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THREE MESOZOIC CROCODILES IN THE COLLECTIONS OF THE PALAEONTOLOGICAL MUSEUM, UPPSALA

by

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Three specimens of two species of Jurassic Crocodile in the Department of Paleontology, Uppsala, have been described. The two specimens are *Metriorhynchus superciliosum* from the Oxford Clay, Peterborough, and *Stenosaurus bollensis* from the Lias E. at Holzmaden. The *Metriorhynchus* material is one skull and mandible, and a near complete skeleton; the *Steneosaurus* is complete and very well preserved. The metriorhynchides both have the characteristic prefontals overlapping the orbits. The complete specimen has the tail flexure at the 27th caudal, but no reversal in the neural spine direction occured. The vertebral column is remarkably complete with 65 vertebrae. The *Steneosaurus bollensis* has very small fore limbs and relatively larger hind limbs. The dermal scutes are abundant and well preserved. This specimen has been subjected to a statistical analysis along with details from a number of other specimens of the same species (Westphal, 1962) to verify the taxonomic position of the specimen, since prior to this description it had been named *Mystriosaurus bollensis.* A discussion of the specimen showed certain palaeoecological significances regarding the depositional environment.

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INTRODUCTION

Amongst the vertebrate collections at the Paleontological Department, University of Uppsala, three specimens of two species of Mesozoic Crocodile were found unrecorded and undescribed. Their preservation is such that a detailed description was thought both necessary and valuable. The two species are: *Steneosaurus bollensis* and *Metriorhynchus superciliosum*; one of each species is nearly complete and a second specimen of *Metriorhynchus* has just the skull and mandible remaining.

The *Steneosaurus* (R. 161) comes from Holzmaden in Southern Germany, and lies in the original rock matrix, a dark shale, thus exposing only the dorsal view and making a study of the ventral side impossible. The stomach contents have been preserved as a black patch just above the sacral region and these have been analysed under the

microscope and are clearly organic, but whether vegetable or animal is difficult to determine. Stomach stones were identified by Zdansky in the same region. Although this specimen is unrecorded, it is to be suspected that a former Director of the department, Carl Wiman, 'acquired it' from the Senckenberg Museum early on in this century. The title painted on the specimen is '*Mystriosaurus bollensis*, Lias E', but this name is now regarded as being synonymous with *Steneosaurus bollensis* and will be regarded as such here; this point will be discussed later.

The two specimens of *Metriorhynchus superciliosum*, one nearly complete (R. 170) and the other just the skull and mandible (R. 165), both come from the Oxford Clay at Peterborough in England. The acquisition of these specimens is not clear, but the identification is correct as verified in this description. In some respects, the complete specimen is as complete as specimens described by Arthaber (1906), Andrews (1913) and Mercer (1934), but the completeness of the vertebral column is such that one suspects that all the bones may not be from the one specimen.

This description has been based on the last paper dealing with these two species, Andrews (1913) and also to a degree on Westphal (1962). The description has been restricted to the diagnostic features as far as possible, and for general anatomical details of this species, I would refer to Andrews (1913).

SYSTEMATICS

Order *CROCODILIA*
Suborder *MESOSUCHIA*
Family *METRIORHYNCHIDAE* E. Fraas.
Genus *METRIORHYNCHUS* M. v. Meyer (1830)
M. superciliosum Blainv. (1837)

Diagnosis

Based upon the specimens R. 170 and R. 165. Prefrontals overlap orbits and have a distinct pitted ornamentation. Snout enlongated and narrow. Premaxillae are large — usually about 16 % of total skull length. Median line is absent on frontals.

Material

Skull and mandible.

Description (Pl. I, fig. 1).

The prefrontals are clearly seen to overlap the orbits, aided possibly by compressional effects. The premaxillae are 12 cm long. The median line is absent on the frontals, which have strong radial pitted ornament.

Skull — This is very much depressed thus obscuring a satisfactory view from the side, although the detail on the dorsal surface is not affected. The snout is characteristically very elongated and the nasals also are large. The prefrontals are extremely large and partially cover the anterior of the orbit.

Premaxillae — These are 12.0 cm along the median line, and 4.5 cm across the posterior of the nasal opening. The processes appearing at the posterior of the nasal opening splitting the nasal are very indistinct and only one was measured: this was 1.1 cm long. Since the length of the nasal opening is 3.5 cm, the ratio of the process to the nasal opening length is:

1.1 : 3.5 or 3.18

The base of the nasal opening at the anterior is missing where a tooth socket once lay, leaving a large gap. The internal angle between the posterior borders of the premaxillae is 35°.

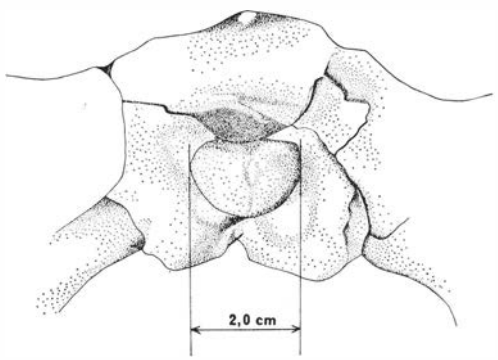

Fig. 1. Anterior view of the occipital condyle of *Metriorhynchus superciliosum* (R. 165). Here, and elsewhere, the numbers on the diagrams refer to measurements in centimetres.

On the palatal surface, the suture between the maxillae and the premaxillae is not visible. On the left side 2 large teeth are preserved and the 3rd is missing; again the right side, only has 2 teeth and the anterior-most is missing, leaving a gap as seen from the dorsal surface.

Maxillae — The distance between the premaxillae and the nasal is 4.5 cm and the length of the aveolar border is 24.0 cm on the left side and 24.5 cm on the right side. The convexity of the snout is not apparent due to the flattening that has occurred.

On the palatal surface these are quite featureless except for the dentition:

left side: 21 sockets with teeth
right side: 24 sockets with teeth

In some cases, the sockets have been formed into one by the disappearance of the intradental bone walls.

Nasals — These first appear 17.0 cm behind the anterior tip of the snout. The length along the median line is 19.0 cm, and the angle between the boundary of the nasals and the maxillae is 16°. The length along this boundary on the left side is 17.0 cm, and on the right side is 20.5 cm. The specimen has been a little displaced laterally and hence this discrepancy. The angles between the borders of the prefrontals and the frontals are:

left side 30°
right side 28°

The surface fabric of this bone is in the form of longitudinal ridges fanning out adjacent to its borders; the depth of these ridges varies steadily from very fine to coarse, going from the inner side outwards. The median furrow is considerably wider here — 1.5 cm at the anterior of the frontal.

