly combined and without evident formal differences are present. In aged individuals they synostose, and the *pars odontoidea* synostoses with the epistropheus.

Epistropheus (Plate XVIII. fig. 6).—Reduction of its diapophysis, the flatness of the lateral and the inferior surface of its centrum, and the absence from this latter of the low keel or ridge, are the most obvious differences.

In vertebræ referable to the front of the neck behind the epistropheus (fig. 3, p. 434), in which the parapophysis is placed very low, the figure of the centrum nearly resembles that of the epistropheus.

With the ascent of the parapophysis on the lateral surface of the centrum, the ventral surface of this becomes narrowed and a low keel arises here at its middle. The terminal surfaces of the centrum have a subcircular outline. In vertebræ referred to the anterior region of the thorax, the centrum assumes a cylindroid form. In a few, in which the parapophysis is passing off the centrum on to the neural arch, the antero-posterior dimension of the centrum is slightly less than in the neck, and in the succeeding vertebræ in the posterior part of the trunk. In these last the centrum is nearly cylindric, contracted at

Fig. 3.

Cervical vertebræ of *Steneosaurus*.

its middle, and dilated at both its ends (fig. 4, p. 435). In the anterior caudal vertebræ the centrum is laterally slightly compressed, its ventral aspect cylindroid. The transverse process in these vertebræ is suturally attached in the level of the neuro-central suture, the sutural impression being shared by the centrum and the neurapophysis. In vertebræ deemed by their smaller size to be situated posteriorly to the above, the centrum is much more compressed laterally, which, with the flatness of the under surface, gives the centrum a parallelopipedal figure (fig. 5, p. 435). In these vertebræ the

Fig. 4.

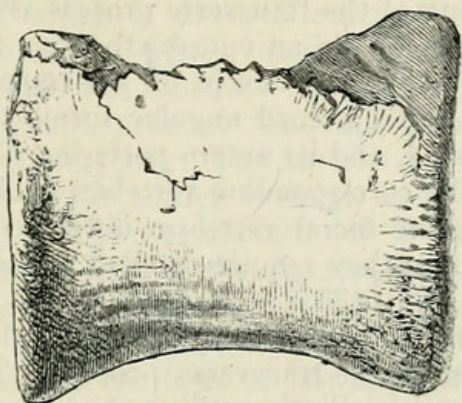
Trunk vertebra of *Steneosaurus*.

Fig. 5.

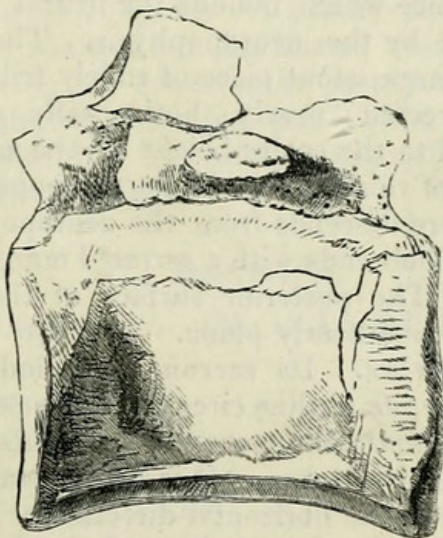
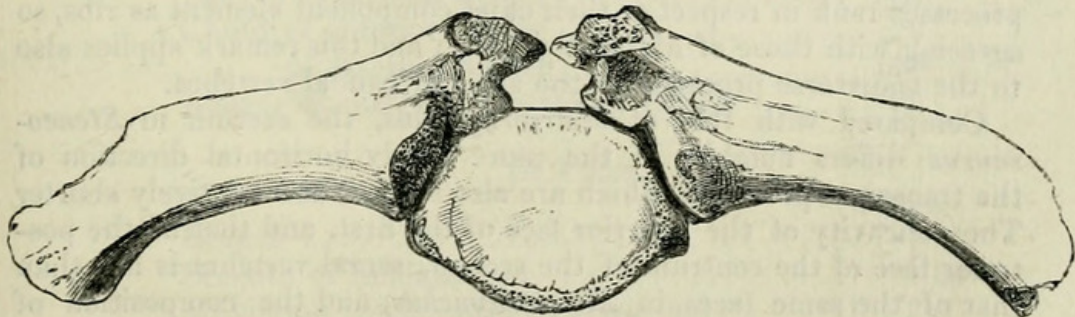
Caudal vertebra of *Steneosaurus*.

Fig. 6.

