

# THE CROCODILE OF MARANSART

(DOLLOSUCHUS DIXONI [OWEN])

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## INTRODUCTION AND HISTORICAL

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In one of his important monographs, and under the heading « *Gavialis Dixoni* », Professor Owen (1850, p. 46) described a new species of Gavial founded on two fragments of the mandible of different individuals, a late cervical or dorsal vertebra, and a femur, all of which had been collected by a distinguished amateur geologist, Frederick Dixon, from the Bracklesham Beds (Middle Eocene) at Bracklesham, Sussex. Dr. Dixon died in 1849 and his collection was purchased by the Trustees of the British Museum in 1850.

Subsequently, in a contribution to Dixon's « *Geology of Sussex* » (1850a, p. 208) issued in December 1850, a year after that author's death, Owen briefly redescribed and figured the specimens, and they again appeared in the second edition of this work in 1878 (1878, p. 253). Since that date only Lydekker (1888, p. 69) has taken any notice of them, and he provisionally referred them to *Gavialis* (?) *dixoni*.

Since 1888 no additional specimens have been discovered in England, and no work has been done upon the species, which has remained thus insecurely perched in the genus *Gavialis*.

In Belgium, however, in 1915, a discovery was made which enables a complete examination of the species to be made, for in that year, unfavourable though it might appear for palaeontological research in that country, an almost complete skeleton of a crocodile was discovered in a quarry at Maransart. As this is one of the most important palaeontological discoveries in Belgium for some years a few remarks concerning the circumstances may be permissible. The site of this interesting discovery is in the province of Brabant, about 25 kilometres from Brussels and not far from the field of Waterloo. The rock in which the specimen was found is a hard calcareous sandstone of Brussellian, i. e. Middle Eocene, age. The stone is now quarried for paving stone but in the past it was

much used for building and such important edifices as the magnificent Hôtel-de-Ville in Brussels and the church of Saint Gudule were built of this material. The sandstone contains water-rolled pebbles of Silurian age. The deposit, and the Brussellian stage generally, are characterized by the presence of the littoral turtle *Lytoloma camperi*, and *Trionyx bruxelliensis*. Winkler has also been found (Winkler 1869, p. 350). The crocodile skeleton was found in association with three fishes, *Odontaspis macrota*, *Pristis lathamii* and *Myliobatis striatus*, which are quite common in the Brussellian; and with four mollusca, namely *Cassidaria nodosa*, *Tellina lyelli*, *Divaricella* sp. ? and the rare *Ostrea elegans*. The last named shell is actually preserved in the crocodile's left orbit.

Thus, despite strong marine representation in the deposit we see also evidences of fluviatile life.

Climatically, both in Belgium and England, the evidence shows that the Middle Eocene (Bracklesham and Brussellian) was warmer than at the present time.

This Belgian « Crocodile de Dixon » was removed to the Royal Museum of Natural History in Brussels and was transformed, with very great skill, into a beautifully prepared skeleton by two of the Museum's preparators, M. Hubert J. Menschaert and M. Jean de Kleermaeker. All this work was accomplished in 1926 and 1927 under the supervision of the late Louis Dollo who placed the specimen on exhibition in the latter year, who wrote the exhibition labels, and who intended to describe the specimen. Unfortunately, in 1931, death made it impossible for this great palaeontologist to undertake the task.

Professor Dollo left no notes beyond the exhibition labels and for several years the specimen was therefore exhibited but remained unexamined and undescribed.

It is, therefore, with a very deep sense of gratitude that I record my thanks to Dr. V. van Straelen, Director of the Museum, for the opportunity of examining and describing this excellent specimen, an honour which has been further greatly increased by sending the specimen to me in London through diplomatic channels. I am therefore also greatly indebted to His Excellency the Belgian Ambassador in London, Baron E. de Cartier de Marchienne, for his great kindness and personal interest. It is indeed an act of great intermuseum and international courtesy to lend a unique specimen, so splendidly preserved, for study in a foreign museum.

Examination already shows that there can be no doubt that the specimens described and figured by Owen as the types of *Gavialis dixonii* can be referred to a skeleton like that from Maransart. Further, while it is clear that the species is distinct, the new skeleton shows that the species cannot be retained in the genus *Gavialis*, but must be referred to a different family of the Crocodylia and to a new genus in that.

As the British Museum specimens are so fragmentary, and as Owen's description of them is quite adequate, there is no need to recapitulate his observations

here, and we may therefore confine ourselves to the description and discussion of the Belgian form.

As has been stated, Dollo left no manuscript, but in the labels he drafted for the exhibition case, which includes plaster casts of the Bracklesham bones, it is recognized that the new skeleton requires a new generic name and Dollo had actually suggested the name *Europaeosuchus*. This name has, of course, no validity and is somewhat cumbrous. It is not, therefore, proposed to establish it here but to use a more appropriate name, which Dollo could not have used, and which bears the memory of that gifted and charming palaeontologist.

## ORDER LORICATA

### SUB-ORDER EUSUCHIA

#### FAMILY TOMISTOMIDAE

Genus DOLLOSUCHUS nov.

#### DIAGNOSIS.

Skull long and comparatively broad, facial contour comparatively flat. Nasals and premaxillae in contact, the former almost reaching the hinder border of the external nares. Internal nares placed as far back as possible, small and circular. Palatal vacuities long and subtriangular. Orbits with a marginal ridge and antero-internal depression; slightly larger than the supratemporal fossae. Maxillae with interdental fossae for the mandibular teeth.

GENOTYPE. — Complete skull and mandible, vertebrae, portions of shoulder and pelvic girdles, limb bones, scutes, etc. Registered number 1748, Musée Royal d'Histoire Naturelle, Brussels.

HORIZON AND LOCALITY. — Middle Eocene (Brussellian), Maransart, Brabant, Belgium.

There is one species, *Dollosuchus dixonii* (Owen).

Syn. : *Gavialis dixonii* Owen, 1850.

*Garialis* (?) *dixonii* Owen, Lydekker, 1888.

*Europaeosuchus dixonii* (Owen), Dollo, MS. 1926.

*Eosuchus dixonii* Owen, Kuhn, 1936.

DIAGNOSIS. — As for the genus.

TYPE-SPECIMEN OF THE SPECIES; two mandibular fragments, an anterior dorsal vertebra, and the right femur. Registered numbers 26125-6, 26128-9. Geol. Dept., British Museum (Natural History), London.

HORIZON AND LOCALITY. — Middle Eocene (Bracklesham Beds), Bracklesham, Sussex, England.

## DESCRIPTION.

In describing the specimen, quite apart from the discussion of the relationships between the different genera, it will be of value to compare it with such other members of this family as are well known and have been adequately described. So far, the most fully described and figured fossil of the family is *Thoracosaurus scanicus* Troedsson, from the Danian of Southern Sweden (Troedsson, 1924), and this account has been largely used. For the recent forms a complete and normal skull of *Tomistoma schlegeli* has been available.

The systematic relationships between these and other members of the family with *Dollosuchus* are discussed later.

**SKULL.** — The skull has the form of an elongated triangle, the greatest width being that between the outer and posterior angles of the quadrato-jugals. The cranial part of the skull is comparatively broad and low for this type of crocodile and the profile is longitudinally concave between the front margins of the supratemporal fenestrae and the swelling behind the opening of the anterior nares. The concavity and the height of the skull are not so marked as in *Tomistoma*. The lateral margins of the skull are, of course, concave externally. The general proportions show that the skull is less elongated than in some related forms. In *Thoracosaurus* and *Holops*, for example, the ratio of maximum length to breadth in the skull is as 3 : 1, in *Tomistoma* and *Eosuchus* the same ratio is 2.5 : 1, and in *Gavialosuchus* and this present skull the ratio is 2.3 : 1. This relative shortness of the skull coupled with the strength of the cranial region is suggestive of a juvenile condition in the specimen being described, and this point will be dealt with later.

The various elements in the skull, and the sutures between them, are very well displayed and leave no room for doubt in deciding their relationships. There has been no compression or distortion and most of the teeth remain in perfect condition. The cavities of the skull are filled with a compact grey-brown matrix which it has not been possible to remove completely, and although the inner elements cannot, therefore, be examined it is possible to describe fully the upper surface of the skull, the palatal surface, and the occipital region.

**Superior Surface (Pl. I, fig. I).**

**PARIETAL.** — The parietals are firmly fused to form a small anchor-shaped bone whose hinder border marks the posterior limit of the skull as seen from above. The posterior border, which is the widest part of the bone, measures 53 mm. across, and is slightly convex posteriorly and concave superiorly. The sutures on either side with the squamosals are short and situated midway on the hinder border of the supratemporal fossae. At these sutural, lateral extremities the antero-posterior diameter of the bone is only 7 mm. From the sutures the

lateral borders of the bone run inwards and forwards forming the inner margins of the supratemporal fossae. Between these margins and the hinder border the surface is pitted, though much less so than in *Tomistoma*, *Thoracosaurus* or *Eosuchus*. In the hinder half of the bone there are two large pits and one or two smaller ones but their effect, together with the concavity of the bone here, is to leave the inner margins of the supratemporal fossae as thin elevated rims which are almost in contact at the closest approximation of the fossae. The least breadth of the parietal at this point is only 5.5 mm., which is very much less than is usual in the other genera of this family. Anteriorly to this, the lateral borders of the parietal diverge forwards and outward until they meet the post-frontals at the inner third of the front margins of the supratemporal fossae. The suture between the parietal and the frontal is in the form of a very wide  $\Lambda$ , with so wide an angle that it is nearly a straight line, and is almost as far forward as the most anterior margin of the supratemporal fossae. The anterior part of the parietal is also less strongly pitted than is usual and is also concave superiorly. The maximum width of the anterior margin is 38 mm. and the length of the parietal in the mid-line is 44 mm. Its most striking features, quite unlike those of *Tomistoma*, *Thoracosaurus* or *Eosuchus*, are the concavity of the bone, with the formation of two thin and high lateral borders to the supratemporal fossae, and the extreme slenderness of the bone in its mid-length.

**SQUAMOSALS.** — The squamosals, forming the postero-external margins of the supratemporal fossae, are also small and slender bones, but are more heavily pitted than the parietal and have the surface slightly convex, giving a somewhat rounded effect to the hinder corners of the cranial table. They are prolonged considerably behind, each ending in a long and narrow ridge running backward and outwards upon the exoccipital and the quadrate. The hinder and inner part of the bone, with the parietal, forms the posterior border of the supratemporal fossae, and the lateral and forward part of the bone, with the post-frontal, forms the upper temporal arch. The suture with the post-frontal is very clearly marked and occurs, on the upper surface, about half way along the outer margin of the supratemporal fossa, but ventrally it continues forwards until it reaches the transverse process of the post-frontal. Neither bone has any outstanding peculiarity which merits description. The greatest width of the bone at the posterior border of the skull is 38 mm. on the left side and slightly less on the right squamosal. The extreme length, from the post-frontal suture to the exoccipital suture is 66 mm. In general shape the squamosals are similar to, but more slender than, those of *Eosuchus* and *Tomistoma*, and have the postero-external ridge more laterally directed than in *Thoracosaurus scanicus* as figured by Troedsson.

**POST-FRONTALS.** — In contrast to the two bones previously described, the post-frontals are comparatively large and stout having actually a greater proportion of this region than the post-frontal of an adult *Tomistoma schlegeli*, though

it is apparently not quite so prominent as in *Thoracosaurus scanicus*. The shape of the bone is, of course, dependent upon the size and shape of the supratemporal fossa of which it constitutes the antero-external border. The breadth of the bone in this specimen at the hinder, squamosal, end is 14 mm., and at its junction with the frontal the width along the suture is 25 mm. The total length is 41 mm. The squamosal end is its narrowest part. The ventral surface of the bone is produced into a short and stout process on the antero-external side which meets a somewhat similar but dorsal outgrowth of the jugal to form the post-orbital bar which separates the orbit and the lateral temporal fossa. The post-frontal's share in the post-orbital bar is greater than that of the jugal, and the whole process is stout, and shorter and thicker than that of the recent adult *Tomistoma schlegeli* used for comparison.

The post-frontal portion of the post-orbital bar, measured on the external surface, is 18.5 mm. long.

**FRONTAL.** — The frontal is diamond-shaped, its greatest transverse diameter being just behind the orbital margin. The hinder edge is slightly rounded and is just excluded from the anterior borders of the supratemporal fossae by the junction of the parietal and post-frontals. The central part of the bone is concave having the external borders, which form the inner boundary of the orbits, elevated. The surface of the bone at the narrowest part between the orbits, and the whole of it anterior to this part, is smooth, but the main portion of the surface is deeply pitted, the pits being on the average about  $4 \times 3$  mm. The frontal is the most ornamented bone in the whole skull.

The surface is more concave and the margins are more elevated than in the living *Tomistoma*, but these margins are not so concave externally as in that genus or in *Thoracosaurus*.

The anterior blade of the frontal is not rapidly contracted in breadth but diminishes quite gradually from the front border of the orbits until it ends in three closely approximated prongs which are intercalated between similar processes on the nasal, into which the blade penetrates for some little distance. The length of the preorbital portion is greater than that in *Tomistoma schlegeli* but less than that in *Thoracosaurus scanicus*.

The principal dimensions are :

Greatest breadth	...	...	...	...	...	...	...	...	...	61 mm.
Greatest length...	...	...	...	...	...	...	...	...	...	92 mm.
Least interorbital breadth	...	...	...	...	...	...	...	...	...	24 mm.
Length of internasal portion	...	...	...	...	...	...	...	...	...	20 mm.
Breadth at posterior nasal limit	...	...	...	...	...	...	...	...	...	12 mm.

**PREFRONTAL.** — The prefrontals are small, elongated, triangular bones. Each forms the anterior half of the medial border of the orbit. From there it extends forwards as a thin wedge between the nasal and the lachrymal. They

appear to be much smaller than those of *Thoracosaurus scanicus* so fully described by Troedsson, although it should be pointed out they are described by him as the lachrymals. The posterior half of each prefrontal is sculptured with a few irregular pits. The maximum length of the right prefrontal is 70 mm., and the greatest width is 13 mm.; the left prefrontal is only 64 mm. long and has a maximum width of 12 mm.

