

On the bone in Crocodilia which is commonly regarded as the os pubis, and its representative among the extinct Reptilia / by H.G. Seeley.

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"On the Bone in Crocodilia which is commonly regarded as the Os Pubis, and its representative among the Extinct Reptilia." By H. G. SEELEY, F.R.S., Professor of Geography in King's College, London. Received October 24, 1887.

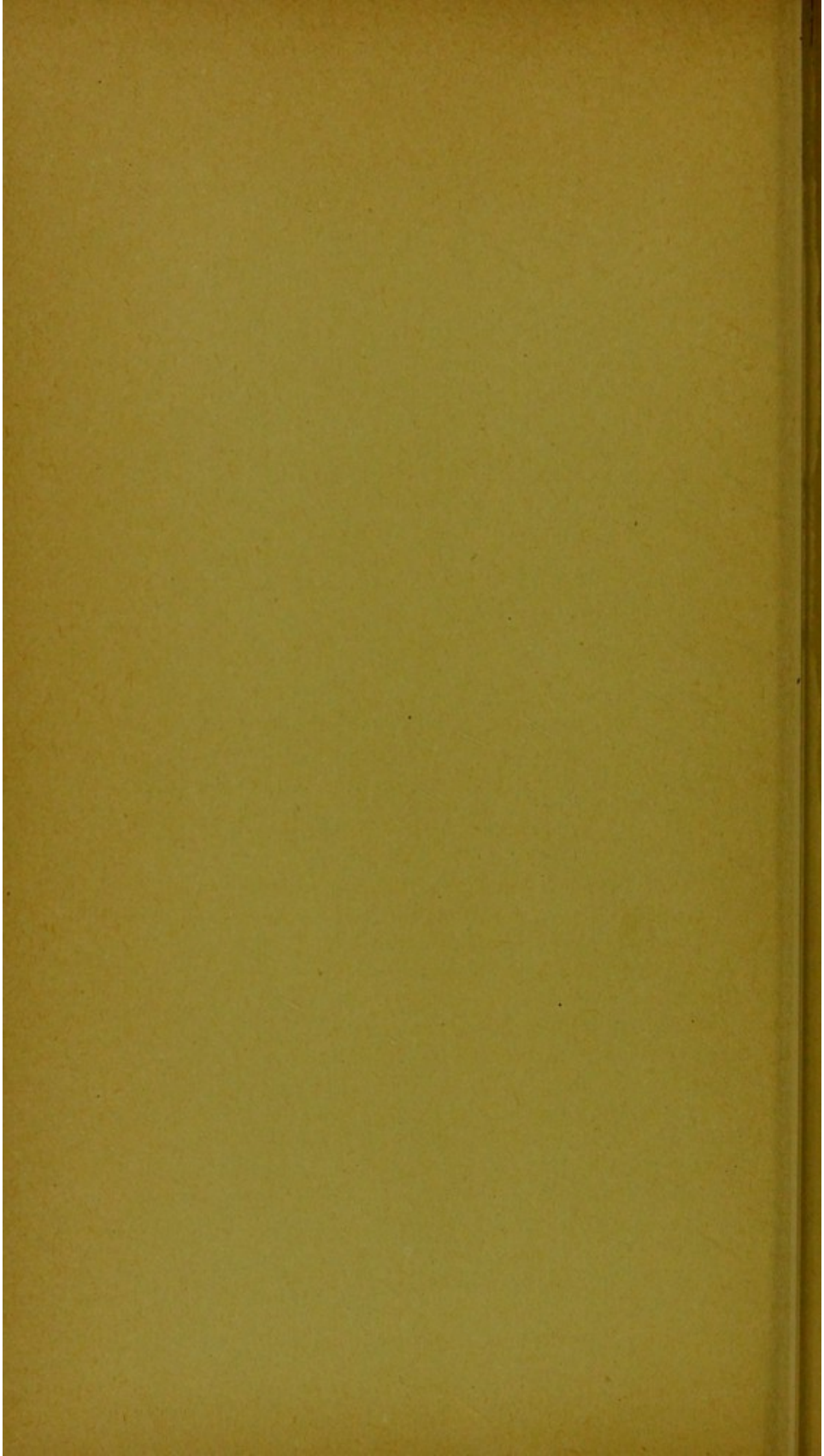
Normally three elements enter into the construction of the pelvic girdle, each of which unites with the other two, and contributes to the formation of the acetabulum for the femur. The ilium and ischium are always more or less ossified, but sometimes the pubis remains represented by cartilage throughout life. Among the Amphibia the pubis is often in this cartilaginous state in its living representatives, so that only two bones and a cartilage usually contribute to form the articular cup for the femur. Among Urodeles the pubic cartilage is perforated by a foramen, which corresponds with the foramen in the ossified pubis of a lizard, and appears to carry the obturator nerve; so that its identification with the pubis is established. But the pubis and ischium are often connate; by which term I designate that embryonic state in which no division of the primitive cartilage into separate elements has occurred. It is not quite so evident that the similarly placed cartilage in certain Anura is homologous with that of Urodeles, since it is not perforated in the same way; and it becomes smaller in aged specimens by the ischium encroaching upon it. It is absent in