Anterior view of first sacral vertebra of *Steneosaurus*.

transverse processes are dwarfing, and they are borne wholly on the neurapophysis distinctly above the neural suture; no trace of sutural attachment of the transverse process is here discernible, and the process appears to be an outgrowth from the arch. Vertebrae posterior to the above are devoid of the transverse process; their centrum retains the flattened angular form, their spinous process is more compressed, and its antero-posterior dimension is relatively greater than in the corresponding vertebrae of *Metriorhynchus*.

Sacrum.—The two sacral vertebrae differ so much from those of *Metriorhynchus* that they require detailed notice.

1st Sacral (fig. 6, p. 435). The centrum has a subcylindric shape. In its anterior half the transverse horizontal dimension is enlarged by the attachment of the transverse process. The anterior terminal surface has an obtusely elliptic outline, of which the longer diameter is horizontal. Its surface is distinctly concave in the horizontal and nearly plane in the vertical direction. The lateral lip and the adjoining part of this surface is contributed by the root of the stout transverse process, and between the upper limit of this and that part of the circumference which bounds the neural canal the lip of this surface is formed by the neurapophysis. The transverse process consists (1) of a large, stout piece of rudely trihedral, slightly fluted cross section, directed nearly horizontally outwards. This is suturally attached to the entire height of the side of the centrum in the anterior half of this latter. Upon the upper surface of this part of the process there descends from the neurapophysis a minor, thin, splint-like part which ends with a serrated margin at a little distance from the arch. The posterior surface of the centrum is nearly circular in outline and nearly plane.

2nd Sacral vertebra. Its sacrum is cylindroid. The anterior face is nearly plane, its outline circular. The posterior face is larger; its outline is less elliptic and more nearly circular than is the anterior face of the 1st sacral vertebra. It is nearly plane in the vertical and distinctly concave in the horizontal direction. Its transverse process is suturally attached to the whole vertical extent of the lateral surface of the centrum. This attachment is separated by an interval from both ends of the latter, the terminal surfaces being formed of centrum only. The structural plane of the transverse process resembles that of the 1st sacral vertebra. Thus the sacral transverse processes rank in respect of their chief component element as ribs, so agreeing with those of *Metriorhynchus*; and this remark applies also to the transverse processes of the anterior caudal vertebra.

Compared with that of *Metriorhynchus*, the sacrum in *Stenosaururus* differs notably in the more nearly horizontal direction of the transverse processes, which are also stouter and relatively shorter. The concavity of the anterior face of the first, and that of the posterior face of the centrum of the second, sacral vertebra is less than that of the same faces in *Metriorhynchus*, and the composition of these faces is also different.

(No part of the pectoral girdle or fore limb has been yet procured by Mr. Leeds.)

Pelvic Girdle.

Ilium (Plate XIX. figs. 3, 4).—A flat, rudely rhombic bone, the longer diameter of which is directed obliquely upwards and backwards. The acute antero-inferior angle is truncated by an oblong surface (*a.i.*), to which was attached the cartilage that connected it with the anterior ischiatic process. The supero-anterior angle projects forwards as a sharp spur (*pa.*). The anterior border is stout, the posterior thin. The upper border is rough and narrow, it widens as the spur is neared. The acetabulum (*a.*) is wide and shallow, its postero-inferior angle (*p.i.*) is the stoutest part of the whole bone. The median surface is strongly impressed by the sutural attachments of the ends of the sacral ribs (*s, s.*). These impressions do not, as in *Metriorhynchus*, rise to the level of the upper border, but they are separated from this by a relatively wide, smooth surface comprising an area of nearly $\frac{1}{3}$ of the whole extent of this surface.

Ischium (Plate XIX. fig. 5).—This resembles very closely that of *Metriorhynchus*, from which it differs slightly by the rather greater excess of its antero-posterior over its transverse dimension.

Os Pubis (Plate XIX. fig. 6).—A paddle-like bone having a long, slender, cylindroid shaft, and a flat dilated ventral extremity. The anterior border is slightly concave, the posterior or inner border still more so. The anterior, abdominal end is thin, and its outline curves outwards and backwards. The pubis is more slender in general form than that of *Metriorhynchus*.

*Dimensions.**Ilium* (left). (No. 2 Leeds's Cat.)

	millim.
Length, upper border	51
„ including spine	78
„ anterior border	53
„ posterior border	57
„ inferior border	57
Longer diameter	87

Ischium. (No. 2 Leeds's Cat.)

	millim.
Length of median border	102
Chord of anterior border	70
„ of external border	100
Longer diameter of acetabular hollow	27

Os Pubis.

	millim.
Length	111
Breadth of ischiatic end	20
Maximum thickness of ischiatic end	7.5
Appropriate breadth of abdominal end	40

Femur (right).—This presents the usual *f*-curve of the Crocodilian

plan. Its length, measured in a straight line, is 248 millim. The proximal articular surface is convex, subtrigonal, borne directly without neck on the proximal end of the bone. The base of the trigone is dorsad, the apex ventrad. The antero-posterior chord is 41 millim., the dorso-ventrad chord is 271 millim., the sagitta is about 2.5 millim. The tuberculum majus and t. minor are more feebly developed. A low, indistinct trochanter is situated on the ventral surface, at about 60 millim. from the proximal end. The distal end presents the usual condylar form.