LACHRYMAL. — The lachrymals are much stouter bones than the prefrontals but like them they have a sculptured surface. They form the anterior margin of the orbits and, together with the jugal, the external orbital border. The latter fact is interesting because, whereas the margin formed by the jugal is always elevated into a crest, this ridge usually flattens out on the more anterior part contributed by the lachrymal. In *Dollosuchus*, however, although the sutural connexion between the two bones is clearly observable, the lachrymal also contributes to the ridge and only the anterior and inner part of the orbit is flattened and somewhat depressed. This is not the condition on the skulls of the recent *Tomistoma schlegeli* that I have been able to examine, and it is also unlike that of *Eosuchus*, where the flattened orbital portion of the lachrymal can be clearly distinguished. Anteriorly the lachrymal retains approximately the same width for about two-thirds of its length and thereafter narrows rapidly to a point. This is somewhat like the condition in *Thoracosaurus*. The maximum length of the lachrymal is 79 mm. and the greatest width, that at the orbital margin, is 24 mm.

JUGAL. — The jugals are long, stout, and prominent bones which form most of the outer border of the orbit and the anterior and outer margins of the lateral temporal fossae, besides supplying the base of the post-orbital bar which, on each side, divides the orbit from the lower temporal fossa. Anteriorly, they are in contact with the lachrymals and the maxillae, and posteriorly they meet the quadrato-jugals. Each jugal is comparatively long and narrow and is pitted quite strongly on the upper and orbital surface of the anterior half. Isolated, the bone would be not unlike a chopper. The orbital margin, as has been mentioned, is raised as a ridge but this dies down at the post-orbital bar to a smooth rounded border. The jugal forms only the front half of the border of the lower temporal fossa and the upper surface then gradually dips down ventrally, in contact with the quadrato-jugal, until it meets the ventral margin of the bone almost at the hindermost angle of the skull. The jugal-quadrato-jugal suture is almost a straight line; the jugal-maxillary suture is long and gently undulating. The extreme length of the bone is 161 mm., and the maximum width is 27 mm.

QUADRATO-JUGAL. — The quadrato-jugal is a wedge-shaped bone which lies between the jugal and the quadrate. Its inner surface forms the hinder margin of the lateral temporal fossa and the outer surface forms the hinder and outermost angle of the skull. Anteriorly the bone is almost of its maximum breadth,

flat, and ornamented only very feebly with faint pitting. The suture with the jugal is long and straight, but the suture with the quadrate is meandering. The broadest part of the bone is about a third of the length from the hinder end. Posteriorly the bone becomes stout and rounded and ends in a pointed projection. The widest part of the skull is across the two hinder ends of the quadrato-jugals. In this specimen there is no trace of the sharp projection of the anterior edge into the lateral temporal fossa which is usually prominent in crocodiles and can be seen, among fossils, on skulls of *Tomistoma*, *Thoracosaurus* and *Eosuchus*. The development of the specimen has been so carefully accomplished that it is difficult to believe that its absence on both sides is due to removal in preparation.

The maximum length of the quadrato-jugal is 89 mm. The greatest breadth is 22 mm., and the breadth at the anterior end is 17 mm. The ventral aspect of the bones is still enveloped in matrix and cannot be seen, although there is no reason to suspect that it varies much from the normal.

**QUADRATE.** — The quadrates are not in any way remarkable and are, of course, partly hidden by the closely applied, overlapping, quadrato-jugals and squamosals. They appear to be quadrilateral, smooth and of uniform thickness except at the hinder, articular, end where two rounded condylar processes are developed. The bones are concave dorsally and slightly concavo-convex or undulating ventrally. The outer border is somewhat irregular, consequent upon the vagaries of the suture, but the inner border is well defined, rounded and concave, and runs forwards and inwards to become concealed under the ex-occipital. The hinder edge is rounded and consists of two well-developed articular condyles separated by a shallow depression. The condyles are subequal in size but the difference in direction of their dorso-ventral axes gives the outer a more prominent appearance. The axes in both cases are directed externally at the upper surface, the inner condyle being at about 20° to the vertical and the outer at nearly 45°. The upper and inner surface of the quadrate just anterior to the inner condyle bears a marked triangular concavity which contains in its anterior angle the small opening for the canal of Stannius. In *Dollosuchus* the depression is seen but is not very marked and the most careful scrutiny fails to discover any opening of the canal. This point is of some interest, for the diagnosis of *Eosuchus*, formulated by Dollo, contains the phrase, « Canal de Stannius du quadratum, pour le siphon mandibulaire, énorme. » The photograph of that skull (Plate I, fig. 5), published here for the first time, fully testifies to this character.

Ventrally the quadrate has a smooth surface which bears, in this case, a moderately prominent and rounded ridge running along the length of the bone from the outer articular condyle. The presence of this ridge saves the ventral surface from being markedly concave both longitudinally and laterally.

The maximum breadth of the articular end is ... .. 33 mm.  
Depth of the inner articular condyle... .. 19 mm.



NASAL. — The nasals are so closely united that it is quite impossible to distinguish any median line dividing them. The posterior, frontal, margin has already been described and it need only be added that the nasals extend forwards, maintaining practically the same width until they reach the hinder edges of the premaxillae where they begin to contract. The anterior end consists, therefore, of a wedge, between the premaxillae, that continues almost to the back of the external nares, for the last definite trace of it is a few millimetres from the narial border in a shallow groove between the premaxillae. This extreme length of the nasals and their close approximation to the nares are sufficient to differentiate this genus from every other member of the family so far figured.

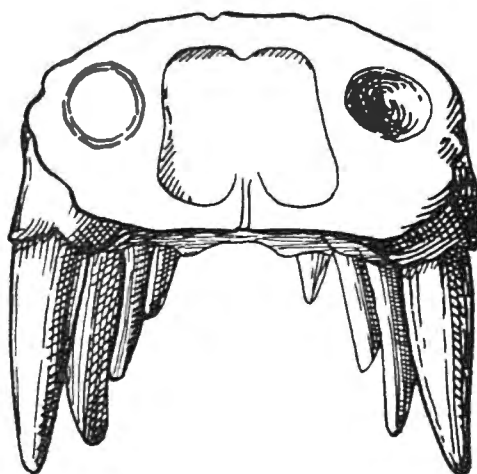


FIG. 1. — Section through maxillae and nasals. Nat. size.

The surface has a few longitudinal furrows and some shallow pits but is nowhere heavily marked. Longitudinally the nasals are concave, the maximum concavity measuring 10 mm. in a length of 250 mm., which indicates the nature of the profile. Laterally, the nasals are gently rounded and not flattened as in the recent *Tomistoma*, for example.

DIMENSIONS :

Maximum length	...	...	...	...	...	...	...	...	...	259 mm.
Maximum width	...	...	...	...	...	...	...	...	...	22 mm.
Width at hinder end of pmx.	...	...	...	...	...	...	...	...	...	16 mm.
Length of portion between pmx.	...	...	...	...	...	...	...	...	...	86 mm.
Distance of anterior end from external nares	...	...	...	...	...	...	...	...	...	8 mm.

MAXILLAE. — The maxillae are the largest bones on the upper surface and they are, being marginal, amongst the most strongly ornamented in this specimen. On account of the comparative width of the nasals the maxillae do not attain their usual prominence on the upper surface. Seen from the side, they are chiefly remarkable for the prominence of the alveoli. The premaxillary portion on each side between the nasal and the maxilla is long and denticulate with the result that the inner borders of the maxillae are arched when seen from the side : posteriorly, there is the long and ascending jugal and lachrymal •

sutures, then the more or less straight nasal border, and anteriorly the long and descending premaxillary suture.

An interesting feature of the upper surface is that at the junction of the maxillary, lachrymal and nasal sutures, and also a little more laterally and posteriorly, there is a tooth embedded in the maxillae. The teeth are apparently crocodilian and are the result of a bite from a small individual. In both places where the bone has been punctured there is a clean round hole without any exostosis. The injury would not be serious although it might be temporarily painful.

On the palatal aspect, the maxillary-premaxillary suture is well-defined and here the longitudinal median division is very clearly marked (Fig. 2b). The bone is laterally convex, particularly in the posterior half and each half is virtually divided again into longitudinal halves by slight ridges connecting the alveoli, indeed the last nine alveoli are definitely cut off from the medial portion of the maxilla by a well-defined ridge several millimetres high. The alveoli are circular, except for a few at the hinder end which are longer than broad. The alveolar margins are elevated, except in the most posterior third of the jaw, and stand out prominently on the side of the maxilla, with deep depressions between them that are in several instances further deepened by fossae for the mandibular teeth. These interdental fossae are not so numerous as in *Tomistoma* but they do exist. They are absent in *Eosuchus* and have not been seen in *Thoracosaurus*. There are fifteen alveoli on each maxilla and altogether sixteen maxillary teeth are preserved, but the teeth will be dealt with later. Three of the alveoli, rather more closely set than the others, are situated under the orbit, another indication that the individual represented was not very aged.

The neurovascular foramina at the alveoli are comparatively large compared with those of *Tomistoma* but are not nearly so prominent as those of *Eosuchus*.

The extreme length of the maxilla along the border of the jaw is 283 mm. The width of each maxilla at the most posterior part of the palatine-maxillary suture is 36 mm. The width across the skull at the front end of the palatal vacuities is 79 mm.

PREMAXILLA (Fig. 2 a, b). — There is no difficulty in distinguishing the line of contact between the premaxillae. Each bone is shaped somewhat like an anvil, having a long wedge-shaped process behind thrust between the nasal and the maxilla, and a somewhat nondescript portion in front marked by very prominent alveoli on the external border and excavated for the external nares on the inner side. In front of the narial opening the bone goes forwards and downwards in a claw-like process which bears one tooth. The upper surface is convex laterally and longitudinally, and is moderately sculptured. The external nares are comparatively large and pear-shaped, being wider in front than behind. The palatal aspect (Fig. 2) shows that the main surface of the bone is occupied by the four alveoli, each with its bony margin produced well above the surrounding

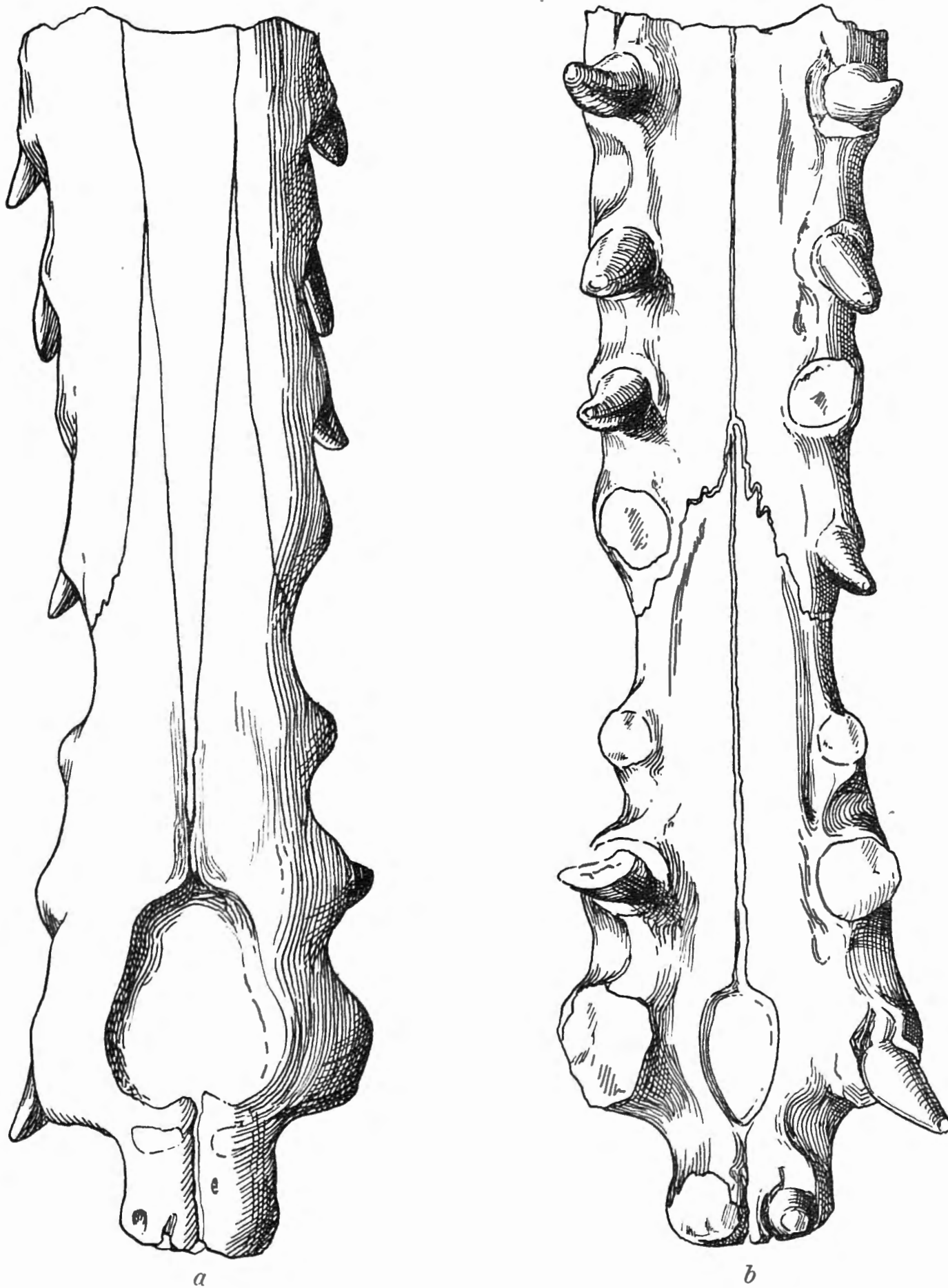


FIG. 2. — Premaxillary region. *a*, upper surface. *b*, palatal surface.  
Approximately nat. size.

surface. The second alveolus, in particular, makes the bone very broad here so that its contraction to the usual limits in front seems sharp. The premaxillary-maxillary suture is a small-angled  $\Delta$ , rather like that figured as *Crocodylus champsoides* (= *Crocodylus spenceri*) by Gürich (1912), whose upper surface is also more like that of the Belgian specimen than any of the others in that interesting plate. The anterior palatine vacuity is long, narrow, and almond shaped. The most striking feature of the bone is its comparative narrowness in front.

Maximum length of premaxilla (upper surface)...	...	147 mm.
Maximum length of premaxilla (palatal surface) ...	...	110 mm.
Width (between 4th tooth and maxillary suture) ...	...	28 mm.
Maximum width (at 2nd tooth) ... ..	...	50 mm.
Minimum width (at anterior end) ... ..	...	20 mm.