Prefontals — The dorsal surface is heavily pitted, with the greatest concentration at the centre of the bone. The maximum length on the left side is 6.0 cm and on the right side 4.5 cm; the maximum width is 5.0 cm on both sides. The distance between the left and right prefrontal at the anterior most point is 6.5 cm. As is characteristic with family Metriorhynchidae, the prefrontals overlap the orbits quite considerably forming an upper shield.

Lachrymal — This bone is present but owing to the effects of compression it is very obscure and measurements cannot be reliably made.

Frontal — The length along the median line is 13.0 cm, and the maximum width, just posterior to the supra-temporal vacuity, is 11.5 cm. The angle of divergence from the anterior of the frontal from the nasals is 35°.

The surface fabric is pitted in a faintly radiating pattern from a point lying central on the median line. The process projecting back across the bar separating the supra-temporal vacuities extends 5.0 cm — approximately half the distance of this bar length. The median trough is absent from 2.0 cm posterior from the anterior of the frontal. A faint trace starts again at the extreme posterior of the frontal.

Parietal — This is 6.0 cm along the median ridge, and 4.0 cm wide at the posterior (posterior of triangular part).

The vertical overlap by the frontal is very slight where it meets the parietal on the median ridge. The median furrow reaches maximum development here having a depth and width of 0.5 cm.

Apart from the suture joining the frontal, the other sutures joining the alisphenoid and the pro-otic are obscured on the left by the effects of compression on the inner wall of the supra-temporal vacuity. On the right side, the suture between the squamosal and the parietal is just visible as is the suture to the pro-otic; however the alisphenoid is still obscured.

Squamosal — These are present and complete on both sides but heavily fractured owing to compression. The sutures joining the squamosal to the prefrontal are clearly seen, and, less distinctly, the suture joining the parietal. These pass directly on to the quadrates below but the suture is very indistinct.

Post-Frontal — Again this bone on each side is heavily fractured, with many chips missing during the reconstruction, but otherwise it is quite com-

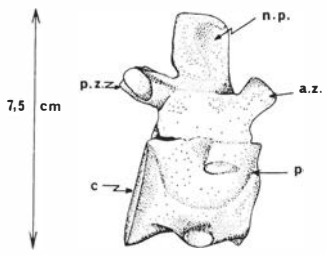

Fig. 2. The second cervical vertebra of the *Metriorhynchus superciliosum* (R. 170). p — parapophysis; np. — neural spine; pz. — posterior zygopophysis; nc — neural canal; c — centrum.

plete. The suture joining the prefrontal to the frontal is very clearly seen, having the characteristic 'V' shape. This bone is completely devoid of any ornament, which often occurs on *M. superciliosum* and on other species as well. This absence may well be a factor of age or sex and will be discussed in the statistical summary.

The post-frontal has a curved inner border giving the supra-temporal vacuity a curved hypotenuse to its right triangular shape. There is a slight variation in the size of these vacuities but no significance is attached to this.

Jugal — On the right side, this bone is complete and in position, but the left side is displaced posteriorly. The right jugal passes anteriorly into the maxillae and the lachrymal, although the suture to the latter is not seen. On the left side, the jugal passes into an indistinct region of compressed bone beneath the prefrontal overhang. On both sides the jugal is missing, and so is the posterior part of the post-orbital bar.

Quadrate — This is well preserved except for a slight compression against the squamosal. The articular facets are all seen very clearly and for the most part still maintain their shape. The quadrato-jugals are missing completely, as are the wings of the basioccipitals, thus revealing a little more of the quadrate.

On the palatal side, the preservation is equally good, although the left side has better preserved articulation facets than the right. The anterior longitudinal ridge is very prominent on both sides leading up to the pterygoids.

The length along the centre is 8.5 cm and the widths is 4.0 cm on the left quadrate; the right has a small fragment missing.

Basioccipital — This is well preserved although not fully complete. The occipital condyle has a convex surface and the small hollow at the centre is not clear owing to a slight infilling of sediment that has not been worked out. The condyle is slightly oval: 1.5 cm laterally and 1.75 cm across vertically.

The median eustachian tube is identifiable but very indistinct. The basisphenoids are present and complete with the characteristically rough surface.

On the palatal surface, the exoccipitals are very fragmentary and incomplete and it is difficult to discern if they extend above the foramen magnum. At the sides on the lower part of this foramen, fragments are definitely present.

Palatal Surface (Pl. I, fig. 4). The preservation of this surface is much worse, although most of the bones are present in some form.

Palatines — Only the anterior 10.0 cm remain and the anterior-most tip is also missing. The bone is rather fractured and its borders very obscure. The median groove is present but the sides are so poorly preserved that the furrow is very disjointed.

Parasphenoid — This also is fragmentary, but it does form a continuous bone from beneath the palatines to the basisphenoid. On the right side, a fragment of the pterygoid is present.

Mandibles (Pl. I, figs. 2, 3). Each of the mandible halves has been fractured in the same place, at the anterior suture of the surangular on the outer surface. Hence they will be described as the anterior and posterior left and right.

Anterior left — The symphysis as the anterior end on the lower side facing inwards is reduced in thickness so that a series of pit structures, lying between the dental sockets, occurs. On the upper side, the dentary is complete although fragmentary at the anterior tip. The length along the interior upper border of the dentary is 26.0 cm, with 19

tooth sockets (and fragmentary teeth). The splenial is present and well preserved. On the outer side the splenial shows through between the anterior of the angular and the posterior of the dentary seen as a triangular bone. Behind the suture of the dentary and the splenial, the splenial thickens considerably and assumes a strongly convex shape.

Posterior left — This is very well preserved and fully complete.

The *angular* clearly shows a radiating fabric which is characteristic of the genus. The suture joining the surangular and the angular is clearly overlapping as seen on the inner and outer sides.

The *coronoid* is complete except for the anterior part where the posterior section of the mandible has broken away from the anterior part.

The prearticular in this specimen is present although the boundary sutures are not seen. It extends back into a deep furrow which is formed by the overlap of the post-articular facet.

The *articular* has well formed post and anterior facets for articulation with the quadrate; the ridge between the two facets is clearly seen.

Anterior right — Essentially equal and opposite to the anterior right except for the tip which is missing along with the front tooth. The length of the dentary is 24.5 cm. 18 teeth are present including one very small tooth; unfortunately, the corresponding tooth on the left side is missing and the socket is not well enough preserved to be able to say if this tooth is just small or whether it was regenerating.