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Normally three elements enter into the construction of the pelvic girdle, each of which unites with the other two, and contributes to the formation of the acetabulum for the femur. The ilium and ischium are always more or less ossified, but sometimes the pubis remains represented by cartilage throughout life. Among the Amphibia the pubis is often in this cartilaginous state in its living representatives, so that only two bones and a cartilage usually contribute to form the articular cup for the femur. Among Urodeles the pubic cartilage is perforated by a foramen, which corresponds with the foramen in the ossified pubis of a lizard, and appears to carry the obturator nerve; so that its identification with the pubis is established. But the pubis and ischium are often connate; by which term I designate that embryonic state in which no division of the primitive cartilage into separate elements has occurred. It is not quite so evident that the similarly placed cartilage in certain Anura is homologous with that of Urodeles, since it is not perforated in the same way; and it becomes smaller in aged specimens by the ischium encroaching upon it. It is absent in

the genus *Hyla*; such absence, considered with the presence of a pubis in *Dactylethra*, would support the conclusion that the pubis and ilium are connate in *Anura*.

In the young of *Crocodylia* the same three elements contribute to the formation of the articular cup for the femur, the ilium above, the ischium behind, and a cartilage in front.

Professor Hoffmann* regarded this cartilage as the pubis, and then the bone which is anterior to it, and had previously been identified as the pubis, became the pre-pubis.

Professor Huxley questioned this identification, and regarded the bone as the ossified part, and the cartilage apparently as the unossified portion of the pubic element of the pelvis.† This cartilage is well known to decrease in dimensions with the age of the crocodile, but it does not disappear by augmenting the extent of the supposed pubic bone; though if it were really a pubic cartilage, its ossification should cause the anterior bony element to extend into the acetabulum. But instead of disappearing in this way, ossification has the effect of continuing to exclude the supposed pubic bone from the acetabulum; so that the cartilage in the young animal does not give rise to a separate osseous element in the adult, but disappears by so ossifying as to approximate the ischium and ilium. At first there is a gap between the ischium and ilium anteriorly, which the cartilage fills, but eventually in old animals these bones almost meet each other, and the cartilage is ossified. Thus in the adult animal the acetabulum is formed by two bones, one being the ilium, and the other in the position otherwise occupied by the ischium and pubis. Therefore it follows, either (1) that the pubic cartilage, if originally distinct in the young, becomes incorporated by ossification with the ilium and ischium; or that (2) the pubis in crocodiles does not enter into the acetabulum, but is a pre-acetabular ossification. I am aware of no exception to the law that the pubis contributes to the os innominatum when it has a separate existence, and therefore it seems to me more probable to suppose that ischium and pubis should be connate, like the same elements in some salamanders, and undivided, than that crocodiles should so differ in plan of the skeleton, as to have the pubis removed from connexion with the ilium, and from the acetabulum. If the former view prevails, then the acetabular cartilage in crocodiles is never a pubic cartilage, but only the unossified part of the ilium or ischio-pubic bone which

* 'Niederl. Archiv Zool.,' vol. 3, 1876, p. 144.