**Palatal Surface** (Pl. I, fig. 3).

**PALATINE.** — The palatines are smooth, longitudinally concave, especially posteriorly, and laterally gently rounded. They form almost the whole of the median border of the palatal fenestrae but the anterior end of the fossae and the anterior fifth of the inner border are formed by the maxilla. They are straight, and almost the same breadth all along their length, and together they form a wedge which runs forward for some distance into the maxillae and separates their hinder ends. In *Tomistoma* the palatines have much the same sort of appearance but the anterior wedge is very short. In *Eosuchus* they are broader with more concave sides and the forward extension is much greater, and *Eosuchus* and *Thoracosaurus scanicus* both have a lateral extension of the palatines which is lacking here. (See Pl. I, fig. 6). The only noteworthy feature of this region is the sharp upward rise in the palatal surface just in advance of the palato-ptyergoid suture which is more marked than in the skulls of other genera that I have been able to examine.

Maximum length ... ..	...	127 mm.
Breadth at pterygoid suture ... ..	...	32 mm.
Breadth at midway along palatal fenestrae ... ..	...	23 mm.
Breadth at anterior end of palatal fenestrae ... ..	...	14 mm.

**PTERYGOID.** — The pterygoids are broad and short compared with those of *Tomistoma schlegeli*, and not so wing-like as those of *Eosuchus* or, to a lesser extent, *Thoracosaurus scanicus*. The anterior edge has almost a straight line suture with the palatines and forms, with the transpalatines, the hind borders of the palatal fenestrae. The lateral borders are partly overlapped by the transpalatines but are visible as straight and thick edges. The inner (medial) borders are raised into a slight ridge where the two pterygoids meet. This ridge runs for little more than half the length for posteriorly there open the comparatively small posterior nares, which too have a raised margin. The surface of the pterygoid forwards and a little outwards of the nares is depressed into a small,

but very obvious, hollow on each side. The hind edge of the pterygoid is only a little concave posteriorly.

Breadth of united pterygoids at posterior border	...	134 mm.
Breadth at anterior border	... ..	116 mm.
Length in mid-line...	... ..	50 mm.

TRANSPALATINE. — On account of the width of the pterygoid, the transpalatines are small but stout bones, articulating with the maxilla and jugal at the edge of the skull and closely applied to the outer margins of the pterygoid. They call for no special mention.

Length along skull margin	... ..	70 mm.
Maximum width between jugal and pterygoid edges...	...	55 mm.
Width at anterior edge...	... ..	41 mm.

**Occipital region (Pl. I, fig. 4).**

SUPRA-OCCIPITAL. — The supra-occipital has only about 1 square millimetre of its area on the dorsal surface of the skull, where the highest part of the suture with the parietal projects on to the median, concave, part of the parietal. In shape the posterior surface is rather like the outstretched wings of a butterfly with a strong median crest and well-developed lateral processes and muscle-scars for the attachment of the cervical muscles (*M. occipito-cervicalis medialis*). The surface is concave both laterally and vertically and the whole bone is wide and short. The maximum width is 46 mm., the height is 18 mm. The suture with the united exoccipitals is much nearer the roof of the foramen magnum than in the skulls of *Tomistoma schlegeli* I have examined, but Troedsson's figure of the bone in *Thoracosaurus scanicus* is more comparable, although the bone is more triangular in that species.

EXOCCIPITALS. — These are broad wing-like bones, having, as indicated, a short suture where they meet in the mid-line, and long sutures with the squamosals above until they finally come to rest against the squamosals upon the upper surfaces of the quadrates. A horizontal ridge divides them in this form into upper and lower surfaces each gently concave dorso-ventrally. The bones are, of course, strongly concave towards the posterior. Their lower border forms the roof of the foramen magnum but no pronounced lip, as in *Tomistoma schlegeli*, is produced here. The exoccipitals also form the side walls of the foramen magnum and project ventrally for some distance on the sides of the basioccipital.

The maximum breadth of each is	... ..	78 mm.
The maximum height is	... ..	48 mm.

BASIOCCIPITAL. — The basioccipital is of peculiar shape and forms the prominent occipital condyle and the floor of the foramen magnum. The occipital condyle is of comparatively small size, comparatively more high and narrow

than in *Tomistoma* or *Thoracosaurus*. The floor of the foramen magnum is deeply grooved. The basioccipital runs ventrally from the condyle until it meets the pterygoids just behind the hinder border of the internal narial opening. This region is elongated and somewhat pentagonal in shape. The upper half of the sides is produced into a ridge and the upper half of the middle line is also produced into a very prominent ridge. This ridge probably extended down all the middle but the distal half has been broken away in the specimen.

The maximum height of the basioccipital is ... ..	58 mm.
Height of occipital condyle ... ..	15 mm.
Breadth of occipital condyle ... ..	18 mm.
Breadth of bone below condyle ... ..	35 mm.
Least breadth of bone below condyle ... ..	16 mm.
Breadth of ventral (palatal) end... ..	24 mm.

None of the other bones of the brain case can be examined.

#### Vacuities of the Skull.

The *supratemporal fossae* are rounded and sub-circular but for a forward extension on the anterior border and slightly to the external side. Their transverse diameter is very slightly greater than the antero-posterior. Their margins are narrower than in *Eosuchus*, *Thoracosaurus*, or *Tomistoma*, particularly so on the hinder border where the bone is only a few millimetres in thickness. Their close approximation in the middle line has already been referred to. At first sight it is difficult to determine whether they are larger or smaller than the orbits, but a careful estimate of the relative areas shows that the orbits are a little larger. In this important respect the skull most resembles *Holops*, which has the vacuities equal in size. In *Thoracosaurus* the orbits are slightly smaller than the supratemporal vacuities, while in *Tomistoma*, *Eosuchus* and *Gavialosuchus* they greatly exceed them in size.

Their principal dimensions are :

Maximum antero-posterior diameter ... ..	43 mm.
Maximum transverse diameter ... ..	47 mm.

The *orbits* are ovoid, the long axis running from back to front and inwards so that if the axis was produced in each orbit they would intersect about 30 mm. in front of the most anterior rim of the orbits. They are a little broader than those of *Tomistoma*, but not quite so broad as the orbits of *Eosuchus* or *Thoracosaurus* appear to be. The orbital margin is raised except for the most anterior and inner border.

The maximum length of the orbits is ... ..	52 mm.
Maximum width ... ..	37 mm.

The limits of the *lateral temporal fossae* have been sufficiently described earlier and there is nothing of importance to add. The fossae are narrower and more elongated than in *Tomistoma schlegeli*. The length here from the post-orbital bar to the middle of the quadrato-jugal border is 47 mm.

The *anterior nares* form here a large pear-shaped opening, broader in front than behind, and, at its widest part, bounded laterally by only a thin strip of premaxilla. The actual size of the opening is greater than that in a much larger skull of *Tomistoma*, and also of the larger skull of *Eosuchus*. The maximum length is 34 mm., and the maximum width 27 mm.

The *anterior palatine vacuity* is also comparatively large, being long and almond-shaped. The length is 23 mm., the greatest width 11 mm.

The *posterior palatine vacuities*, or palatal fenestrae, are long and sub-triangular, the base of the triangle being the practically straight edge of the palatine bones. Compared with the other genera in the family they appear to be a little narrower than is usual. They also have more of the maxilla in the anterior and inner border than *Eosuchus*, *Thoracosaurus* or *Tomistoma*. The greatest length is 101 mm. : the greatest width 37 mm.

The *posterior nares* have a circular opening at the very back of the skull. In shape and size it is like that of *Tomistoma*, and is smaller than those of *Eosuchus* and *Thoracosaurus*. It is not like that of *Gavialosuchus*. It is about 20 mm. in diameter.

The *foramen magnum* is like that of *Tomistoma schlegeli*, that is, broad and low, and not subcircular as figured for *Thoracosaurus scanicus*. Its floor is excavated and strongly concave from side to side. Its breadth is 24 mm., and the maximum height 15 mm.

The only other foramina that need be mentioned are the well-marked, triangular openings of the carotid foramen on each exoccipital at the level of the occipital condyle.

THE PRINCIPAL DIMENSIONS OF THE SKULL ARE :

Total length (from quadrate angle to tip of snout) ...	480 mm.
Length in middle line... ..	428 mm.
Greatest width... ..	207 mm.
Width across lateral edges of squamosals ... ..	121 mm.
Width at hinder end of orbits... ..	145 mm.
Length of region behind post-orbital line ... ..	63 mm.
Length of region in front of post-orbital line ... ..	365 mm.
Width of snout at 10th maxillary tooth (anterior end of palatal fenestrae) ... ..	79 mm.
Width of snout at 1st maxillary tooth ... ..	39 mm.
Distance between the above teeth ... ..	178 mm.

**Mandible** (Pl. I, fig. 7).

Like the upper jaws and cranium this is completely and excellently preserved, and has been developed with admirable skill. Every tooth is present although various stages of growth are exhibited. Compared with the upper jaws, the mandible appears long and the bones comparatively stout. The splenials enter the symphysis which extends to the tenth tooth on the right side. This tooth is not developed on the left side. There are seven teeth posterior to the symphysis, so that the whole condition of the lower jaw is very unlike that of *Thoracosaurus scanicus* where there are six teeth on the rami and seventeen on the symphyseal part. As Troedsson has pointed out in his very full description of *Thoracosaurus*, the length of the symphysis is usually about one half of the length of the mandible measured along the middle line, but that is not the case in this new specimen where the post-symphysial part takes a much larger share.

The total number of teeth is 16 on the left side and 17 on the right.

**ARTICULAR.** — The articular, which forms the surface for articulation with the quadrate, is of the usual form. The actual articular surface is short and broad and consists of two concavities separated by a slight longitudinal ridge. The outer concavity is nearly twice the size of the inner. At the back of this surface there is a prominent transverse ridge which descends posteriorly to the triangular, concave, hinder projection which eventually rises to a prominent process. The transverse ridge has a small foramen pneumaticus on its inner end. From front to back this part of the articular is very concave but a median ridge prevents it from being also laterally concave. This surface serves for the attachment of the *M. occipito-maxillaris*. This process appears to be inclined a little more inwards than is usual and is longer and narrower than in *Tomistoma*. The anterior and lower border forms only the upper part of the hinder border of the inner rim of the mandibular foramen as the angular forms most of the back and lower margins. The angular also runs almost to the very hindermost knob of the articular. The external surface is covered by the surangular and angular.

Maximum length of articular	...	...	...	...	...	...	84 mm.
Width across transverse ridge	...	...	...	...	...	...	37 mm.

**ANGULAR.** — The angular is a keel-like bone applied to the lower and outer surface of the articular and forms, as its name suggests, the angle of the jaw. It forms the hinder, and most of the lower, border of the external mandibular foramen on the outer surface, and continues for some distance in front of that foramen as a thin wedge. Internally, its front margin is bifurcated so that between it and the splenial there is formed the small, elongate, internal foramen. The upper margin on the inner surface forms the floor of the lateral vacuity whose posterior border it forms with the articular. The rounded inner ridge at the angle of the jaw is very well developed.



The greatest length is about 260 mm.; the greatest breadth 41 mm. Both of these are measured on the outer surface.

**SURANGULAR.** — The surangular forms the upper surface of the hinder part of the jaw, from the front of the articular surface of the articular to the hind end of the alveolar row. It has a moderately broad extension on the outer surface and forms the upper border of the posterior part of the external mandibular foramen. It overlaps the articular end in a suture upon the transverse ridge of that bone, although a very narrow extension passes from there almost to the end of the jaw. Internally it is in no way remarkable and forms the upper limit of the lateral vacuity.

Its extreme length is 203 mm. The greatest breadth — or depth — is just behind the external foramen and is 27 mm.

**CORONOID.** — There is absolutely no trace of the coronoid on either side. Although every suture of the neighbouring bones is well preserved there is nothing to indicate the existence, or the former presence, of this bone.

**SPLENIAL.** — The splenial is a long narrow bone, with smooth surfaces, which forms the inner wall of the lower jaw. The inner surface is slightly convex longitudinally and a little concave dorso-ventrally. It forms the elevated inner border of the hinder part of the alveolar row, and, as has been stated already, it enters into the mandibular symphysis, although only to a small extent. In *Cavialis* the symphyseal portion and the posterior-ramus portion are approximately equal. In *Thoracosaurus scanicus* the symphyseal portion is half of the post-symphyseal length, in *Tomistoma schlegeli* the proportions are intermediate between these two, but in this specimen the symphyseal part is only one fifth of the total length. The splenials diverge from the alveoli only just a little before entering the symphysis. The maximum length of the splenial is 225 mm. Its maximum height is at its hinder end and is 50 mm. On the lower surface of the jaw the splenial retains the same width until only a short way behind the symphysis. Its average width is 9 mm.

**DENTARIES.** — The symphyseal part has the dentaries separated in the middle-line and it is clear that they are of fairly uniform width. The inner margin is practically straight but the lateral border consists of a line of outstanding alveoli with a concavity, and sometimes a deep notch for a maxillary tooth, between them. The development of the alveoli and the condition of the teeth are irregular, but the 4th tooth is about the most prominent. Each alveolus has two nutritive foramina, one a little in front, or at the side, of it and the other a little in the rear. The front of the dentary is formed by the borders of the prominent alveoli of the 1st teeth, with a median depression between them. The under surface is convex from side to side and a little convex longitudinally. The surface is much sculptured by a series of short longitudinal markings.

In the post-symphysial part, the dentaries form the outer surface of the jaw until they reach the external mandibular foramen where they are in contact with the splenial and angular below and the surangular above. They form the entire outer margin of the alveolar row which is, of course, formed by the upper surface of the dentaries alone. In the symphysial portion, as has been indicated, the alveoli are circular openings whose inner edge is almost on a level with the surface of the dentary, but whose outer surface is prominently elevated above the surface in front, to the outside, and the back of it. The alveoli are, with the exception of the first and the fourth, of uniform size. The first alveolus is 12 mm. in diameter and the fourth is approximately the same, but the average diameter of the others is only 8 mm.

In the post-symphysial parts of the rami the alveoli are not so prominent laterally, for the side of the jaw is more vertically inclined and actually inclines a little inwards in its upper part. The posterior teeth therefore come to lie in a groove, the alveoli being separated by deep concavities, some of them being interdental pits for the accommodation of the maxillary teeth. On the right side the 10th and 11th alveoli are large but posteriorly there is a gradual diminution in size and the last alveolus although still 8 mm. in length is quite narrow. On the left ramus the 10th alveolus and tooth have not been developed.