Posterior right — Again very similar to the posterior left except that most of the coronoid is absent and only the anterior-most part remains. Owing to the fracturing of the posterior angular and surangular, the reconstruction necessary had led to a faulty placing of the articular. Thus the facets are pointing in the wrong direction vertically and also slightly laterally. The process directing down from the posterior facet is missing.

The *prearticular* is present but it is not so well preserved as on the right mandible and it also is slightly displaced.

Genus *METRIORHYNCHUS* H. v. Meyer (1830)
M. superciliosum Blainv. (1867)

Diagnosis

See above, specimen R. 165.

Material

A near complete skeleton (specimen R. 170). Remaining 4 to 5 caudals are missing, and most vertebrae have only centrum complete. Manus is absent and pes has phalanges missing. Both girdles are complete. Skull is complete (except teeth) but heavily fractured in places. Mandibles complete, but in a poor condition.

Description

The skull of this specimen is essentially very similar to the first specimen so only the features which are different from that specimen will be described to avoid repetition. The overall length is 286 cm. There is a flexure at the 27th caudal vertebrae, but no reversal of the neural spines occurs; 40 caudal vertebrae are present which added to 25 sacral, dorsal and cervical vertebrae makes a total of 65. A deep notch occurs in the coracoid where, in other genera, a foramen is present.

Skull (Pl. II, figs. 1, 2, & text-fig. 1). — The total length is 65.0 cm and the length from the tip of the snout to the basioccipital is 59.0 cm. The preservation is generally good except, again for compression obscuring a side view.

Premaxillae — This is 12.0 cm long medianly. The nasal opening is rather fragmentary and the posterior processes have been fractured. The maximum dimensions of the nasal pit are: 4.5×2.0 cm. The angle of convergence of the pre-maxillae posteriorly is 35°.

The region just anterior to the nasal pit is considerably more elevated than in the first specimen thus giving a more pronounced pit-like appearance from the side. On the palatal surface 6 sockets are present, of which 4 have teeth in.

Maxillae — The length between the premaxillae and the nasal is 5.5 cm. The length along the aveolar border on the left side is 29.0 cm, and

on the right side it is 28.5 cm. The longitudinal ridge markings are quite pronounced.

On the palatal surface the dentition on the left side contains 24 sockets of which 7 have teeth, and on the right side there are 20 sockets but only 5 teeth. The distance between the anterior socket of the maxillae and the posterior socket of the premaxillae on the right is 2.25 cm and on the left it is 2.0 cm.

Nasals — The length along the median line is 17.0 cm and the angle between the nasals and the premaxillae is 20°. The aveolar boundary on the left side is 13.0 cm and on the right it is 14.5 cm. The angle between the frontals and prefrontals is 35° left and right. The median furrow here is quite wide — 1.0 cm. The surface fabric is as in the first specimen.

Prefrontals — The maximum length is 8.0 cm on the right, and on the left it is 9.0 cm; the width is 5.0 cm on both sides. The maximum distance between the two prefrontals is 9.0 cm at the anterior-most point.

Lachrymal — As in the first specimen this bone is very much obscured, perhaps even more so here.

Frontal — The length along the median line is 14.5 cm, and the angle of divergence from the nasal is 38°. The maximum width, anterior to the supra-temporal vacuity, is 13.5 cm.

The median line is totally absent along the length of the frontal and the only relief is the heavy pitting. The posterior extension of the frontal along the inter-vacuity ridge is 4.5 cm, which again is about half the length of this ridge.

Parietals — The median furrow is absent; the distance across the posterior part of the triangular surface is 4.5 cm. The width of the ridge at the posterior is 1.5 cm. Again, the only clear suture is that joining the frontal, although one can see the alisphenoid and pro-otic, which are badly preserved.

Squamosal — These are almost identical to those of the first specimen and need no further discussion here.

Post-Frontal — Again this is very similar to the first specimen except that there is a slight pitting on the surface. These two specimens have so far had a remarkable resemblance, thus this feature of relief on the post-frontals bears no intraspecific significance, and it is difficult to determine if this is a factor of age, sex or just individual variation.

Jugal — This bone is missing on both sides.

Quadrate — The width of the posterior facet is 3.5 cm on both the left and right. The quadrato-jugals are missing.

Basioccipital — The occipital condyle is well preserved and the central pit is clearly seen. The foramen magnum, although a little distorted, is also clearly seen.

The basisphenoids are complete, retaining their rough surface. The exoccipitals on the palatial surface are much more complete in this specimen, although far from perfect, being distorted by compression.

Palatines — These are only present anteriorly and what remains is very heavily fractured and poorly preserved. The median line is visible.

No other palatal bones are present except for the ventral surface of those bones already described.

Mandible (Pl. II, figs. 3, 4; Pl. III, figs. 1, 2, 3). This is all in one piece but is heavily fractured and thus much detail is obscured.

Right part of the mandible — Total length is 65.0 cm. The anterior tip has been broken off and the remainder is in bad condition. The dentaries contain 20 sockets of which 10 have fragmentary teeth. The dentary itself is well preserved and is 28.5 cm along the oral surface.

The *symphysis* is very much in the same condition as in the first specimen — worn away slightly to show the roots of the tooth sockets.

The *splenial* is very well preserved still having the original surface fabric and is the one bone unaffected by fracturing.

The *surangular*, however, is in very poor condition though one can still see the suture joining this

Table I. Dimensions of the vertebrae of *Metriorhynchus superciliosum*:

Vert. no.	Length of Centrum	Height of Centrum	Height of Spine
1	3.0	3.0	1.5
2	2.7	3.0	+2.7
3	3.2	2.7	4.2
4	3.2	2.7	4.2
5	3.5	2.5	+3.0
6	3.7	2.5	—
7	4.0	2.7	+2.7
8	4.0	2.5	—
9	4.0	3.0	—
10	4.0	2.7	+3.2
11	4.0	2.7	4.7
12	4.0	2.7	—
13	4.0	3.0	—
14	4.0	2.7	5.5
15	4.0	2.5	—
16	4.0	2.5	5.0
17	×3.5	3.0	—
18	3.5	2.7	—
19	3.2	2.7	5.5
20	3.0	2.7	—
21	3.5	2.5	—
22	×3.5	2.5	—
23	3.0	2.5	—
24	2.7	2.5	—
25	2.5	2.7	5.2
26	3.0	2.5	—
27	3.0	2.5	—
28	3.0	2.7	—
29	3.5	3.0	—
30	4.0	2.7	—
31	4.0	2.7	—
32	4.0	2.7	—
33	4.2	3.0	—
34	4.0	2.7	—
35	4.0	2.2	—
36	4.0	2.5	—
37	4.0	2.5	—
38	4.0	2.5	—
39	4.0	2.5	—
40	3.7	2.2	—
41	3.5	2.5	—
42	3.5	2.2	—
43	3.5	2.5	—
44	3.5	2.2	—
45	3.5	2.2	—
46	3.2	2.2	—
47	3.2	2.0	—
48	3.0	2.2	—
49	3.2	2.0	—
50	2.7	1.7	—
51	2.7	2.0	2.2
52	2.0	2.0	2.5
53	2.2	1.7	2.0
54	2.2	1.7	2.5
55	2.0	1.7	1.7
56	2.2	1.7	—
57	2.2	1.7	—
58	2.2	1.5	—
59	2.2	1.5	—
60	2.0	1.5	—
61	2.0	1.2	—
62	1.7	1.2	—
63	1.5	1.0	—
64	1.5	0.7	—
65	1.5	1.0	—

× Cracked
\+ Incomplete

to the angular below. The angular, although badly preserved, does still show the original pattern on the surface which is very faint and is not radiating as in the first specimen. Anteriorly these two bones are in much better condition leading into the dentaries.

The *coronoid* is only present at the coronoid angle and here it is very fragmentary; the depth of the mandible at the coronoid angle is 6.5 cm.

The posterior and anterior facets of the articular are present, and still retain their original form. The posterior tip of the articular process is also present and well preserved. The prearticular is absent.

Left part of the mandible — The total length is 63.5 cm. The bone has essentially the same preservation except for the following details.

There are only 19 sockets of which only 6 have fragmentary teeth, including the anterior most which is absent with the tip on the right mandible.

The *coronoid* is complete and well preserved, and the depth of the bone at the coronoid angle is 6.0 cm.

The *symphysis* is in a very poor state owing to heavy fracturing and pieces missing.

The *surangular* also is very poor with a large hole in the centre, but the angular is a little better.

The *articular* however is very good and the facets although more worn than those of the right mandible, still retain their shape.

The *prearticular* is present but fragmentary.

Vertebral column (Pl. III, figs. 4, 5, & text-fig. 2). — A total of 65 vertebrae are present giving a total length of 227.0 cm. No chevrons are present in the caudal region and a great deal of the neural spines are missing.

The *atlas* and *axis* are fused together and are not fully preserved. The arch of the axis is the major feature apart from the centrum, but it is broken off before the postzygopophysis is reached. The arch of the atlas is just visible but dorsally much reduced by fracturing. The anterior wedge bone is present and the position of the articulation with the rib of the atlas is clearly seen. The rib of the atlas is missing on both sides. The diapophysis is missing.

Six *cervical vertebrae* are present and are the best preserved of the column. The definition taken here for a cervical vertebra is that which considers the parapophysis to be borne on the centrum, and where the parapophysis lies on the neutral spine the vertebra is the dorsal. The anterior and posterior zygopophyses are present in all 6 vertebrae as are the bases of the parapophyses. The neural spines are complete in vertebra 2 and 3, but the remainder have the tops broken off. The ends of the centra are all biconcave (as is the case in all vertebrae in this specimen). The diapophysal process is only partially present on vertebra 1 and 3; the remainder have this process broken off at the base.

The *thoracic-lumbar vertebrae* amount to 16 of which 15 have ribs attached on both sides. The distinction between the dorsal and cervical vertebrae is very clear using the criteria mentioned above. The centra are generally unaffected by compression; the vertical diameter is the same as the horizontal diameter. Of the 16, only 5 vertebra have complete neural spines. The diapophysial processes are generally, except one, near complete, and have the facet still present for the articulation of the ribs. The posterior and anterior zygopophyses are generally absent leaving the scars and not the processes. The neural canal can be seen in all vertebrae where the neural spine is partially remaining.

Two *sacral vertebrae* follow the dorsals and again these are very distinct. The first has no neural spine, but the second has a fully complete one. The lateral processes, sacral ribs, are complete in both and on each side with the facet for articulation with the ilium well preserved. The zygopophyses are absent on the first sacral, but on the second the anterior zygopophyses are imperfectly preserved.

There are 40 *caudal vertebrae* included in this reconstruction and the question of whether these are all from this one species is difficult to answer. If they do all come from this one specimen, then it is, to my knowledge, the greatest number of caudal vertebrae to be preserved in this species.

The *tail flexure* occurs at the 27th caudal — which is greater than the specimens described by Andrews (1910). The 40th caudal is by no means the last, and probably the 44 observed by Fraas in *Geosaurus* is also true in this species.

Only 4 caudals have a well preserved neural spines with zygopophyses, and 2 others have remnants. These 6 vertebra (25—30) lie on the flexure of the tail. The first 2 from the sacral end have good zygopophyses, while in the second 2 they are fragmentary, and in the 5th and 6th the neural spine is the only structure.

The effects of compression have made the vertical dimension of the centra greater than the horizontal. Andrews (1910) indicates that in the vertebra posterior to the flexure, the neural spines point in the opposite direction anteriorly. Unfortunately, the spines are not well enough preserved to provide

Table II. *Average dimensions of each type of vertebra:*

Width of Neural Spine	Height of Neural Spine	Diameter of Centrum	Type
2.5 cm	4.5 cm	3.5 cm	Cervical
4.5 cm	5.5 cm	5.0 cm	Thoracic-lumbar
—	5.0 cm	3.5 cm	Sacral
3.5 cm	4.5 cm	2.5 cm	Caudal A.
1.5 cm			Caudal B.

N.B. The caudal vertebrae have been divided up into two groups since, for the measurements of the neural spines, the caudals differ too much for averages to be taken; the averages are more meaningful.

definite evidence for or against this, but from this reconstruction the little evidence there is does not agree with Andrews.

Shoulder girdle and Fore limb (Pl. III, fig. 6). The shoulder girdle is complete and very well preserved, but the fore limb has the carpals and ulna missing.

Scapula —

Maximum length	right	7.3 cm	left	7.0 cm
Width at articular end	„	2.0 cm	„	2.0 cm
„ at shaft	„	1.0 cm	„	0.7 cm
„ at upper end	„	1.5 cm	„	1.5 cm

The two sides vary more than one would expect and thus may be a factor of post-mortal deformation. The facets at both ends are well preserved as is the glenoid cavity.