† 'Roy. Soc. Proc.,' vol. 28, 1879, p. 394. Prof. Huxley's language is not quite clear on this point. He says (p. 398) "It is the osseous portions of the pubes which are commonly described as the entire bone." "These apparently anomalous elements of the pelvis are readily moveable upon their fibro-cartilaginous connexions with the acetabulum. But in no essential respect do they differ from ordinary pubes."

occupies the place of the pubis, and so it is manifest that if the pubis enters into the acetabulum in crocodiles, it must be found in the anterior process of what is commonly named the ischium, which fills the anterior corner of the pelvic basin. And since no exception to this position of the pubis among vertebrates is known, by which it articulates with the ilium, the conclusion is legitimate, in the absence of evidence to the contrary, that a bone which does not unite with the ilium by bony union, and which is carried in front of a process which occupies the usual position of the pubis, cannot be the pubic bone. It would be equally unprecedented for the pubis and ischium to be connate in a reptile, were it not that this condition is already established in the existing Amphibia, and were there not strong reasons for regarding the crocodiles as descended from extinct allies of the Amphibian class; while in an early stage of development all the pelvic elements in crocodiles are connate. Hence I concur with Professor Huxley in regarding Professor Hoffmann's identification of the pelvic acetabular cartilage as the pubis as untenable.

Professor Hoffmann regards the bone which is commonly identified as the pubis as being the pre-pubis.* Professor Huxley, on the other hand, regards it as being a portion of the pubis, and bases his identification mainly on the relations of this bony element to the pelvic muscles. There is an *à priori* objection to the latter interpretation, because it would introduce a joint in the middle of the pubis, making one part connate with the ischium, and the other part a free bone. Of such a condition I am not aware that vertebrate osteology offers any example, and the improbability against it being a true interpretation seems to be great. That a bone may ossify from several centres is evident from the bones of Mammalia and certain young birds and lizards; but in crocodiles none of the bones are thus characterised, and therefore I can only conclude with Hoffmann, that the ossification is a distinct element of the skeleton, which is connected with the pubic portion of what I term the ischio-pubic bone, and is in the position of the pre-pubic bone; but it does not necessarily follow that it is identical with the pre-pubic cartilage, which has been termed by Hoffmann and Huxley the epipubis. For the cartilage, whether in Amphibians or Mammals, is developed from the median line of the pubic symphysis; while in crocodiles the pubes do not form a symphysis, because they are not developed distally, and the pre-pubic ossification is situate immediately below the acetabulum, in the position of the pectineal process; so that while the Amphibian cartilage is in the position of the marsupial bones of mammals, the crocodilian

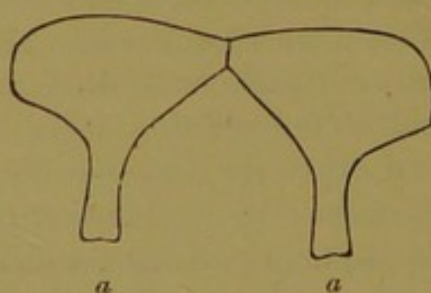
* Professor Haughton ('Ann. Mag. Nat. Hist.,' vol. 1, 1868, p. 282) bases the nomenclature of the bones on the muscular anatomy, and terms the reputed pubis the marsupial bone; the ischium then becomes the pubis; while the ilium is the ilium in its anterior part, and the ischium in the posterior part.

bone corresponds in position with the pre-pubic bone of Ornithosaurs, which is always developed on the anterior pubic border towards the acetabulum, at some distance from the pubic symphysis. The extinct allies of the Crocodilia may throw some light upon the nature of this ossification.