**TEETH.** — The teeth in both upper and lower jaws show the same characters, and these characters to some extent vary with the position of the tooth. The anterior teeth, along most of the region in front of the palatal vacuities above and on the symphysial border below, are long, slender, conical and slightly curved. There is a distinct longitudinal striation which becomes finer on the posterior teeth and two of the striae are appreciably developed to form lateral edges, although they do not affect the cross-section very obviously. The striae die out just at the apex of the tooth which is smooth. The first tooth on each side, above and below, is curved backwards and its lateral edges are directed laterally. On both upper and lower jaws the following teeth tend to have the lateral edges twisted through an angle of about  $45^\circ$  so that the curved, posterior, aspect of the tooth faces backwards and inwards. The rotation continues as one traces the teeth backwards until one finds that the last five or six teeth, again both above and below, have their « lateral » edges at the back and front. Further, they are reduced in height, flattened laterally, and have the flutings much finer and more numerous. Particularly in the lower jaw of this specimen there is no doubt that two distinct types of teeth are discernible. All the teeth are beautifully preserved and there is no difficulty in distinguishing all their features which bear out Owen's description of *Gavialis dixonii*. The teeth in the upper jaw are both more numerous and larger in size. The average size of an upper tooth (not one of the last six) is 18 mm., and the diameter at the alveolar rim is 8 mm. The hindermost teeth average 11 mm. in height and their diameter from front to back is in each case 8 mm., although from side to side they only measure 5 mm. which indicates their quite different shape from the anterior teeth.

In the lower jaw there is considerable variety in the size of the teeth, the fourth, the largest, being 22 mm. long, but the others average about 13 mm. The diameter of the latter teeth is 7 mm. There are about 24 longitudinal lines on each of these teeth, and on some of the larger teeth very fine markings exist between them. The hindermost six teeth average 10 mm. in height and they are all 8 mm. from back to front and only 5-6 mm. from side to side. Their striations are too fine and numerous to count.

The dental formula is  $\frac{4+15}{16-17}$ .

#### Vacuities in the mandible.

Little need be said of these. The external mandibular foramen is ovoid, being 55 mm. long and 22 mm. at its widest. Its borders are quite smooth. The lateral vacuities have prominent borders. They are 96 mm. at their longest part and 45 mm. at their deepest. The internal mandibular foramen is very narrow. It is 22 mm. long and only 5 mm. at its widest.

#### THE PRINCIPAL DIMENSIONS OF THE LOWER JAW ARE :

Maximum length from tip to end of articular ... ..	530 mm.
Maximum width across ends of articulars ... ..	200 mm.
Maximum width at hinder end of symphysis ... ..	58 mm.
The width at the front of the jaw is probably ... ..	36 mm.
but the two dentaries are displaced here.	
Length of the symphysis ... ..	198 mm.

VERTEBRAL COLUMN. — A considerable number of vertebral centra, fragments of apophyses and chevrons are present on the skeleton from which there can be selected 24 centra in excellent and almost complete condition. Of these 4 are cervicals, 5 dorsals, 4 lumbar, and 11 caudals. Professor Dollo has marked the estimated position of each on the centrum and his suggestions appear to be quite correct on comparing the vertebrae with the whole series of a recent *Tomistoma schlegeli*. In describing the type-specimens of *Gavialis dixonii*, Owen described and figured a rather worn and incomplete centrum which was also in the Dixon Collection but which had no certain association with the other crocodilian remains. He selected it as the only available Bracklesham crocodilian procoelous centrum of comparable origin to the mandibular fragments, and he estimated its position in the series as the last cervical or first dorsal. A fuller and comparative description of what vertebrae are present is therefore essential.

The four *cervical vertebrae* are excellently preserved and are typically crocodilian in appearance. They resemble quite closely the cervicals of *Crocodylus americanus* fully described and figured by Mook (1921).

All the vertebrae but one are procoelous, longer than broad, and high, with a long neural spine.

Among the cervicals preserved are the delicate pro-atlas and the stout centrum of the axis. The pro-atlas is a small V-shaped bone of very delicate struc-

ture. Anteriorly it is pointed and posteriorly it broadens out considerably. The hinder border is concave. The upper surface is convex, and the lower surface correspondingly concave. The upper surface has a slight median ridge running from front to back. At its widest point the bone is 31 mm. across.

The centrum of the axis is quite characteristic. Of stout construction, it is broadest in front and tapers behind, and the neural spine is long antero-posteriorly and low vertically.

The pre-zygapophyses are broken off and the post-zygapophyses are incomplete. The odontoid surface is convex and square in front view, and firmly

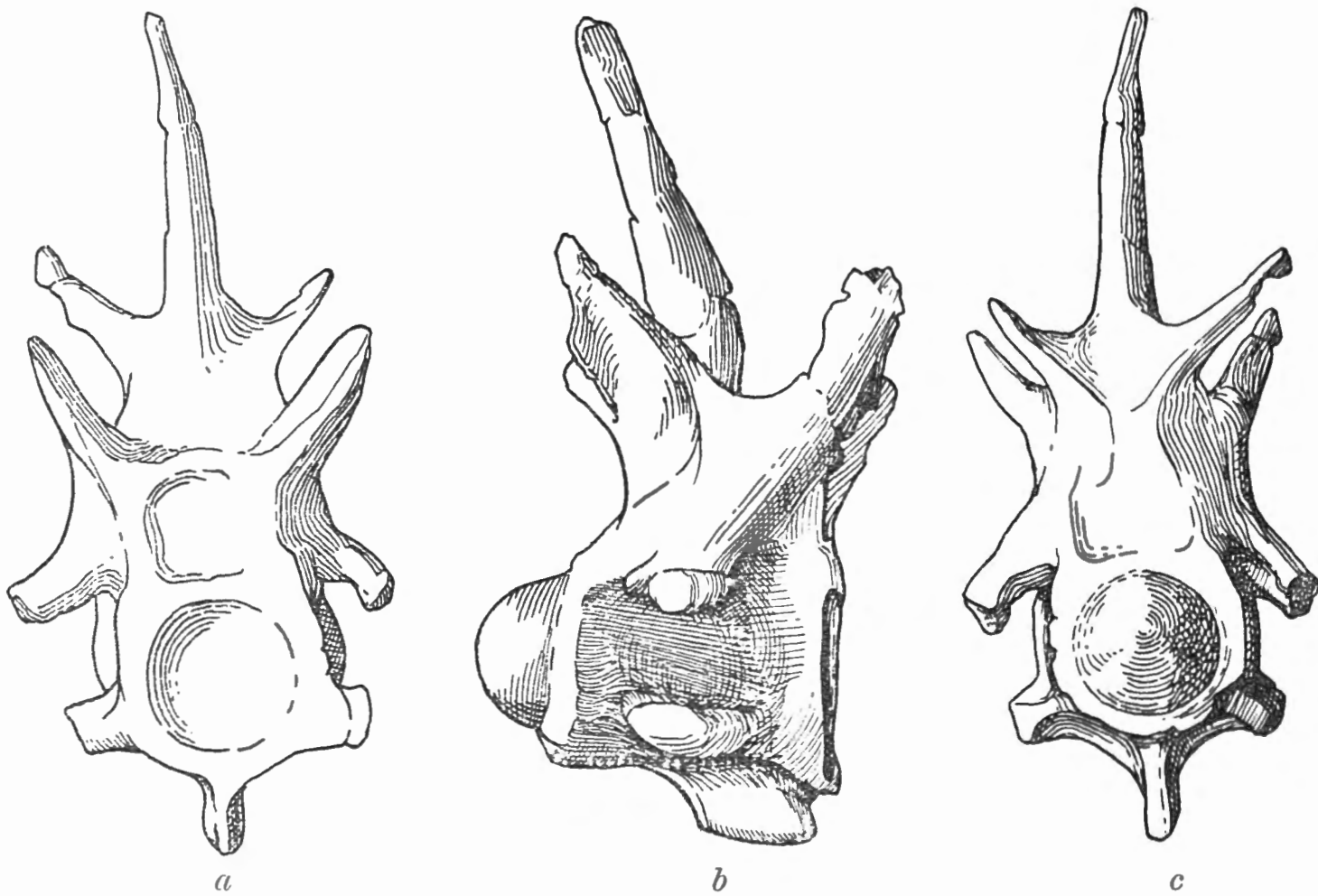


FIG. 3. — 5th Cervical vertebra. *a*, anterior view. *b*, lateral view. *c*, posterior view. Nat. size.

fused to the centrum. The diapophyses are at the very front edge and the parapophyses just below and behind them. On the concave lower surface a slight hypapophysis is developed just in advance of the middle length and a slight keel is developed. The dimensions are given later.

The next centrum in the series is probably the third cervical. The anterior articular surface has an almost square outer border but within there is a well-rounded and deeply excavated sub-spherical surface. The pre-zygapophyses are long and narrow, and directed forwards and upwards at about  $45^\circ$ . They are set a little lower than the post-zygapophyses and are not so extended laterally as these

processes. In this vertebra the hinder limit of the post-zygapophyses is just beyond the back of the articular ball. The neural spine is moderately short, but long from back to front, with the anterior edge rounded and the posterior edge straight. The spine projects backwards but not quite so far as the post-zygapophyses.

The centrum itself is a little broader than high and not quite twice as long as broad. The sides are markedly concave longitudinally and slightly concave vertically. The lower surface is definitely concave longitudinally, although the hypapophysis intensifies the curve. There is no keel on the inferior surface in this vertebra.

The upper articular process for the rib, the diapophysis, is a stout projection slightly to the front of the mid-length and vertically just on the level of the neurapophysial suture. The ventral process, the parapophysis, is a stout and rounded projection on the front and lower edge of the side, just behind the anterior articular rim. The processes are here separated by a wide groove. On the ventral surface between the two parapophyses a short and thin hypapophysis is developed. Its front end is not quite so anteriorly placed as the front ends of the parapophyses.

The remaining cervical vertebrae are identified as the 5th and 6th. They are in every way larger than the vertebra just described. The neural spine (Fig. 3) is longer and much narrower, and the pre- and post-zygapophyses are more vertically directed. In the fifth vertebra they are both nearly of the same lateral expansion, but in the sixth, as in the third, the post-zygapophyses are more extended laterally.

The neural canal in all of them is broad, high, and squarish in section.

The centrum is as high as it is broad and is only one and a half times as long as broad. Compared with those of the third cervical, the diapophyses are longer and stouter, and project more laterally. They are situated about the middle of the length but originate more dorsally on the neurapophyses. The parapophyses are longer and thicker. The hypapophysis is narrow but is considerably longer.

All the vertebrae have a very well-developed posterior hemispherical articular surface.

#### DIMENSIONS :

	C. 2.	C. 3.	C. 5.	C. 6.
Length of centrum . . . . .	53 mm.	40 mm.	40 mm.	40 mm.
Breadth of centrum (anterior end) . . . . .	23 mm.	22 mm.	25 mm.	25 mm.
Height of centrum (anterior end) . . . . .	25 mm.	20 mm.	24 mm.	25 mm.
Spread of pre-zygapophyses . . . . .	—	22 mm.	36 mm.	33 mm.
Spread of post-zygapophyses . . . . .	—	24 mm.	34 mm.	39 mm.
Width across diapophyses . . . . .	33 mm.	35 mm.	42 mm.	49 mm.
Width across parapophyses . . . . .	27 mm.	24 mm.	30 mm.	33 mm.
Length of hypapophysis . . . . .	13 mm.	8 mm.	15 mm.	16 mm.
Total height . . . . .	—	76 mm.	93 mm.	93 mm.

**DORSAL VERTEBRAE.** — There are five dorsals preserved and they are all typically crocodilian in appearance and characters. The first dorsal is of very much the same size and appearance as the 6th cervical described above, but it is slightly larger, has a longer and stouter neural spine, and more strongly developed pre-zygapophyses. The diapophyses have become laterally directed processes projecting horizontally from the base of the pre-zygapophyses and the parapophyses have almost disappeared, being represented on each side by merely a swelling with a slight dorso-ventral ridge. The hypapophysis is slightly longer and as deep or deeper than in the cervicals. The anterior articular cup is larger in size and deeper. The neural canal is still very large. The other dorsals represented are the 2nd, 3rd, 5th and probably the 9th, and the chief differences in them are that, as one goes backwards in the series, the pre-zygapophyses become more flattened and directed externally, the neural spine becomes shortened vertically and longer antero-posteriorly, and both the parapophyses and the hypapophysis disappear from the centrum. The centrum itself changes little in size, but with the loss of the lateral and basal processes the lateral and ventral surfaces become more concave.

The transverse process becomes strongly developed until in the 9th dorsal it forms with the pre-zygapophysis a strong, broad, wing-like process.

**DIMENSIONS :**

	1st dorsal.	2nd.	3rd.	5th.	9th.
Length of centrum . . . . .	39 mm.	40 mm.	41 mm.	42 mm.	43 mm.
Breadth of centrum at anterior end.	27 mm.	27 mm.	27 mm.	27 mm.	26 mm.
Height of centrum at anterior end.	24 mm.	23 mm.	24 mm.	25 mm.	26 mm.
Width across pre-zygapophyses . . .	38 mm.	39 mm.	38 mm.	44 mm.	47 mm.
Width across post-zygapophyses . . .	37 mm.	39 mm.	38 mm.	40 mm.	35 mm.
Width across diapophyses . . . . .	57 mm.	76 mm.	86 mm.	110 mm.	122 mm.
Length of hypapophysis . . . . .	15 mm.	16 mm.	13 mm.	14 mm.	—
Total height . . . . .	95 mm.	87 mm. (*)	80 mm. (*)	81 mm.	70 mm. (*)

(\*) Incomplete.

The vertebral centrum figured by Owen when establishing the species *Gavialis dixonii* is described as answering « to the last cervical or first dorsal in the existing Crocodilians ». On comparing it with these vertebrae its general similarity to the first dorsal in every detail is noticeable, but it is very much smaller, for its length is only 30 mm., its breadth at the front end 21 mm., and its height there 20 mm. The centrum must have belonged to quite a small specimen and certainly not to the same individual to which the mandibular fragments described by Owen belong.