Tibia (right).—Its length is 113 millim. The proximal end is stout. It is obscurely divided into two areas—(1) a narrower, corresponding to the inner femoral condyle, and (2) a wider, outer or posterior area, answering to the outer femoral condyle, the outer border of which is slightly emarginate, as if for the fibula. The distal end is set obliquely on the shaft, so that its postero-external angle is in a lower level than the antero-internal angle. Its articular surface is narrow, of rhomboidal outline, with shallow trochlear groove. The lengths of the tibia and femur are as 113:248, so that the tibia relatively to the femur is much shorter than in *Eusuchia*.

INTEGUMENTAL ARMOUR.

The collection does not contain, I believe, any scutes which, by associated interment, can claim to belong to *Metriorhynchus*; but it includes some fine examples which were found buried with bones of *Steneosaurus*. The largest and best preserved of these scutes are of oblong figure, with rounded-off angles. A low keel divides their outer surface into two unequal areas, of which the wider is 44 millim., the narrower 18 millim. across. In a second specimen, these dimensions are 42 millim. and 17 millim. The larger area is quadrilateral. It is indented with a pattern of lines and long pits which radiate from the highest point of the keel, diminish as they recede from this, and cease near the border of the scute. The anterior border is thin, and a submarginal tract of the surface within it is smooth, unornamented, and plainly articular, being, where in undisturbed natural position, overlaid by the posterior border of the scute next in front of it. The lesser one is crescentic, quite smooth, and it was doubtless overlaid by the applied border of the adjoining scute. The smooth submarginal band of the larger area and the crescentic lesser area meet in a tongue-like projection, in which the keel runs out anteriorly. This tongue, when the scutes are articulated, is received in a corresponding hollow in the deep surface of the scute next in front. The whole of the deep surface is smooth, its grain radiates from a point beneath the highest part of the keel, where the scute is thickest.

In their form and in their plan these scutes correspond so closely to those placed in single series along each side of the dorsal middle line of the trunk in D'Alton and Burmeister's figure of the '*Gavial of Boll*,' that there cannot be any doubt of their having also occupied

this position, and formed a buckler covering the back from the neck to the tail, as in *Teleosaurus temporalis*, with which E. E. Deslongchamps identifies the above-mentioned 'Gavial.' Whilst their imbricated arrangement permitted some gliding of the scutes on one another, and thus gave some degree of flexibility to the trunk, the tongue-like processes must have imparted great security when the limits of this mobility were approached. In their form and in the position of their tongue these scutes differ from those of the Purbeck Wealden *Goniopholis*. From those of the Wealden *Bernissartia* they differ in having one and not a double keel, and in having a tongue, which the scutes of *Bernissartia* want.

The skeletons of these Peterborough Mesosuchians, so far as their plan is illustrated by their remains in the Leeds Collection, differ from those of the Eusuchia (1) in the amphiœelous character of all their vertebræ except the two foremost and the two sacral; (2) in the absence of the largely developed carina which so strongly characterizes the cervical vertebræ in Eusuchia; (3) their atlas differs in possessing a diapophysis placed on its pleurapophysis; (4) their epistropheus differs in having a well-developed diapophysis in the level of its neuro-central suture, and a parapophysis on its centrum.

In *Gavialis gangeticus* I find the capitular and the tubercular costal articulations both placed wholly on the *pars odontoidea* and the second cervical riblet to articulate exclusively with this. In *G. gangeticus*, *Crocodylus niloticus*, and in *Alligator mississippiensis* I do not find any trace of a diapophysis on the atlantal neurapophysis. In *C. niloticus* the capitulum of the second rib rests wholly on the *pars odont.*; and the tuberculum costæ is borne chiefly on this, but to a very small extent also on the centrum of the epistropheus. In another example of this Crocodile the capit. and the tuberc. costæ are both wholly borne on the *pars odont.* In *C. americanus* the second rib articulates wholly with the *pars odont.* In *Alligator lucius* I find the capit. costæ resting on the *pars odont.*, and the tuberc. costæ articulating with a rudimentary diapophysis situated on the neural arch of the epistropheus just above the neuro-central suture. The plan of the articulation of the second rib is plainly subject to variation in individuals of the same genus and even species. Dr. G. Baur, in an example of *Gavialis gangeticus* examined by him, found the capitulum only of the second rib articulating with the *pars odont.*; and a minute diapophysis on the neural arch of the epistropheus, with which the tubercle of the rib was probably connected by ligament. Dr. Baur also found in *Alligator mississippiensis* the capit. costæ articulating chiefly with the *pars odont.* and by a minute facet with the true centrum of the epistropheus. In *Croc. americanus*, Schneid., Baur also found the capit. costæ articulating with the *pars odont.*; and the tuberc. costæ touching the neurapophysis of the epistropheus, but without articular facet on this latter (43). These discrepancies and those observed by Koken (44) make it very desirable that these details should be examined in larger numbers of individuals of the same species. So far as the