First, in the Teleosauria the bone is much more slender and less expanded at its anterior end, in all the species from the Lias and Lower Oolitic rocks. The diminution in size of the bone in Oxford clay representatives of the group is more marked, and in some undescribed types in the collection of A. Leeds, Esq., is reduced to a mere bony style without any expansion at either end, comparable in form and substance to a lucifer match. One stage more of diminished development would obliterate the bone altogether, but no such condition has yet been discovered. It has the same osseous attachment as in Crocodilia, and the ischio-pubic bone is of the same type in Teleosauria as in Crocodiles.

In the Ornithosauria the plan of the pelvis is different. First, there is the complete ossification of the three constituent bones, with the ilium prolonged in front of the acetabulum as well as behind it, the ischium and pubis united by symphysis, and all three bones contributing to form the imperforate acetabulum. Secondly, there is a pre-pubic ossification in front of the pubis, with a narrow attachment below the acetabulum. These pre-pubic bones vary in form in the different genera. In *Dimorphodon* they are triangular; in *Cynorhamphus* they are shaped like a capital T, and so expanded anteriorly that

Pre-pubic bones of *Cynorhamphus suevicus*,
after Quenstadt. Restored.



a, attachment to the pubic bones.

the cross bars from the two sides met in the median line; in *Rhamphorhynchus* the shape is T, an inverted capital L, but the bones of the two sides are united together into a transverse bow-shaped bar. Other modifications are found in the group, but the most common are approximations to the form of the pre-pubic bones of crocodiles. Since these bones have the same relations to the pubes which the pre-pubic bones of crocodiles exhibit, I regard them as being homologous, and if the distal part of the Ornithosaurian

pubis were not developed, the homology would be supported by a similar plan of pelvic construction.

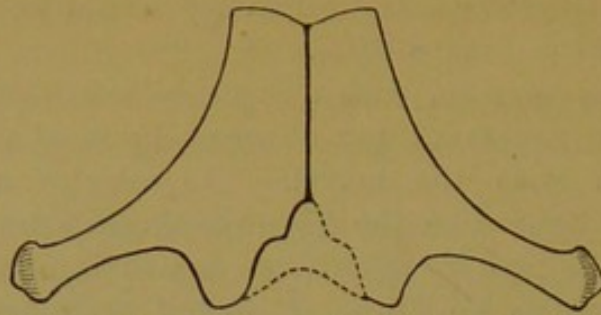
Finally, there is some evidence that a similar structure is developed in the abdominal region of the allies of *Iguanodon*, without being in direct union with the pelvis. As long since as 1841 Dr. Mantell, F.R.S., figured in the 'Philosophical Transactions' (Pl. 8, fig. 2) an undetermined Wealden bone, which is now in the British Museum, registered as No. 2218. It is not quite perfect, but is suggestively similar to the pre-pubic bones of Ornithosaurs. A thick sutural surface shows that it met a similar bone in the median line. Subsequently Mr. S. H. Beckles, F.R.S., obtained another specimen into which two such bones entered as constituents, which was exhibited during the British Association Meeting at Brighton, in 1872, and ultimately described and figured by Mr. J. W. Hulke, F.R.S.*