**LUMBAR VERTEBRAE.** — There are four lumbar vertebrae in the skeleton and they resemble the latest dorsal very closely. The neural spines are shorter vertically and antero-posteriorly than in the dorsals, but the zygapophyses are broad and strongly developed. The diapophyses are also long, broad and well-developed but not quite so much so as in the later dorsals. The centra look long and

narrow although each is a little shorter than the preceding centrum. No hypapophysis is developed, but the first three lumbar have two longitudinal ridges running along the whole ventral surface. The surface between these ridges is concave longitudinally and laterally. The fourth lumbar has a faintly developed median ridge. All the centra are strongly procoelous.

## DIMENSIONS :

	1st lumbar.	2nd.	3rd.	4th.
Length of centrum. . . . .	45 mm.	43 mm.	40 mm.	37 mm.
Width of centrum at anterior end . . .	28 mm.	27 mm.	27 mm.	25 mm.
Height of centrum at anterior end . . .	23 mm.	22 mm.	21 mm.	21 mm.
Width across pre-zygapophyses . . . .	49 mm.	51 mm.	50 mm.	45 mm.
Width across post-zygapophyses . . . .	45 mm.	45 mm.	43 mm.	38 mm.
Width across diapophyses . . . . .	104 mm.	108 mm.	102 mm.	96 mm.
Total height . . . . .	65 mm.	64 mm.	65 mm.	65 mm.

SACRAL VERTEBRAE. — The skeleton as a whole is so well preserved and has been so well collected, that it is strange to record that there is no trace of the sacral vertebrae or any fragment of them. The next vertebra in the series is the first caudal.

CAUDAL VERTEBRAE. — Altogether 11 caudal vertebrae are preserved and without exception they bear out the common features of such crocodilian centra. The spines are moderately high in the most anterior vertebrae but the posterior ones have a high, thin, and narrow spine. The first caudal has a biconvex centrum, and apophyses and transverse processes not unlike those of the lumbar. The spine is sub-triangular and short. The next centrum in the series is probably the sixth caudal. Here the centrum is long and narrow with two well-developed longitudinal ridges marking the lateral edges of the lower surface which is concave in both directions. The upper portion of the centrum and the apophyses are entirely missing, but on one side there is a transverse process (diapophysis) still well developed. The next in the series are considered to be the 13th to the 20th, and the 22nd. They all show the customary long and narrow centrum, with a squarish and shallow-cupped anterior articular surface. The pre-zygapophyses are small and directed forwards like a pair of little horns. The post-zygapophyses are very small. The neural spine is tall and thin and situated to the rear of the middle of the length. The lateral margin of the lower surface is produced into a ridge which is specially prominent in the hinder half, where a deep concavity lies between the two ridges.

## DIMENSIONS :

	1st.	6th.	13th.	14th.	15th.	16th.	17th.	18th.	19th.	20th.	22nd.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Length of centrum. . . . .	43	43	45	47	46	44	44	44	43	42	40
Width at anterior end . . . . .	20	20	16	17	16	15	14	13	12	12	11
Height at anterior end . . . . .	19	19	16	15	16	14	14	13	11	12	11
Length of neural spine from neuro-central suture . . . . .	40	—	45	45	44	45	50	52	—	50	33

There is, of course, no indication of the total number of centra in any of the vertebral regions.

**RIBS AND CHEVRONS.** — There is also a considerable collection of ribs from various parts of the vertebral column.

The ribs are very characteristic in the crocodiles and those of this specimen conform so well to type that there is little need to describe them in any detail here. Only six cervical are preserved and they are all closely alike, differing only in their size. Three are from the right side of late cervical vertebrae and three from the left side of a late and two early cervicals. They all agree in being formed of a longish bar of bone which is rather excavated posteriorly. This bar is carried longitudinally, parallel to the length of the cervical series, and from it, a little in front of the middle of the length, two stoutish processes are given off vertically. The upper and longer of these processes articulates with the diapophysis, the shorter and stouter with the parapophysis. The articular surface of the latter process is larger than the other. The four largest cervical ribs are each 47 mm. long.

A number of dorsal ribs are also present and these again are quite typical. They are stout and well curved and the anterior ones have distinct tubercular and capitular processes. These ribs, at least in the series here preserved, appear much more robust than, although not so long as, the later ribs which have only capitular processes with merely a tubercular facet. The posterior ribs are less strongly curved than the anterior. The longest rib in this series measures 122 mm.

**CHEVRONS.** — Five chevrons have been preserved and they are all of the usual crocodilian pattern. They are all from the posterior part of the series for they have a V-shape with two distinct and separated articular surfaces. Seen in cross-section, the distal end, in all but one of the chevrons, is remarkably thin, although when seen in side-view it is expanded to be the broadest part of the bone. The dimensions of one such chevron bear out the characters sufficiently.

Greatest length...	...	...	...	...	...	...	...	...	59 mm.
Width (lateral) of proximal ends	...	...	...	...	...	...	...	...	15 mm.
Width (lateral) of distal end	...	...	...	...	...	...	...	...	2 mm.
Width (antero-posterior) of distal end	...	...	...	...	...	...	...	...	10 mm.

The chevron which does not show this flattening is the largest and is 71 mm. long.

**STERNUM AND VENTRAL RIBS.** — One of the most remarkable features of the specimen is the preservation of long, narrow, frond-shaped bones, much broken, but associated with elongated, thin, straw-like bones. These can only be the remains of the sternal ribs and the abdominal splint ribs. There is no trace of any part of the sternum itself, although the underlying interclavicle is preserved, or of the xiphisternal horns, but the preservation of any of the abdominal rib-series in a fossil crocodile is unusual.



The sternal ribs appear to be seven in number and to be all from the left side of the skeleton. They are long and narrow and bear a superficial resemblance to certain Chelonian plastron bones which is typical. For their length and breadth they are quite thick but not unproportionately so when compared with those of a recent crocodile or Gavial. Each is broken into several pieces and the most satisfactorily reconstructed specimen measures 121 mm. in length, 24 mm. at its widest, and is 5 mm. in average thickness.

The abdominal splint ribs are also fragmentary, but are thin and like twigs, and are preserved in sufficient number and extent as to leave no doubt as to their identity. The longest portion, which is perhaps complete, is 82 mm. long and 3 mm. in diameter and has the typical, irregular curving shown by these ribs (Fig. 4). In all there are eleven abdominal rib fragments of reasonable size, two of which may possibly be complete.



FIG. 4. — Abdominal splint rib. Nat. size.

**PECTORAL GIRDLE.** — The pectoral girdle in the crocodiles consists of the scapula, coracoid, and the median, unpaired, interclavicle, and here the interclavicle and the two coracoids are perfectly preserved but there is no trace of the scapulae. The loss of these two important bones is all the more remarkable considering how well otherwise the skeleton has been recovered.

**CORACOID (Fig. 5).** — As stated, both the right and left coracoids are in excellent condition, and neither shows any unusual feature. For comparison with them there have been used the bones of an adult *Tomistoma schlegeli*, and in general they are closely similar. The fossil coracoid is, however, shorter and broader comparatively. The proximal surface, for the articulation with the scapula, is sub-triangular, being considerably broader behind than in front. Antero-posteriorly the surface is convex, but at the broadest part, i. e. at the hinder end, the surface over a small area is slightly concave. Externally to this the glenoidal facet projects as a prominent process with an almost circular surface.

On the upper surface, in front of the scapular part, the margin of the coracoid dips sharply downwards and forwards, and this part occupies a greater proportion of the surface and is more angular than in the recent *Tomistoma*. In *Tomistoma* and most species of *Crocodylus* the coracoid foramen is conspicuous about midway between the proximal and anterior angle and the glenoidal facet. Indeed, the foramen is usually a little nearer the former than the latter. In *Dollosuchus*, however, though still conspicuous, it is situated very near the base of the glenoid process and is largely overshadowed by it. The anterior margin of the coracoid is strongly concave, much more so than in *Tomistoma schlegeli* or in *Crocodylus americanus* (Mook 1921). The distal and front angle comes to be a little triangular projection. The distal border is thickened and rounded,

forming nearly the quadrant of a circle. The posterior border is very slightly concave, but almost straight and so is different from that of the other species quoted above where the proximal half of the margin is concave and the distal convex. Further, in the Belgian specimen a ridge is developed on the proximal part of the edge and this ridge runs upwards to the base of the process for the glenoidal facet.

The outer surface of the bone is smooth and, over most of its surface, convex externally. The upper quarter is made concave by the development of the glenoidal facet. Longitudinally, the coracoid is, of course, strongly convex.

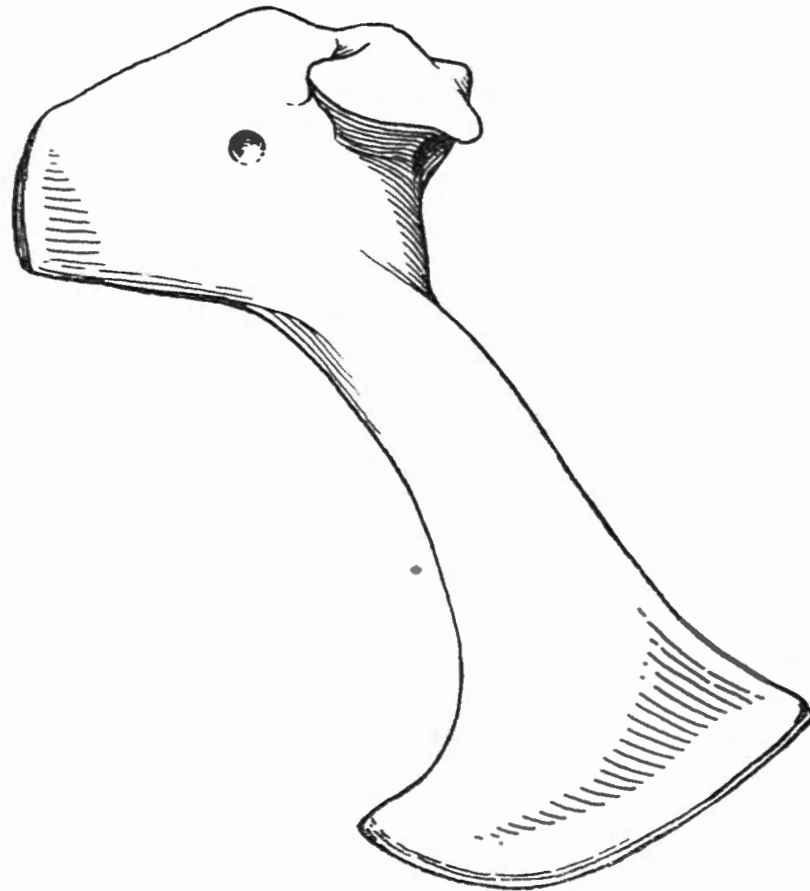


FIG. 5. — Left coracoid. Nat. size.

The internal surface is correspondingly strongly concave. The inner aspect of the coracoid foramen is not circular, like its external opening, but is ovoid and is nearly three times as large as the other. It is much nearer the hinder border.

The thickest part is the proximal end and the width gradually diminishes from there distally. The thinnest part is just a little above the distal border, but at the border the bone is a little expanded again, and has the margin of uniform thickness.

The coracoid is much shorter than the humerus and the femur, slightly shorter than the ischium and the ulna, and longer than the radius and the pubis. These relationships differ considerably from those given by Mook (1921) for *Crocodylus americanus*, as typical of the Crocodylia, notably in the length here of the ulna and the shortness of the pubis.

## DIMENSIONS OF THE LEFT CORACOID :

Total length	... ..	100 mm.
Length (antero-posterior) of proximal surface	... ..	50 mm.
Length (antero-posterior) of distal surface	... ..	47 mm.
Least antero-posterior length of shaft	... ..	16 mm.
Maximum thickness of proximal end	... ..	31 mm.
Maximum thickness of distal end	... ..	5 mm.

**THE INTERCLAVICLE.** — The interclavicle is long and narrow and shaped like a feather, although the margin is so thin that it has not been wholly preserved. Indeed, what actually remains is the thickened median portion with a little of the thin bordering bone. Ventrally, the bone is flat but dorsally it is strongly convex from side to side on account of the thick median rib. Posteriorly the thin lateral borders to this rib are not developed so that the hinder part of the interclavicle is merely an oval rib of bone (Fig. 6).

Although it cannot be stated that the entire interclavicle is preserved the dimensions of the bone here are : Length, 126 mm. Greatest width, 19 mm.



FIG. 6. — Interclavicle. Nat size.

**THE FORE LIMB. — HUMERUS (Fig. 7).** — The entire left humerus is preserved but only the proximal half of the right. It has no outstanding features but it is comparatively short and broad, and the deltoid ridge is proportionately long. The proximal end is of uniform thickness and is angular, being divided into two articular surfaces, an upper and horizontal and an inner and lateral. The latter is larger, and set at a greater angle to the former, than in recent specimens of *Tomistoma* or *Crocodylus* that I have been able to examine. The figures of the right humerus of *Thoracosaurus scanicus* are too poor for comparison. The outer surface in the proximal third is practically straight but distally the border is slightly concave. The inner surface is markedly concave for all of its length. The deltoid crest is well developed and reaches its maximum elevation almost at a third of the length of the bone distally. In the recent *Tomistoma schlegeli* the same point is reached at a quarter of the length. The ridge is sharp on the proximal side of the crest, but distally it is rounded and soon merges with the shaft of the bone.

The distal articular surfaces are ordinarily developed and show no feature worthy of special mention. In side view the bone is, as usual, somewhat sig-

moidal, and the curving appears to be more marked here than is usual. Seen from either end it is noticeable that the planes of the proximal and distal ends are not parallel but are set at an angle of about  $35^{\circ}$ .

The humerus is only a little shorter than the femur but it is much longer than any of the other limb or girdle bones

DIMENSIONS OF THE LEFT HUMERUS :

Total length ... ..	155 mm.
Breadth of proximal end ... ..	42 mm.
Breadth of horizontal surface of proximal end... ..	30 mm.
Breadth of inner surface of proximal end... ..	22 mm.
Breadth of distal end... ..	35 mm.
Circumference of shaft ... ..	50 mm.
Index of circumference over length... ..	.316
The index in the humerus of <i>Crocodilus ameri-</i> <i>canus</i> is... ..	.410

These measurements are sufficient to indicate the general features of the humerus.