limited material accessible to me shows, the plan of connection of the second rib in *Allig. lucius* approaches that in these Mesosuchia more closely than does that in *Crocodylus* and *Gavialis*. This I had not expected, and, in association with it, it should be remarked that in *Alligator*, as was noticed by D'Alton and Burmeister (45), the division of the vertebral end of the rib is better marked than it is in *Crocodylus* and *Gavialis*.

The structural differences of the sacral vertebræ in the two Mesosuchian genera which form the subject of this paper have been already described; it remains to compare their plan with that occurring in the *Eusuchia*. In *Steneosaurus*, as also in *Gavialis*, *Crocodylus*, and *Alligator*, the anterior terminal surface of the first sacral vertebra, whilst principally composed of the true centrum, receives a considerable lateral accession from the root of the sacral rib, and a smaller complement from the neurapophysis. In *Gavialis*, *Crocodylus*, and *Alligator*, the posterior terminal surface of the second sacral vertebra also receives a large lateral accession from the root of the second rib, and in *Alligator* also a small complement from the neurapophysis; but in *Steneosaurus* and in *Metriorhynchus* (as illustrated by these remains) no part of the posterior surface of the second sacral vertebra is contributed by the rib. In *Metriorhynchus* the rib does not contribute any part of the anterior terminal surface of the first sacral vertebra; and the accession to this surface from the neurapophysis is minute and inconstant. In *Steneosaurus* the accession to the posterior terminal surface from the neurapophysis is also a vanishing quantity.

Thus in the plan of the sacral vertebræ there is a close agreement between that in *Steneosaurus* and in the *Eusuchia* mentioned which is not observed in *Metriorhynchus*. In *Steneosaurus* the plan of the sacral ribs also is very similar to that in *Eusuchia*, whilst in *Metriorhynchus* there are obvious differences, notably their greater length and slenderness, and their pronounced downward bend.

The near resemblance in several skeletal details between these Mesosuchia and *Alligator*, to which attention has been called, and the very near resemblance of the dermal armour to that of *Jacare* is interesting as suggesting that the Alligatoridæ may not have descended through the Gavials and Crocodiles; that these three genera may not represent successive phases of evolution, but rather three distinct lines of descent. This is not the generally accepted view, and it appears not to accord with the supposed first appearance of the three genera in time.

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Since writing the above, my attention was lately most kindly called to some remains of *Geosaurus* in the Nat. Hist. Mus., Cromwell Road, by Mr. Lydekker, who at the same time pointed out to me such close structural correspondences between these and certain *Metriorhynchian* remains from the Oxford Clay, collected by Mr. Leeds, identical with those here described, as are suggestive of a very near affinity between these *Saurians*.

Oct. 27, 1888.

EXPLANATION OF THE PLATES.

PLATE XVIII.

Metriorhynchus.

- Fig. 1. Side view of synostosed atlas and epistropheus (axis). *d'*, diapophysis of axis; *d*, diapophysis of atlas.
2. Anterior view of a cervical vertebra. *d*, diapophysis; *p*, parapophysis; *prz*, prezygapophysis; *psz*, postzygapophysis.
 3. Anterior view of trunk vertebra.
 4. Posterior view of second sacral vertebræ.
 5. Caudal vertebra.

Steneosaurus.

6. Side view of epistropheus.

PLATE XIX.

Metriorhynchus.

- Fig. 1. Ilium; left, outer view. *pa*, preacetabular process; *a.i*, anterior ischiatic process; *p.i*, posterior ischiatic process; *s*, sacral impressions; *u*, upper border; *a*, acetabular hollow.
2. Inner view of same bone.

Steneosaurus.

3. Ilium; left, outer view. Lettering as in figs. 1 and 2.
4. Inner view of same bone.
5. Ischium. *a*, anterior border; *m*, mesial symphyseal border.
6. Os pubis.



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