Coracoid —

Maximum length	right	7.3 cm	left	7.3 cm
Width at lower end	„	4.0 cm	„	4.0 cm
„ of shaft	„	1.7 cm	„	1.5 cm
„ at upper end	„	5.0 cm	„	5.0 cm

This is a characteristically large, double-headed axe-shaped bone and does not reflect the irregularities of the scapula. The foramen of the articular (upper) end is absent and occurs in the form of a deep notch. The glenoid fossa is well preserved but the reconstructer has placed the whole bone at an incorrect angle to the scapula such that the glenoid cavity and the glenoid fossa are fully 4 cm apart.

Humerus —

Maximum length	right	7.0 cm	left	7.0 cm
Width at head	„	2.0 cm	„	1.7 cm
„ at distal end	„	1.7 cm	„	1.5 cm

Again the variation is very slight. The facets at each end are in very good condition and the deltoid crest is also present although a little worn.

The *Ulna* is present as a fragmentary circular bone with a diameter of 2.0 cm on the right side only.

Pelvic girdle and Hind limb. — These are well preserved: the limb is not fully complete, though more so than the fore limb.

Ilium —

Maximum length along:				
dorsal border	right	6.5 cm	left	6.7 cm
Acetabular border	„	5.0 cm	„	5.0 cm

The anterior angle of the ilium is complete. Here again the reconstruction has been a little erroneous: the pubis and ischium are a very long way from the ilium to which they are supposed to be suturally attached.

Ischium —

Maximum length of symphysis	right	8.5 cm	left	8.5 cm
Width at anterior end	„	2.2 cm	„	2.2 cm
„ at neck	„	3.0 cm	„	3.0 cm
Maximum width	„	10.5 cm	„	10.5 cm

Again this bone on both sides is well preserved, clearly showing the anterior process and the acetabulum which here articulates with the femur instead of with the ilium, as it did in life.

Pubis —

Maximum length	right	9.5 cm	left	9.25 cm
Width at neck	„	1.0 cm	„	1.0 cm
„ at upper end	„	1.5 cm	„	1.5 cm

The *symphysis* is quite curved and not too long: length curved 5.25 cm, length direct 4.00 cm.

Both bones are well preserved with the articulation surface to the ischium and femur having a near original form, being slightly convex and oval.

Femur —

Length straight	right	13.0 cm	left	13.0 cm
Length curved	„	3.5 cm	„	3.5 cm
Width at proximal end	„	13.7 cm	„	14.0 cm

This bone has been fractured badly but no pieces are missing. The head of the femur is in good condition having a considerably bulbous form, and articulates with the ischium (acetabula) and the pubis. The distal end is imperfect but the tip holding the condyle is very smooth and complete, fitting well against the tibia and fibula.

Tibia and *Fibula* —

Tibia length	right	7.8 cm	left	7.8 cm
Fibula length	„	7.8 cm	„	7.8 cm

These are again well preserved being a little under half the length of the femur. The tibia is the wider bone particularly at the proximal end. The fibula has the greater width at the distal end along the articulation surface, while the tibia

does not increase in width from its neck along this surface.

Pes — The phalanges in this specimen are absent, and the 4 bones represent the continuation of the limb on both sides. Metatarsal 2 on the right side is fractured and half missing. The metatarsal 1 is characteristically very wide at the proximal end being twice the thickness of the others at this point. At the neck and the distal end however, it assumes similar proportions to the other three.

The metatarsals are flattened slightly giving an oval shape in cross section. The metatarsal 5 is missing.

The following dimensions apply to both the left and right:

	length	prox.end	dist.end
Metatarsal I	7.0 cm	2.5 cm	0.75 cm
„ II	—	—	0.75 cm
„ III	7.5 cm	1.0 cm	0.75 cm
„ IV	8.0 cm	1.0 cm	1.00 cm

Order *CROCODILIA*
Suborder *MESOSUCHIA*
Family *TELEOSAURIDAE* Geoffroy (1825)
Genus *STENEOSAURUS* Geoffroy (1825)
S. bollensis Geoffroy (1825)

Diagnosis

See Andrews (1910 (2)).

Taxonomy

This large teleosaurian has been named as *Mystriosaurus bollensis,* but by some this is regarded as synonymous with *Steneosaurus bollensis.* Andrews (1910) provided a definite distinction between the two, but this depended on the specimen having well preserved ventral nares, which is rarely seen, and certainly not here. All other features fit with descriptions of *Steneosaurus bollensis.*

Material

A nearly complete skeleton. (Specimen R. 161)

Description

The overall length of this specimen is 3 m 64 cm, excluding an indefinite number of caudal vertebrae which are missing. The preservation on the dorsal surface of the skull is good but the detail is very indistinct; otherwise, the rest of the skeleton has been well 'developed' — again on the dorsal surface only. Where I have used the terms left and right, these are with respect to the observer, except where stated.

Skull (Pl. IV; Pl. V, figs. 1, 2, & text-fig. 3). — The length of the upper skull from the basioccipital to the tip of the snout is 75.0 cm; the total length including the articulars of the mandibles is 85.0 cm. There has been a considerable displacement between the upper and lower jaws of approximately 2.0 cm, but this is not enough to permit anything to be said about the mandibles. The only parts of the lower jaw that is visible are the articular bones protruding from under the quadrate on each side. Here the posterior and anterior facets are clearly seen but are directed straight upwards instead of at an angle owing to post-mortem alteration.

The *teeth* are present on the right side only and although displaced they are mostly well preserved. The largest teeth are found on the premaxillae and immediately posterior to it on the maxillae. The preservation of the teeth on the maxillae may be described as:

left	25 (16)	14 (7)	right	— upper jaw
	23 (16)	1 (—)		— lower jaw

where the number in brackets represents the teeth preserved and the number outside is the number of sockets seen. The left and right here are with the respect to the specimen and not the observer. The premaxillae has 3 teeth on the upper jaw, and only 1 is visible on the lower.