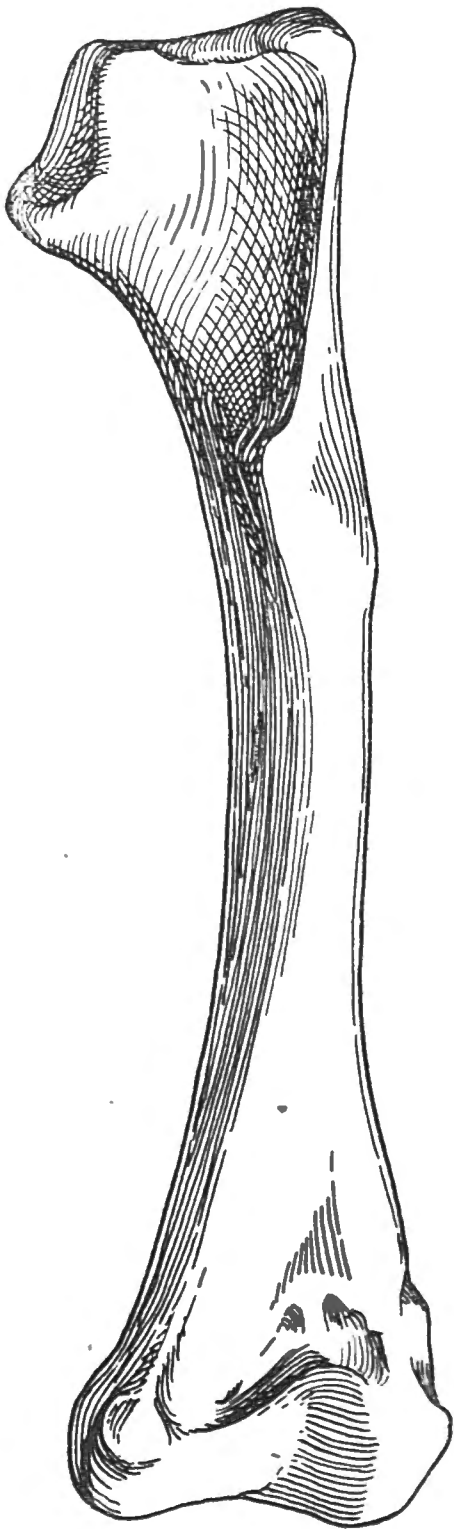


FIG. 7. — Antero-ventral aspect of left humerus. Nat. size.

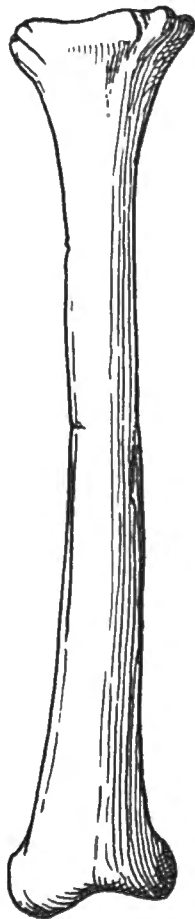


FIG. 8. — Left radius, anterior view. Nat. size.

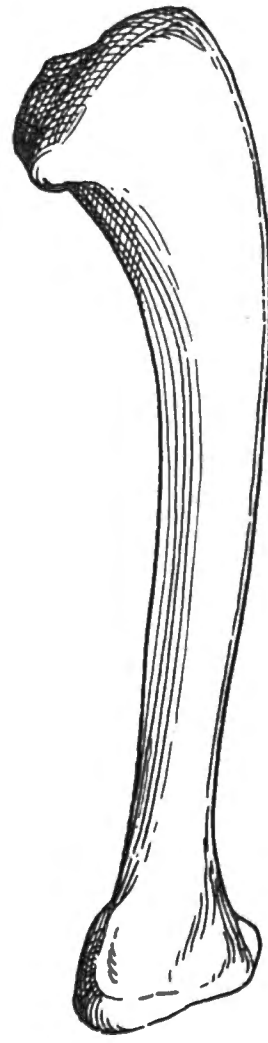


FIG. 9. — Left ulna, lateral view. Nat. size.

**RADIUS** (Fig. 8). — Both radii are present in good condition. Each radius is a relatively small bone, shorter and more slender than the ulna. The proximal end is expanded antero-posteriorly and but very little laterally, and the distal extremity is thin and also expanded fore and aft. The ulnar and the anterior surfaces are straight; the former has a long, slightly developed ridge running the whole of its length near the hinder border. The radius is shorter than most of the limb and girdle bones but in this specimen it is longer than the pubis.

**DIMENSIONS OF THE RADII :**

Total length...	94 mm.	94 mm.
Maximum diameter, proximal end ...	21 mm.	19 mm.
Maximum diameter, distal end ...	19 mm.	18 mm.

**ULNA** (Fig. 9). — The left ulna is preserved entire but the articular head of the right has been broken away. Apart from this deficiency, both bones exhibit the same features. The ulna is a thin curved bone, much thickened at its proximal end, and slightly thickened at the distal end. Both ends are elongated antero-posteriorly. The shaft is somewhat flattened and has a strongly concave anterior, and a convex posterior, border. The proximal articular surface is large, and faces upwards and forwards, but it has no olecranon process. The distal articular end faces downwards and inwards, and on the inner surface there are two small oblique processes.

The ulna is larger than the radius, coracoid and pubis, it is almost the same size as the ischium, but it is smaller than the humerus or the femur.

**DIMENSIONS OF THE LEFT ULNA :**

Total length ...	108 mm.
Antero-posterior diameter of proximal end...	27 mm.
Width of proximal end ...	22 mm.
Antero-posterior diameter of distal end...	20 mm.
Width of distal end ...	9 mm.

**CARPUS AND MANUS.** — Considering the excellent condition of much of the skeleton, the remains of the carpus and manus are disappointingly few and fragmentary. The whole series, as represented here, consists of the radiale, pisiform, and metacarpals I, II, III and V of the right hand, and metacarpals I, II and IV of the left, with 3 small phalanges. All these bones are quite typically crocodylian and call for little description. The radiale, as usual, is short and stout, slightly expanded distally and much expanded proximally. The upper articular surface is kidney-shaped and very slightly concave; the lower surface is sub-oval and a little more deeply cupped. Both lateral borders are strongly concave. The length of the radiale is 25 mm., so that the length of the radiale divided by the length of the radius is .266, which agrees well with the figure of .262 in *Caiman sclerops* and .274 in *Caiman niger* and *Crocodylus americanus*.

The pisiform is very small and is only 17 mm. in its greatest diameter.

Of the metacarpals, the first of the right hand is short but broad, the second is stout and is the same length as the third which is, however, more slender. The fourth, from the left hand is slender and about the length of the first, but the fifth is quite small.

Their dimensions from the right hand are.

	M. I.	M. II.	M. III.	M. IV.	M. V.
Length ... ..	27 mm.	35 mm.	35 mm.	—	20 mm.

**PELVIC GIRDLE AND HIND LIMB.** — The pelvis and the hind limb elements are more fully represented than those of the shoulder girdle and fore limb. There remain the proximal articular portions of both ilia, the two pubes and the two ischia.

**ILIUM.** — The portion of the left ilium consists merely of the upper part of the acetabular region and is too fragmentary for description. The right ilium is more complete but unfortunately the postero-dorsal spinous portion has been broken away so that it is impossible to give the dimensions of the bone. The

articular, acetabular, part is perfectly typical and requires no elaboration here. Seen from the outside, the bone is deeply concave but dorsally the margin is rounded and moderately thick. The antero-posterior length of the distal, articular, end is 63 mm.

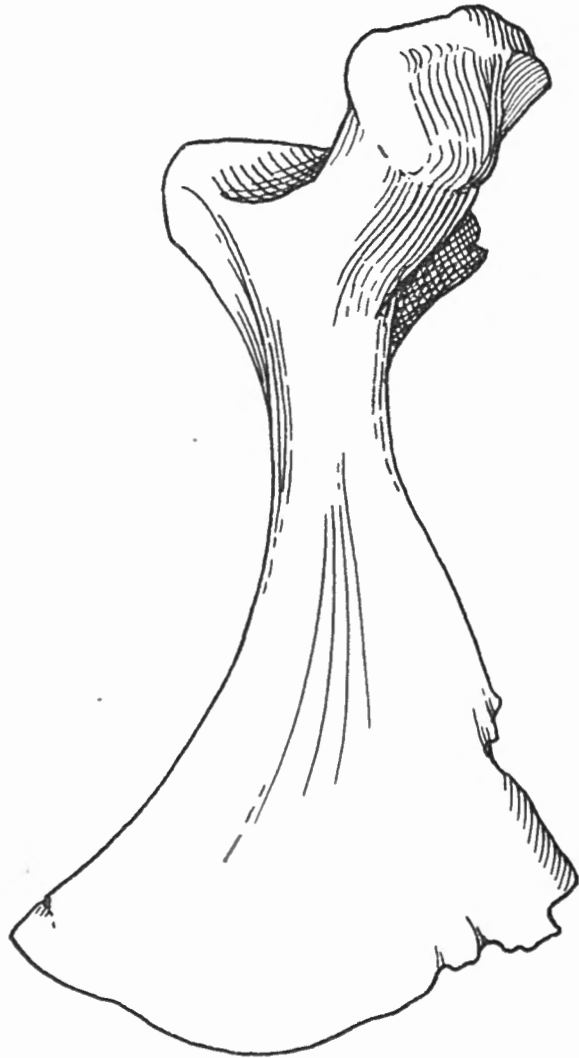


FIG. 10. — Right ischium, external view.  
Nat. size.

**ISCHIUM.** — Both ischia are nearly complete. They are large bones, much larger than the pubes, and of rather complex shape. They are much expanded both proximally and distally, but whereas, the latter expansion forms a broad, almost flat, plate, the upper expansion is formed by two articular heads connected by a projecting neck (Fig. 10). The smaller and anterior of these proximal processes articulates with the anterior iliac process and with the pubis, and it excludes the pubis from any contact with the ilium. This anterior process arises on a forwardly directed, nearly horizontal, neck which protrudes from just below the principal articular surface of the ischium. This surface is irregular, somewhat angular, and broader than long. Distally to the head the shaft is triangular but soon it expands to the broad, thin and curved distal

end. The distal ends of the ischia meet in the middle line. The bones are quite typically crocodilian in size and appearance.

DIMENSIONS OF RIGHT ISCHIUM :

Maximum length, oblique ... ..	109 mm.
Antero-posterior length, proximal end ... ..	48 mm.
Greatest length, distal end... ..	58 mm.

PUBIS. — Both pubes are also present, but the right has lost a piece of the distal margin. The left pubis is, however, quite complete and undistorted. It is the smallest of the girdle bones, and is even shorter than the incomplete ilium, and the radius and ulna. Mook has shown (1921) that in *Crocodilus americanus*, at least, the pubis, though short, is longer than these elements.

The pubis is roughly triangular in outline, with the head a little expanded transversely and the distal end greatly expanded and thin (Fig. 11). Longitudinally it is curved and very slightly twisted, so that in its natural position in the skeleton it is concave dorsally and convex ventrally, and the longer diameter of the proximal end is not quite parallel to the plane of the distal end. The shaft of the bone is oval and the thickness decreases constantly distally. The inner margin is more concave than the external. Both pubes meet in the middle line.

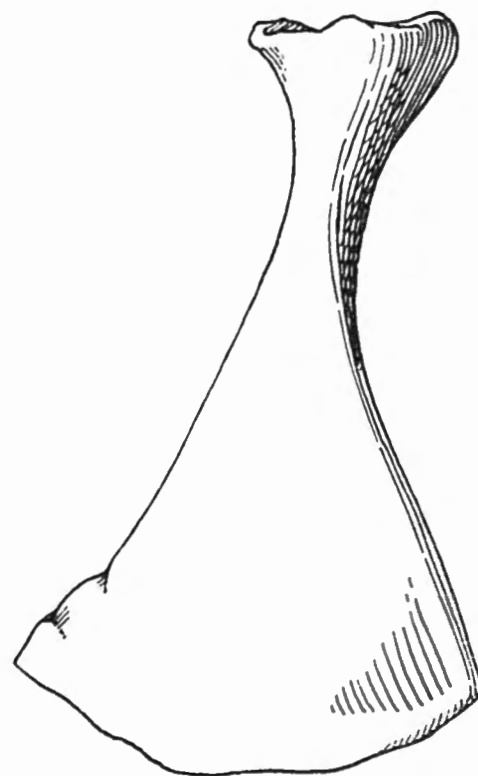


FIG. 11. — Left pubis, ventro-lateral view. Nat. size.

DIMENSIONS OF THE LEFT PUBIS :

Total length ... ..	83 mm.
Maximum diameter of proximal end ... ..	23 mm.
Minimum diameter of proximal end ... ..	13 mm.
Breadth of distal end ... ..	49 mm.
Thickness of distal margin ... ..	2 mm.

THE HIND LIMB. — FEMUR (Fig. 12). — The entire and well-preserved left femur is present but the right femur is rather fragmentary and lacks most of the shaft and the distal articular end. The left femur is long and stout and is both longer and broader than the incomplete and worn right femur assigned to *Gavialis dixonii* by Owen. It is, however, much shorter, comparatively broader, and more curved than the corresponding bone of *Tomistoma schlegeli*. The fourth trochanter in both specimens of *Dollosuchus* is more prominent than in the modern *Tomistoma* and extends further distally.





TARSUS. — Neither tarsus is complete, but from the right limb there is the calcaneum (fibulare), the fused astragalus (tibiale and intermedium) and centrale, and the small, rounded ossicle representing the fused 1-3 tarsalia. All these bones are quite well preserved and of quite typical form. Their shape is very irregular and the calcaneum has a very prominent heel.

DIMENSIONS :

Maximum diameter of right astragalus, etc. ... ..	30 mm.
Maximum length of right calcaneum ... ..	40 mm.
Maximum diameter of tarsalia 1-3 ... ..	21 mm.

From these figures it appears that these bones are large compared with the dimensions of the tibia and fibula, yet there can be little doubt of their association.

METATARSUS. — The metatarsals of both sides are fairly well represented. There remain the complete second and third, and the fragmentary first and fourth, of the left foot, and the four complete metatarsals and seven phalanges from the right.

The metatarsals are all long and comparatively stout, with moderately expanded distal and proximal ends. The first digit is stouter than the others and the third is the longest. The metatarsals are all long compared with the phalanges.

DIMENSIONS :

	Left foot.		Right foot.			
	M. II.	M. III.	M. I.	M. II.	M. III.	M. IV.
Length.	80 mm.	82 mm.	73 mm.	81 mm.	83 mm.	73 mm.