Bones, like that figured by Mantell, have long been in the British Museum. And Professor Cope has figured a pair of similar bones in *Diclonius mirabilis*.† Mr. Hulke interpreted Mr. Beckles' specimen as consisting of the clavicles and interclavicle. Mr. W. Davies, F.G.S., had interpreted the isolated bones like Mantell's No. 2218, as clavicles, and his determination had been accepted by Professor O. C. Marsh; so that until M. Dollo regarded them as parts of the sternum they had been regarded as clavicles. Dr. George Baur, of Yale College, subsequently in 1885† suggested that the supposed sternal apparatus of *Iguanodon* should be turned round, so that the supposed clavicles would become posterior processes of the sternum, and this view has been supported by Cope and adopted by myself. I suppose that the interpretation of the Beckles specimen was a consequence of its condition of preservation, by which fractures came to simulate sutures. Those fractures which are assumed to limit the clavicles, so as to allow the supposed interclavicle to extend between them, follow very different courses from the natural limits of the bones. If Mantell's fossil already referred to is superimposed upon Mr. Beckles' specimen, then it is manifest that the broad part of the specimen is made up of two such bones which meet by median suture, and extend for two-thirds the length of the specimen. Some trace of the transverse suture may perhaps be seen which separates these bones from a thin ossification which extends beyond them. Hence there can be no interclavicle between the supposed clavicles; and the evidence for the identification of the clavicles disappears. Turning the specimen so that the supposed clavicles point posteriorly, they will be found to make a remarkable approximation in form to the pre-pubic

* 'Geol. Soc. Quart. Journ.,' vol. 41, 1885, Pl. XIV, p. 473.

† 'American Naturalist,' Feb. 1886, p. 154.

‡ 'Zoologischer Anzeiger,' No. 205, p. 561.



? Pre-pubic bones of *Iguanodon*, restored from No. 2218, Brit. Mus.

bones of the crocodile. Professor Huxley* figured the ventral aspect of a *Crocodylus acutus* at about the close of embryonic life, in which a considerable fibrous development was found anterior to each pre-pubic bone. This condition varies with age. In a large adult crocodile from Abyssinia, in the British Museum, the fibro-cartilages anterior to the pre-pubic bones are united in the mesial line, anteriorly, so as to form one mass. A similar condition is seen in younger specimens. And if such a structure were sufficiently ossified to be preserved in a fossil state, it would closely reproduce the form of the anterior portion of Mr. Beckles' fossil, while the marks of lateral attachment in this part of the fossil correspond with the grooves for the last pair of abdominal ribs. Therefore I regard this specimen as probably representing in the *Iguanodon* the pre-pubic bones of crocodiles, as well as the cartilage connecting them with the ribs, which Huxley terms the epi-pubis. On its mode of attachment to the pubis I offer no suggestion, and there is no evidence available. But since the bone in crocodiles and Ornithosaurs is attached in the region of the pectineal process, it is probable that it is connected with the extension of the pectineal process in Dinosaurs, which Professor O. C. Marsh has named the pre-pubis, and I would bring the pubic bone in the Ornithischia into harmony with the process in Crocodiles by suggesting that the distal part of the bone, like the anterior process, is entirely absent, so that only the sub-acetabular part which supports the pre-pubis remains in crocodiles; and I suppose that if the pubis had been prolonged distally in the crocodile, it might have included the foramen for the obturator nerve.

If this interpretation of Dr. Mantell's undetermined bone should be sustained, it would contribute a new and distinctive element to the *Iguanodont* pelvis, as remarkable as the pubic modification in an Ornithosaur or Crocodilian, and distinct from either. The evidence from the fossil allies of crocodiles by no means demonstrates the nature of what I have termed the pre-pubic bones, though it shows that pre-pubic ossifications exist which cannot be confounded with the pubis, which may resemble the Crocodilian bone in form and in

* 'Roy. Soc. Proc.,' vol. 28, Pl. 8.

being anterior in position to the acetabulum, and in similar isolation from the ilium.