It is difficult to determine the full extent of the bones of the dorsal surface. Only the left suture is visible, joining the maxillae and the premaxillae. The nasal opening is poorly preserved and the posterior processes of the pit are missing. The premaxillae are parted in the middle, causing a great rift in the nasal opening. The original

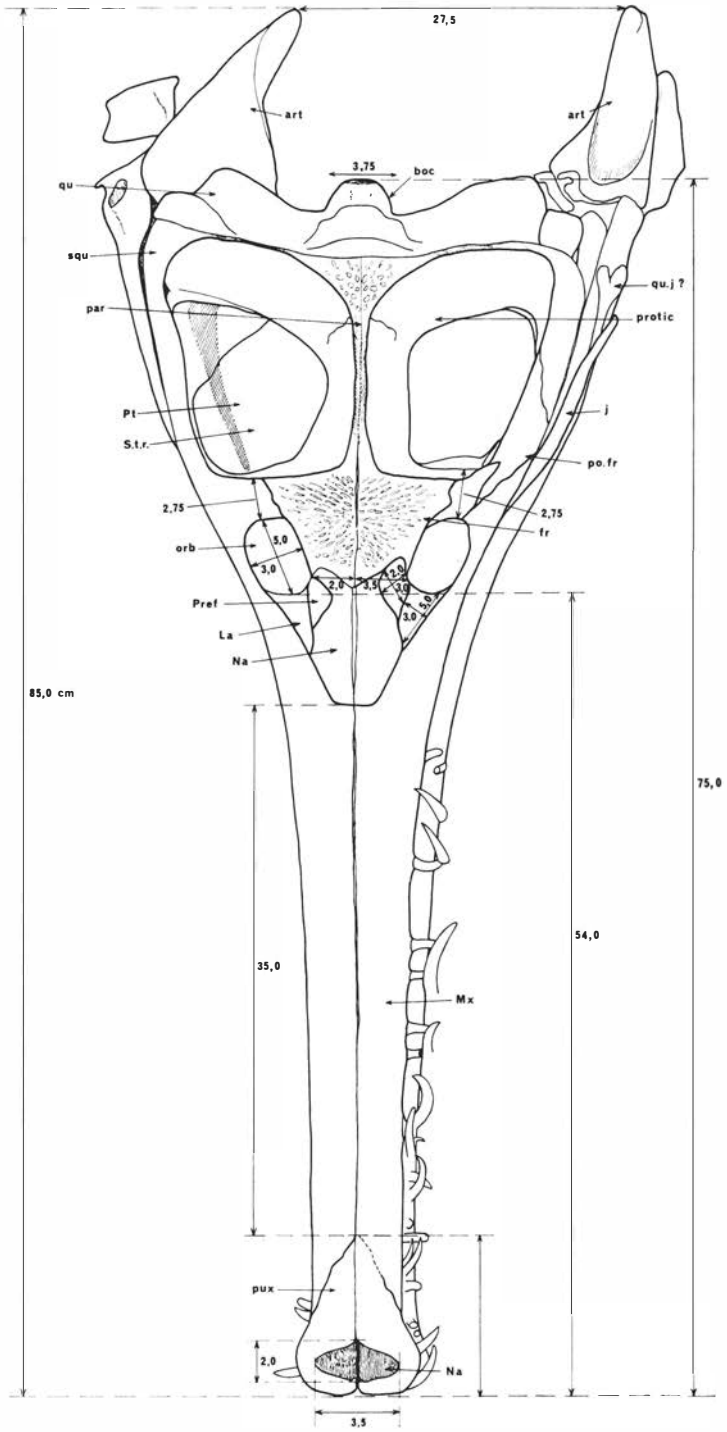

Fig. 3. A diagram of the dorsal view of the skull of *Steneosaurus bollensis* (R. 161). qu.j. — quadrojugular; j — jugular; po.fr. — postfrontal; fr — frontal; Mx — maxillae; pmx — premaxillae; Na. — nasal; prefr. — prefrontal; Orb. — orbitals; S.t.v. — supratemporal vacuity; Pt — pterygoids; par. — parietals; Squ. — squamosals; qu. — quadrates; boc. — basioccipitals; art. — articular.

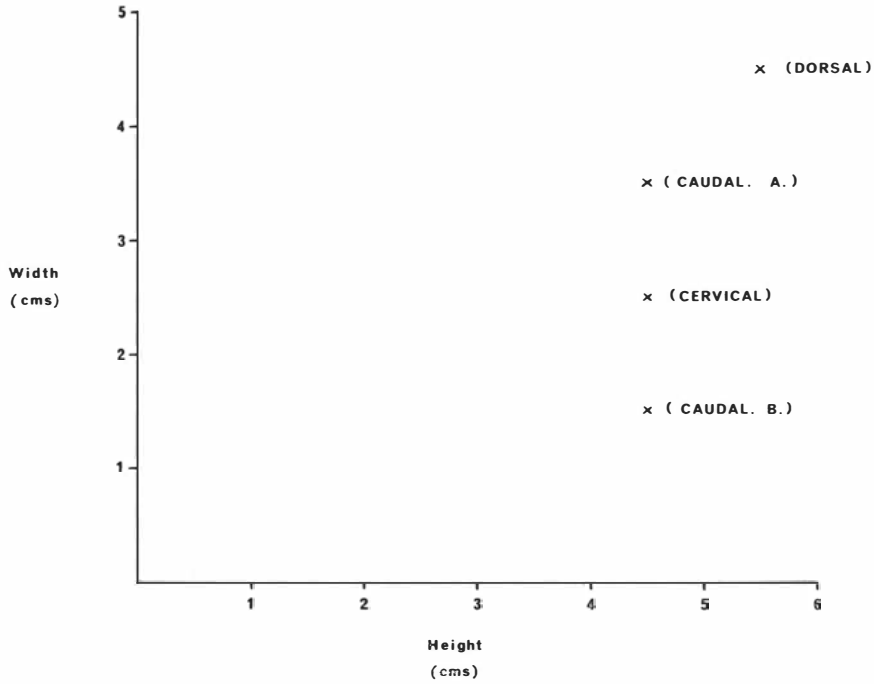

Fig. 4. A graph representing the height and width of the different groups of vertebrae from *Steneosaurus bollensis* (R. 161).

nasal openings can still be seen although not well.

The maxillae are present but the suture joining these to the postfrontals are obscured in the effects of displacement of the jaws. The convexity is not apparent across the snout owing the compression.

The *lachrymal*, *prefontals* and *nasals* are all ill-defined but just discernible; the anterior border to the nasals is not seen definitely, but there is a marked change from very smooth to a heavily pitted surface of the frontals around the region where the suture should be. The marked relief of the frontals radiates around a point at the centre of the bone on the median line, which is very marked here.

The suture joining the frontals to the post-frontals is, however, clearly seen owing to a crack that has occurred along this line of weakness during diagenesis.