PHALANGES. — So far as can be determined the phalanges are phalange 1, digit I, phalanges 1 and the unguis of digit II, phalanges 1 and 2 of digit III, the first phalange of digit IV, and a fragmentary unguis. All appear to be from the right foot. They share the general character of stoutness, but not length, with the corresponding metatarsals. They are all quite typically crocodilian and differ in no obvious degree, other than of size, from the phalanges of a modern *Tomistoma schlegeli*.

SCUTES. — Associated with the foregoing remains there is a large collection of dermal scutes. As to their actual position it is a little difficult to be definite, but they are all small, more or less circular, and rather like the marginal rows in *Crocodylus*. Some are flat while others are ridged. The majority are small, a little broader than long, the breadth being about 29 mm. The upper surface is pitted and has a series of small radially arranged canals. Neither these nor the pittings are regularly arranged or very prominent. The middle of the scute

is raised into a longitudinal ridge. The under surface of these scutes is smooth and concave from side to side.

Other scutes, probably belonging to a median row, possess very much the same characters but the median ridge is not developed and the upper surface is convex and subconical. The general shape of these scutes is oval, with pits and radial markings, and with a rather irregular margin. A beautifully preserved scute of this kind measures 35 mm. across and 30 mm. from back to front, yet the maximum thickness is only 5 mm. Some of the scutes are very small.

There are other fragments of flat, feebly sculptured bone which look like scutes or pieces of a chelonian neural plate, and not improbably these are portions of the ventral, sternal, ribs.

There is no trace of any large, quadrangular scutes such as are characteristic of the median rows in modern crocodiles. Nor is there any evidence of keel-less, articulated, scutes as have been figured and described for *Thoracosaurus*.

The number of scutes preserved is only a small fraction of the number that the crocodile possessed, and most of them appear to belong to the lateral rows. Their small size in some cases is noteworthy, but otherwise they show no features which call for additional description or comment.

AGE OF THE SPECIMEN. — In various parts of the description reference has been made to apparently youthful features of the skull. The comparative breadth of the cranial table, for example, has been mentioned and the number of maxillary teeth under the orbit. Although these features are among those in which age is indicated, when taken in conjunction with the state of the sutures, the relative size of the orbits and supratemporal fossae, and the actual size of the latter (for they are usually very small and slit-like in young crocodiles), it is clear that the specimen is not immature, but an adult and by no means of advanced age. Any further growth would not have affected the main characters upon which the diagnosis and description are based.

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## COMPARISON WITH OTHER FORMS

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The preceding description, with the frequent comparisons to *Thoracosaurus* and *Tomistoma*, will have shown sufficiently how different the new genus is from these older established forms. It will be convenient, however, to recapitulate some of these points and to note the essential differences with a wider range of genera. Most of the characters are those of the skull, as this region is quite well known in most of the genera referred to, although remains of the body skeleton are in many cases practically unknown.

*Thoracosaurus*, in general, has a longer and narrower skull (the length being three times the breadth) with larger lachrymals. As in *Dollosuchus* the supratemporal vacuities are broader than long, but they are larger than the orbits. Small antorbital fossae are reputed to be present. The facial profile is flatter than in *Dollosuchus*, and the teeth are more numerous in both upper and lower jaws. *Thoracosaurus* has no interdental fossae.

*Holops* is a genus very closely allied to *Thoracosaurus*, but it differs from it in having no antorbital fossae and having the orbits and supratemporal vacuities equal in size. Otherwise, the differences enumerated for *Thoracosaurus* serve to distinguish *Holops* also from *Dollosuchus*. In the last-named, however, the development of the hypapophysis in the axis has given rise to a median keel on the inferior surface of the centrum. This is not developed in *Holops*. Both *Thoracosaurus* and *Holops* share the primitive feature of having the frontal entering the margin of the supratemporal fossae.

*Tomistoma* is obviously quite distinct in the many features and proportions instanced throughout the preceding description. Here, the skull is a little longer compared with that of the new genus and has a much more concave facial profile. The supratemporal vacuities are quite different, since they are longer than broad and only about half the size of the orbits. The number of teeth in both upper and lower jaws is a little greater.

*Eosuchus*, described by Dollo in 1907 but figured here for the first time (Pl. I, Figs 5, 6), is also clearly unlike the new genus although both come from the Eocene of the same country. *Eosuchus* has a slightly longer and narrower skull in which the supratemporal fossae are much smaller than the orbits and are longer than broad. The facial contour is rather flat and the interorbital space is convex. The internal narial opening is not so posteriorly situated as in *Dollo-*

*suchus*. The canal of Stannius is very greatly developed. The splenial region of the mandibular symphysis is concave.

*Gavialosuchus* is closely similar to *Tomistoma* and so is distinct from *Dollosuchus*. The skull, although having much the same length to breadth ratio as in the last named genus, has the middle of the facial region broader and the upper surface more concave longitudinally. The cranial table is relatively large compared with that of other genera. Other points of interest are the very small size of the squamosal, at least in *Gavialosuchus americana* (Mook, 1921), the angulation of the inner narial opening, and the large size and shortness of the teeth generally. The large size of the teeth relative to the size of the skull is a resemblance between *Gavialosuchus* and two genera from the Argentine, doubtfully referred to the family Tomistomidae. These are *Leptorhamphus*, Ambrosetti, and *Oxysdonsaurus* of the same author.

Rusconi (1935) in discussing *Leptorhamphus* draws attention to the size of the teeth compared with the relatively small size of the jaw and suggests that in this it is possible to see some relationship with *Gavialosuchus*. However that may be, it is at least clear that *Dollosuchus* is quite distinct from these genera.

The second genus, *Oxysdonsaurus*, is based upon an isolated tooth, again of comparatively large size, and which is quite unlike any of the teeth of the new European genus.

A third South American form, *Gryposuchus*, from the Amazon region, and represented by the end of the upper jaw, has been described by Gürich (1912). The palatal aspect of the premaxillaries is much shorter and broader than in *Dollosuchus*, and on the dorsal surface the arrangement of the nasal, maxillary and premaxillary sutures is entirely different.

There can be no doubt whatsoever, therefore, that this new crocodile is a perfectly distinct form belonging to the family Tomistomidae.

On the other hand, when compared with the English specimens named *Gavialis dixonii*, there can be no doubt that the two are specifically identical although differences in the size of the individuals concerned are obvious. The types of the species come from certainly two, and possibly three, individuals, one larger than the Belgian form and the other, or others, smaller.

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## SYSTEMATIC POSITION

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The establishment of a new genus of undoubted Tomistomid characters creates the opportunity of reviewing briefly the membership of this important family. There is no point here in tracing the nomenclatural evolution of it as modern research has greatly clarified the limits of the main families, and much of the confusion in older works was caused by their authors' difficulty in deciding whether *Tomistoma* was a Gavial or a Crocodile.

Of recent reviewers the earliest we need consider is Gürich. In creating his new genus and species, *Gryposuchus Jessei*, and discussing its affinities, he states : « Während für *Tomistoma* noch Raum ist bei den eigentlichen Crocodylidae, müssen die besprochenen tertiären und jungkretazeischen Formen einstweilen zu einer Familie zusammengefasst werden, die zwischen Crocodylidae und Gavialidae steht, und zu dieser Familie gehören *Gavialosuchus eggenburgensis*, « *Gav. macrorhynchus* » bei Gervais und « *Thor. macrorh.* » bei Koken und endlich die vorliegenden Formen « *Gryposuchus Jessei* Gür. » The misspelling of the name of *Gryposuchus* is one of the several misrepresentations of generic names in the paper, and some unfortunately have been repeated by subsequent authors.

Later, and again following the description of a new form, Troedsson (1924), who was particularly concerned with *Thoracosaurus*, remarks that « at least 3 families of long-nosed crocodiles can be distinguished :

Fam. THORACOSAURIDAE n. nov. DANIAN.

*Thoracosaurus* LEIDY (incl. *Holops* COPE).

Fam. TOMISTOMIDAE Miocene — recent time.

*Tomistoma* MUELLER.

Fam. GAVIALIDAE DANIAN (?) — recent time.

*Hyposaurus* (?) OWEN. *Gavialis* OPPEL. »

Since that date the new edition of Zittel's Palaeontology (1932) has appeared with a classification which, so far as the family Tomistomidae is concerned, is wider and more comprehensive than any of those previously given.

The family is there suggested to contain eight genera, *Thoracosaurus*, *Holops*, *Eosuchus*, *Tomistoma*, *Gavialosuchus*, *Gryposuchus*, *Leptorhamphus* (a misprint for *Leptorrhamphus*), and *Oxyodontosaurus* (a misprint for *Oxysdonsaurus*).

Finally, in 1934, Mook (1934) published a short paper on the evolution and classification of the Crocodilia in which he recognizes *Tomistoma* and the other genera which are included above in the same family merely as genera within the wide family Crocodylidae. He, also, refers to the genus *Oxyodontosaurus* Ambrosetti. In the original description Ambrosetti (1890) clearly gives the name as *Oxysdonsaurus* which is not nearly so euphonious as the revised version. No revision of the name has been published so far as I am aware, and such an emendation would not be permissible in any case, so that the less pleasant, but original, generic name must stand.

If we examine the genera enumerated above we find that they range in time from the Upper Cretaceous to the present time and that a great geographical range exists.

The oldest genera are the closely allied forms *Thoracosaurus* and *Holops*.

*Thoracosaurus* was established by Leidy in 1854, the type-species being *T. neocesariensis* (De Kay). The original specimen came from New Jersey but since that time other species have been named. *T. macrorhynchus* Blainville has been found in the calcaire pisolitique of the Marne, France, and in the Maastrichtian of Holland. Another, and one of the best preserved species, is *T. scanicus* Troedsson from the Danian of Malmö, Sweden.

The genus *Holops* was created in 1869 by Cope with *H. brevispinis* Cope as the type-species. There has continually been much confusion between this genus and the preceding one and although Hay (1902) lists six species, Troedsson (1924) places them all in the synonymy of *Thoracosaurus*. This is probably incorrect because the two genera differ in the relative size of their supratemporal vacuities to the orbits, a character of some consequence and constancy, and while *Thoracosaurus* has on each side an antorbital vacuity none is present in *Holops*. It is possible, however, that the antorbital vacuities of *Thoracosaurus* are not natural but are the result of accident.

Both genera are alike, and differ from the other Tomistomidae, in having the frontal in the margin of the supratemporal vacuities which is a primitive feature, but they are the oldest genera in the family and this slight difference is scarcely sufficient to justify the erection of a special family for them as we have seen that Troedsson has done.

The next genus in stratigraphical order is *Eosuchus* Dollo, the type and only species being *Eosuchus lerichei* Dollo (1907). This is known by the excellent skull figured here (Pl. I) and some other fragments and is a perfectly distinct and valid genus of Tomistomid character. Its age is Lower Landenian.

*Dollosuchus dixonii*, occurring in the Bracklesham of England and the Bruselian of Belgium, is the next in ascending stratigraphical order, although three

species of *Tomistoma* are also known from the Middle and Upper Eocene of Egypt.

The genus *Gavialosuchus*, which is very closely related to *Tomistoma*, was founded by Toulou and Kail (1885), the type-specimen being the incomplete skull of *Gavialosuchus eggenburgensis* from the Miocene of Eggenburg, Austria. Another species, *G. americana* (Sellards) comes from the Miocene of Florida and has been very fully described by Mook (1921).

Andrews (1906) and Joleaud (1930) have placed the genus in the synonymy of *Tomistoma*, the former author contending apparently that the only real criterion is whether the nasals are in contact with the premaxillaries or not. If they are in contact the specimen belongs to *Tomistoma*. Joleaud includes nearly all the genera and species in the group under *Tomistoma*, in describing a remarkable form, *T. brumpti*, but it is interesting to note that in discussing the relationships of this species he finds it convenient to re-arrange the various forms into groups, a process rendered more exact and satisfactory if the genera had been left as they originally were.

The difficulty with *Gavialosuchus* is that some fragments of rostra described by various authors as *Tomistoma* have certain resemblances to the same part of the rostrum of *G. eggenburgensis* Toulou & Kail. The particular specimen in which the matter has been raised is *T. (Melitosaurus) champsoides*. This was stated by Lydekker (1886) to be identical with the Austrian species.

This particular question cannot definitely be settled as the most important part of the skull for diagnostic purposes is the cranial portion. A superficial resemblance in the tips of the snouts of most of the specimens in this group is easily to be found. It is significant that although a large number of species of *Tomistoma* have been described most of them are very fragmentary. In nearly every case where a complete skull has been found fossil it is easy to demonstrate its difference in many constant and important features from the modern *Tomistoma*.

For this reason alone, the genus *Tomistoma* is the least satisfactorily defined of the whole group when fossils are considered. Amongst its many members from the Middle Eocene until the present day, very few of the species are known from a satisfactory specimen. Those which have been recorded are, briefly, as follows, in ascending stratigraphical order. *Tomistoma kerunense* Andrews (1905, 1906) comes from the Middle Eocene of the Fayum, Egypt. The type, in Cairo, is an imperfect rostrum without the premaxillary region. The back of a skull has also been found. The species is closely related to the form *T. gavialoides* mentioned later. *T. africanum* Andrews (1901, 1906) is also from the Middle Eocene and occurs in the bed above *T. kerunense*. The type is a nearly complete mandible, without teeth, in the Geological Museum, Cairo. There is another specimen in the British Museum consisting of the front ends of both upper and lower jaws closely joined which shows that the premaxilla had five

teeth. The number of mandibular teeth is 20 on each side, 15 being in the symphyseal region.

*T. gavialoides* Andrews (1905, 1906), Upper Eocene of Egypt, is known from a skull which has not the hinder end of the palate (with the inner narial opening) nor the tip of the snout. The orbits, supratemporal vacuities, and the proportions of the post-cranial region are quite unlike those of the modern *Tomistoma*, according to Andrews, and the number of teeth 22-23 is larger than is usual in *Tomistoma*. There are five teeth in each premaxilla, a number common in many of the fragments referred to the genus, although the adult recent *Tomistoma* has only four. Dr. Mook, who has examined probably more crocodiles than any other authority, tells me that the number of teeth is unexpectedly constant and that a variation of two in number is usually to be regarded as more than an individual variation.

The next species are Miocene in age and from a wide range of localities. The most fully described of these is the rostrum and portions of the cranium figured under the name of *Tomistoma calaritanus* by Capellini (1890). The specimen is from the Miocene of Cagliari, Sardinia. Its author states that it is nearest to *Gavialosuchus eggenburgensis* but there are many obvious differences. The Italian species appears to be a true *Tomistoma*, although again much of interest is missing in the specimen and it has 5 teeth on each premaxilla.