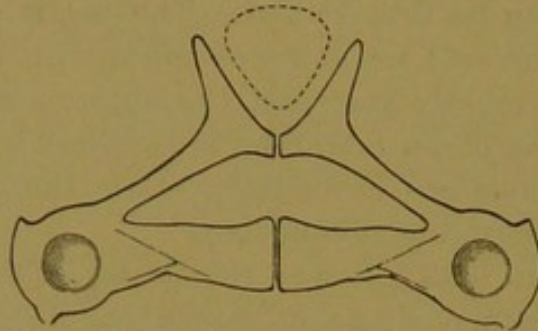
In the current identification of this bone every consideration has been made subordinate to the embryological evidence as stated by Rathke. Yet although his excellent description unaccompanied by figures has been regarded as conclusive that the bone under discussion is the pubis, it seems to me necessary to reconsider the evidence before the matter can be thus settled. The pelvis of a crocodile in that stage of development which corresponds with the middle period of incubation, if I rightly interpret the author's meaning, is apparently more like that of an emu than is the adult animal in so far as the ischium and pubis are concerned; while the relative shortness of the pubis is suggestively Iguanodont.

Rathke's statement is as follows: the ilium, ischium, and pubis of each side unite to form a single unbroken cartilaginous mass. The two ilia are short, rather broad, plates, as in the full-grown animal, and extend somewhat outward beyond the transverse processes of the sacral vertebræ. The ischia were also similar to those of the full-grown animal, consisting of tolerably thick plates, somewhat expanded transversely at their median union, but are not so broad in proportion to their length as in the full-grown crocodile. The pubis was somewhat shorter than the ischium, and in proportion to the other parts of the pelvis was much shorter than in later life, and not directed so much forward. It extended downward nearly parallel to the ischium, almost along its whole length, only separated from it by a small interspace, and uniting with it at its upper end. Ventrally the pubes are widely separated, and have the hinder small half of the connexion with the yolk-sac opening between them. They preserved a similarity in shape to that of the mature crocodile, but the distal ends were not so wide in proportion to their length, and the other parts are not so slender as in later life. And on a subsequent page the author again remarks, "The direction of the pubis in embryonic life remains different to that of the adult, but in the middle of the embryonic period there comes to be a division in the cartilaginous plate which hitherto had represented the ilium, ischium, and pubis."

The early condition of the pelvic elements is so interesting in its parallelism of the ischium and pubis, and in the subsequent change of direction of the reputed pubis, that I applied to Professor W. K. Parker, F.R.S., for help. He at once sent me three examples of *Crocodylus palustris*, one about mature in the egg, another with the head 3 cm. long, the body about 4.5 cm., and the tail about 7 cm., which was about half grown, and a smaller specimen about a third grown.

On examination I found that the pubes in the half-grown specimen were developed as in the adult, even to the fibrous extensions in front of the bones and behind them, and the only important difference was

the presence of the median notch between their anterior corners for the hinder half of the yolk sac and a direction rather less anterior. In the smallest specimen the element which Rathke terms the pubis does not diverge anteriorly from the ischium to the same extent as in the adult, but the elements have the usual form and meet in the middle line, and the difference is unaccompanied by any divergence



Pelvic cartilage of *Crocodilus palustris*, showing the relations of the pre-pubic plates to each other when one-third developed in the egg.

of plan in the pelvis. The unsegmented cartilage is a different kind of evidence from the same cartilage divided into elements which become permanent as ossifications. And I hold segmentation which occurs subsequently at a distance from the acetabulum, which isolates a bone from the pubic region of the pelvis and the ilium, to be evidence that the structure so separated is pre-pubic; while the only other segmentation separates the ilium from the bone which supports the pre-pubis. From this it follows that the pubis has never been distinct from the ischium, and is not developed distally in crocodiles. The notch which defines the anterior part of the ischio-pubic bone corresponds with the great notch in the acetabulum of the mammalian pelvis, and that notch is situate between the ischium and pubis. The cartilage which completes the anterior margin of the acetabulum seems to me to be inseparable from the ilium; and to be continuous at its border with the fibrous sheath for the head of the femur. I should attribute its existence to the absence of distal development of the pubis, because this would remove the usual pressure of the bone upon the anterior corner of the acetabulum, which stimulates ossification of the ilium.

If the interpretation thus made is morphologically sound, it has an important bearing upon the affinities and classification of the Crocodilia.