The *supra-temporal vacuity* is sub-rectangular and the inner borders of each meet at the median ridge rising very sharply from the palatal surface of the skull. The *lateral-temporal vacuity* is not seen owing to the compression effects. The bones surrounding the supra-temporal vacuity are all present and clearly seen except for their sutures; where these have been seen they have been marked in on fig. 3. At the base of the supra-temporal vacuity, the *pterygoids* are seen and actually form the base.

On the left side on the specimen the displacement enables the *jugal* to be seen leading from the quadrate via a very fractured *quadro-jugal* to

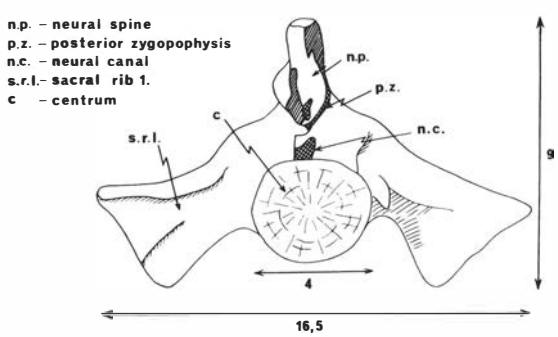

Fig. 5. The first sacral vertebra from *Steneosaurus bollensis* (R. 161). sr. 1 — sacral rib 1.

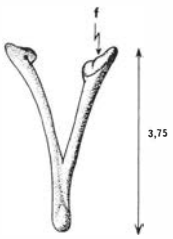

Fig. 6. The 23rd caudal vertebra from *Steneosaurus bollensis* (R. 161). f — facet for articulation with the caudal vertebrae.

a very obscure region to the left of the orbits — presumably once leading to the *lachrymal.*

The *postfrontal* leading from the frontals are clearly seen to join with the squamosals on the right side, but on the left the suture is very indistinct. The *squamosals* are very well preserved and comparatively unaffected by compression; they join with the parietal which is equally well preserved with the upper surface being characteristically triangular and heavily pitted.

Below the squamosals are the *quadrates* and the *occipital.* The left quadrate is rather limited in extent but the right is well exposed on the dorsal surface. The occipital has a very well preserved condyle which is in close proximity to the atlas vertebra; the *foramen magnum* is not seen. Owing to the ventral surface being out of view, the *exoccipitals* and the *basisphenoids* are not seen.

Vertebrae (Pl. V, figs. 2, 3, 4, 5, 6, & text-figs. 4, 5, 6, 7). — All the vertebrae are lying on their side — mostly to the left of the vertebral column — but are relatively unaffected by compression.

The column is almost complete with 50 vertebrae excluding the atlas and axis, which are fused; of the 50, 9 are cervical, 14 are thoracic-lumbar, 2 are sacral, and 25 are caudal with possibly 10—15 caudals missing.

The atlas and axis are in a position which is difficult to examine properly, but the rib of the atlas is clearly seen along with the anterior wedge bone. The arch of the atlas and axis are very obscure and their crests are absent.

The *cervical vertebrae* are all present but leaning over to the left with the neural spines parallel to the surface of the rock matrix. On the other side of the column, opposite to the neural spines, are 8 cervical ribs more or less in their original position these are characteristically hammer-shaped with one "head" thicker than the other. The vertebrae themselves are very well preserved, with the posterior and anterior zygopophyses complete and interlocking with each other. The propophysial and diapophysial processes are present but are fractured near the base and thus do not show the surface for articulation with the cervical ribs. As is characteristic with the rest of the vertebral column, the ends of the centra are biconcave.

The *thoracic-lumbar* vertebrae follow on from the cervicals without a break in line, and these too have their neural spines lying on the left side of the column. Again the same criteria for distinguishing the cervical from the dorsal is used here as for the *Metriorhynchus superciliosum* (see specimen R. 170): whether the lateral processes are on the neural spine instead of on the centrum. Both of these processes are very clear on the right side — facing directly upwards, but are fractured before the articular facets are seen. The preservation of the lateral processes is much better in the anterior dorsals showing a greater curvature, although this may well be due to compression. The lateral processes nearer the sacrum have been fractured much nearer the base and so it is difficult to say

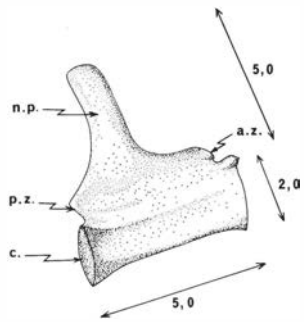

Fig. 7. A chevron vertebra from the 12th caudal vertebra from *Steneosaurus bollensis* (R. 161). (see fig. 2 for abbreviations).

whether the processes were curved or not. The posterior and anterior zygopophyses are again very well preserved and are in their positions as in life, interconnecting with each other.

On the first few dorsals, the neural spine is obscured by scutes, but for the most part the neural spine can be fully seen, showing that they are complete. The centra are very constricted at the centre having deep biconcave ends. The neural spines are very broad and allow for very little reverse flexure of the backbone. There are a number of bony scutes having no surface relief, lying in line with the neural spines and it appears that these may well have formed some type of dorsal ridge in the living animal, as an extension of the spinal ridge.

The two *sacral vertebrae* are the only vertebrae which are not in position, lying out to the right of the specimen. The first sacral has been displaced so that a very good view of the axial or posterior surface is seen. The transverse processes are very well preserved and complete, showing the articulation for the sacral ribs. The neural canal is visible and is almost totally undistorted. The anterior zygopophyses too are in very good condition although a little chipped. From this position, very little can be said about the neural spine except that it is complete and its measurements have been recorded. The second sacral is very fragmentary and no details can be brought from it. The centra are quite round with perhaps a slight vertical expression.

The *caudal vertebrae* are complete except for the posterior 10 to 15, and form a continuous series with the zygopophyses fitting into each other very closely. Only the latter few have been disturbed from the original position. Anteriorly, the caudals seem to be complete, but the anterior-most is in a poor state of preservation with just the centrum remaining. The chevrons for the most part are present although none are in their original position except two which are very nearly so. The articulation facets for the chevrons on the posterior of each centrum are not well preserved. The neural spines of the anterior caudals have a form very similar to those of the dorsals, although not quite as wide; the posterior caudals have very long and thin spines. An intermediary type lies between the two with thick spines but they tend to slope back a little. The centra are constricted about the centre, but appear to be more constricted in a vertically than horizontally, giving a flattened appearance.