*T. dowsoni* Fourtau (1918) is another species known from the Miocene, in this case from Moghara, Egypt, where fragments of the rostrum are exceedingly abundant. The type-specimens are fragments of the upper and lower jaws. There is a more complete skull now in the British Museum, but here again many of the important points are not preserved.

The other Miocene species are *T. champsoides* (Hulke ex Owen MS) and *T. gaudensis* (Hulke). The former is known from the tip of the rostrum and lower jaw from Malta and was first described by Lydekker (1886) (Owen having previously given it the manuscript name of *Melitosaurus champsoides*, first quoted by Hulke [1871]), and the latter name was founded by Hulke in 1871 on an incomplete skull and part of the mandible from Gozo. *T. champsoides* has five premaxillary teeth but there is little to be said about it, but *T. gaudensis* has all the characters of the genus *Tomistoma* according to Hulke's brief description.

The occurrence of a somewhat remarkable species from the Pliocene of Omo, Ethiopia, has been fully described by Joleaud.

The specimens are fragments of the snout and mandible and are remarkable in having the alveoli very outstanding. The total number of teeth is 24 on each side and again each premaxilla has five alveoli. According to Joleaud it is at the gavial end of the varied Tomistomid genus.

The living *Tomistoma schlegeli* is different in many respects from some of these species, but this could well be so without in any way invalidating their



relationship on account of the length of time which has elapsed between the earliest Eocene species and the present day. All the species listed above have five premaxillary teeth while the living form has five only in the very young condition and only four throughout its adult life. As a whole, however, it is obvious that the genus as at present constituted is indefinite and that many of the species bear names which are of no systematic importance although useful for reference.

The remaining genera are even more indefinite than some of the forms referred to above. *Gryposuchus Jessei* Gürich (1912), from the Pleistocene of Brazil, is known only from the end of the upper jaw. The snout would appear to be massive, with sutures on the dorsal surface of the same pattern as in *Thoracosaurus macrorhynchus*, and on the ventral surface like those in *Crocodylus champsoides*. There are only four teeth in each premaxilla. Joleaud referred this form to *Tomistoma* but there is no real indication of its affinities.

The two South American genera, *Leptorrhampus* and *Oxysdonsaurus*, cannot be discussed with any advantage. They are very inadequately known and the latter species is based on a striated tooth whose description Ambrosetti published with a certain reserve. Ambrosetti, their author (1890), considered them to belong to the Gavialidae and Rusconi in a recent paper (1935) has retained *Leptorrhampus entrerrianus* within that family, but he does not mention *Oxysdonsaurus*.

As Ambrosetti published but a meagre description and gave no figure it is impossible to assess the true systematic position of these two genera.

On reviewing the members of the family Tomistomidae enumerated above it is clear that certain characters are of fairly constant importance throughout the series. These are the size of, and relationships between, the nasals and premaxillae, the shape and relative size of the orbits, supratemporal vacuities, and external narial opening, the position of the internal narial opening, the general proportions of the cranial table, the number of teeth and the length of the mandibular symphysis.

In connexion with the last feature, it is interesting and perhaps instructive to record the relative length of the symphysis to the length of the mandible (in the middle line) in various species. The following list, in which a true crocodile is at one end and a true gavial at the other, contains all the fossil Tomistomidae in which it is possible to calculate this ratio.

	L. of mandible. L. of symphysis.	No. of symphysial teeth.	Total no. of teeth.
<i>Crocodylus cataphractus</i> ... ..	3.90	7	15
<i>Dollosuchus dixonii</i> ... ..	2.72	10	17
<i>Tomistoma schlegeli</i> ... ..	2.34	15	20
<i>T. calaritanus</i> ... ..	2.23	12	17
<i>T. africanum</i> ... ..	2.14	14	20
<i>Thoracosaurus scanicus</i> ... ..	2.00	17	23
<i>Gavialis gangeticus</i> ... ..	1.85	23	25

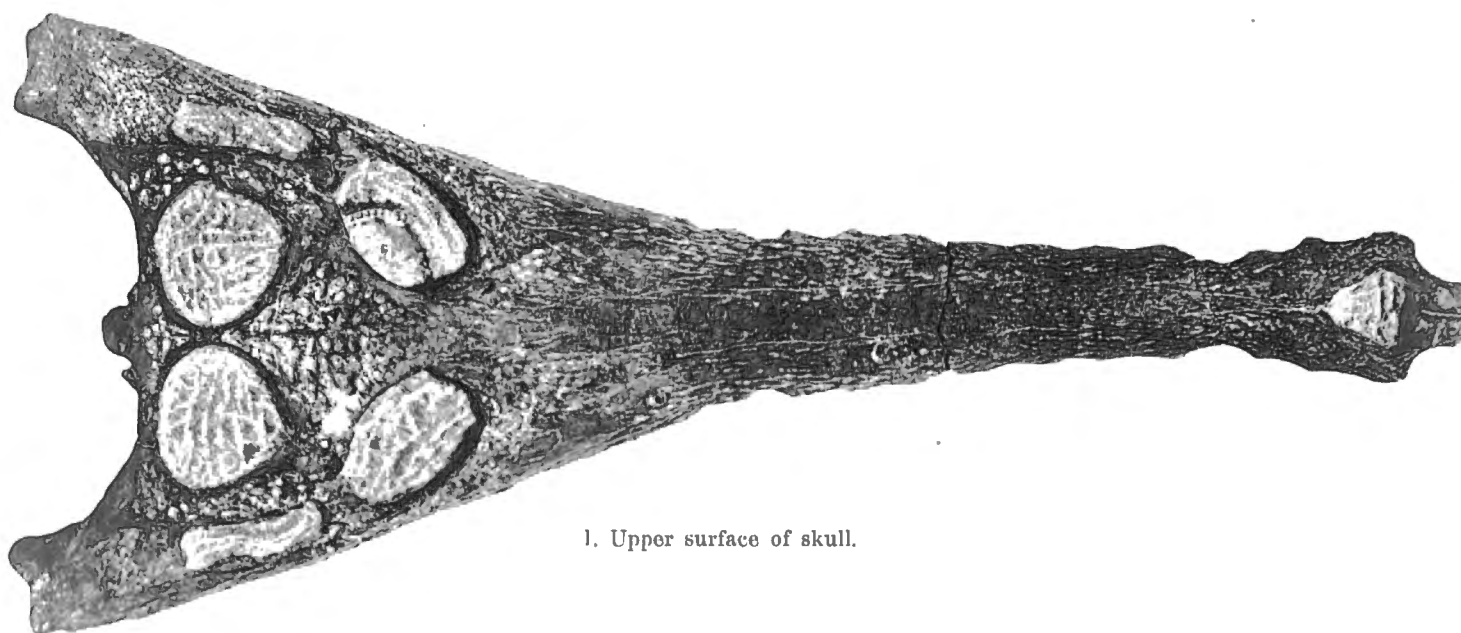
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Mandible. (About  $\frac{2}{5}$  natural size).

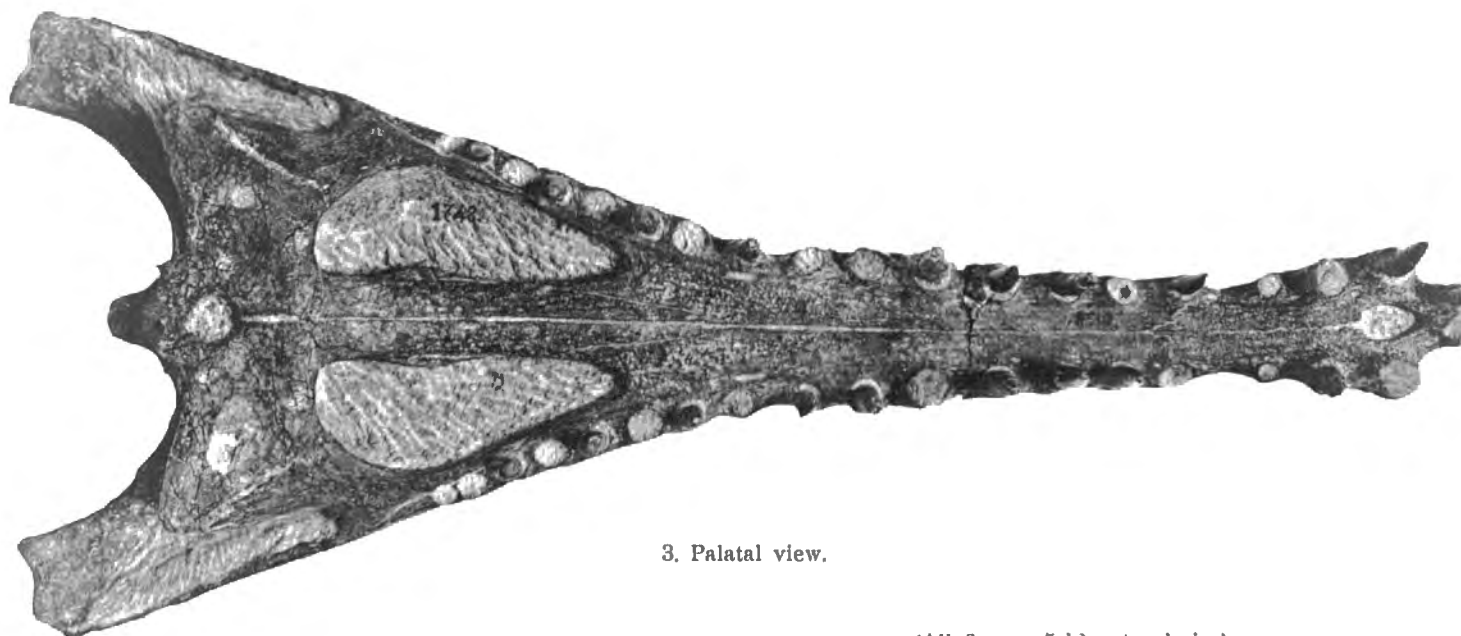
7. — *Dollosuchus dixonii* (Owen).



1. Upper surface of skull.



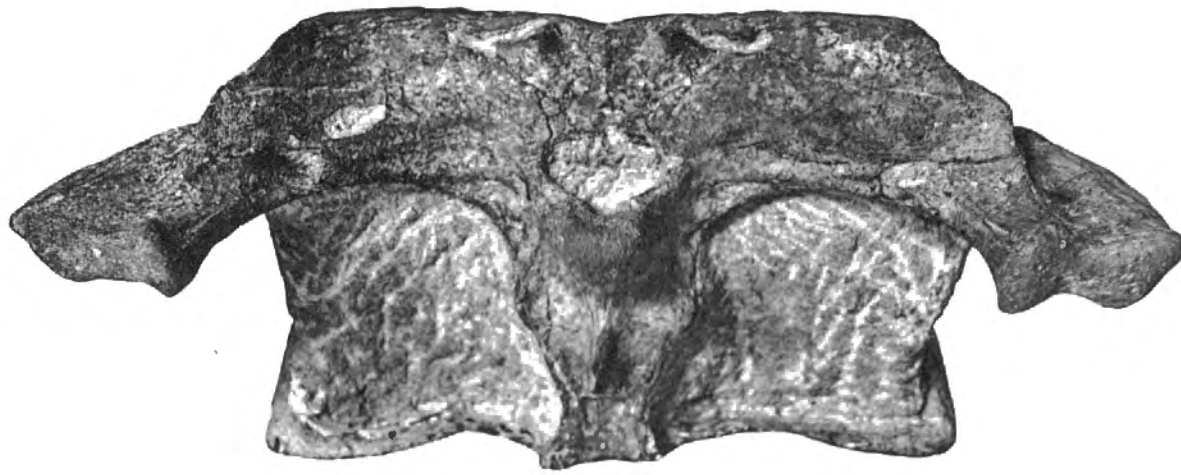
2. Profile of skull.



3. Palatal view.

(All figures 5/12 natural size).

1, 2 and 3. — *Dollosuchus dixonii* (Owen).



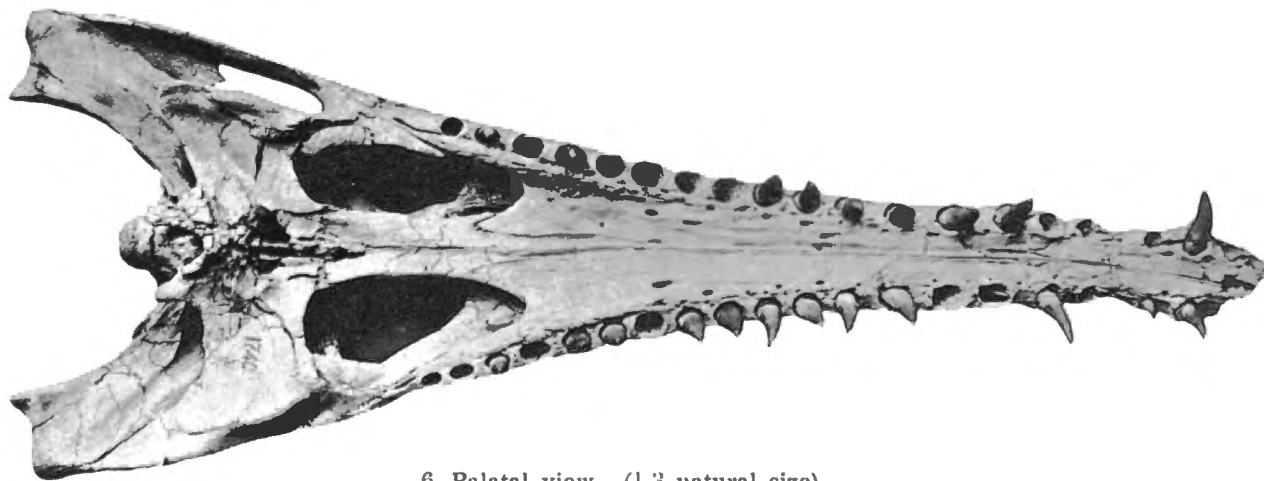
Occipital region of skull. (7/10 natural size).

4. — *Dollosuchus dixonii* (Owen).

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5. Upper surface of skull. (1/3 natural size).



6. Palatal view. (1/3 natural size).

5 and 6. — *Eosuchus lerichei* Dollo.

W. E. SWINTON. — The Crocodile of Maransart.