The caudal rib on each vertebra is broken off near the base, but they all stem from the centrum in each case as in the cervicals. The ribs are missing in the posterior caudals having been decreasing from the anterior back.

The fore limbs and pectoral girdle (Pl. VI, fig. 3, & text-fig. 8). — The *pectoral girdle* is displaced from the vertebral column but it has remained intact within itself, and the fore limb is also attached correctly. The girdle and limb are characteristically very small and form the main body of evidence that the steneosaurs were aquatic animals, since so small a limb could not possibly support an animal with such a head.

The right limb is complete and its relation to the pectoral girdle is clearly seen, while the left limb only shows the radius, ulna and the tarsals and metatarsals.

The left *coracoid* is just visible and is 13.5 cm long; there is a small gap to the right coracoid where the vertebral column should lie. The right coracoid also has a length of 13.5 cm and the diameter at the neck is 1.5 cm. This bone is extremely well preserved with the distal and proximal surfaces showing few signs of wear. On the right anterior edge there is a pronounced ridge which disappears at the neck, and opposite this ridge, on the posterior edge, lies the glenoid fossa which is partially obscured by the scapula which is articulating in it.

The *scapula* is 12 cm long, but is not quite so well preserved, although all the major features are present. This bone has rather a curious shape: the proximal ends is quite as one would expect — dilated at the articulation surface then narrowing to a thin neck — but at the centre, the bone abruptly widens on the one side and this width is maintained to the distal end.

The length of the *humerus* is 17.5 cm. It underlies the scapula and is thus partially obscured. The head does not quite articulate with the scapula

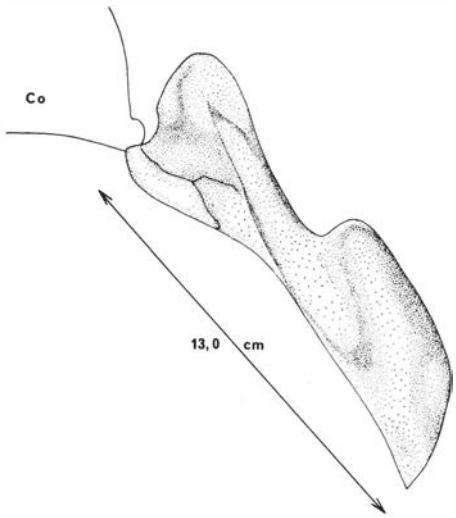

Fig. 8. The right scapula of *Steneosaurus bollensis* (R. 161).

or the coracoid since compression has displaced it a little. The articulation surface of the head is well preserved and quite smooth as it is also at the distal end. The deltoid crest is seen, and the ridge which as in other specimens, runs down from the head. The degree of expansion in the head is unfortunately obscured, but from what is seen he head is certainly not as big as in *S. durobrivensis* (Andrews).

The *radius* and *ulna* lie together at what appears to be a rather sharp angle into the humerus. The ulna is characteristically thickened at the proximal end curving to the much thinner distal end. The direct length of this bone is 11.5 cm. The proximal articulation surface is very well preserved and is partially obscured by the humerus with which it is articulating. The shaft steadily thins and does not thicken at the distal end. The radius forms a straight shaft with a slight expansion at either end for the articulating surfaces. This bone is 10.0 cm long. The radius and ulna on the left side are of similar structure and the same dimensions.

Only one *carpal* is present, the ulnare, which is equivalent to the calcaneus of the hind limb. The carpals of the left limb are slightly better preserved with the radiale, ulnare and pistaforme complete and in their original position. The metacarpals are less perfectly preserved on this side, but are in their exact position and are more complete. The last phalanx is only preserved on the last two digits and absent on the rest. Again, the metacarpals may be summarized thus:

Dig. I — 2; Dig. II — 4; Dig. III — 4; Dig. IV — 4; Dig. V — 3.

The digits are nearly complete but are a little disjointed in positioning. The bones themselves are all very well preserved and the facets at each end are clearly seen. Only on the right hind limb are these well enough preserved to be described. The end phalange on digit 2 is very small and appears to have had no functional significance in life. The end phalange on digit 3 is sub-conical and slightly curved and a little larger than phalange 3. The end phalange on the 4th digit is more elongated than that of the 3rd digit, but still has a conical tip. The end phalange on digit 5 is the longest of these phalanges, again being sub-conical.

These distal phalanges due to their sub-conical shape may be regarded as claws. However, the inconsistency in size makes this a little doubtful, since phalanges 3 and 5 would be well adapted for 'clawing', but not so phalange 1 and 2. It is possible that this arrangement has been developed for an aquatic mode of life. However, a specific study of contemporary aquatic fauna and hydrodynamic models would be required to verify this. The completeness may be represented thus:

Dig. I — 3; Dig. II — 4; Dig. III — 4; Dig. IV — 4; Dig. V — 2.

Pelvic girdle and Hind limbs (Pl. VI, figs. 1, 2, & text-fig. 9). — The pelvic girdle is unfortunately obscured by the sacral vertebrae, scutes and ribs, and all that can be seen is the posterior part of the ischium with the symphysis clearly showing. The head of the femur is also obscured by the sacral vertebrae, but the main part of the shaft is seen and is well preserved. This bone is 31.0 cm long measured directly. Towards the distal end the bone becomes quite flattened, and at the tip the articular facet for the tibia and fibula forms a distinct lip curling back.

The tibia and fibula are both present although the tibia is largely obscured by the fibula. They

Table III. Measurements of metatarsal and phalanx:

Metatarsal	Phalanx		
I	1	—	11.5 cm
I	2	—	3.0 cm
I	3	—	2.0 cm
II	1	—	13.0 cm
II	2	—	3.5 cm
II	3	—	1.5 cm
II	4	—	2.0 cm
III	1	—	13.0 cm
III	2	—	4.0 cm
III	3	—	2.0 cm
III	4	—	1.5 cm
III	5	—	1.0 cm
IV	1	—	11.5 cm
IV	2	—	4.0 cm
IV	3	—	1.5 cm
IV	4	—	1.0 cm
IV	5	—	0.5 cm
V	1	—	2.0 cm

are both in contact with the femur and the tarsals as in life.

The tarsals are complete and in their correct position. The astragalus lies directly between the tibia and the 1st metatarsal, and the calcaneus lies between the fibula and the cuboid which in turn leads to the 4th and 5th metatarsals. The 5th digit is vestigial consisting of only 1 metatarsal. The primary metatarsals of the first phalanges are elongated out of proportion to the remaining phalanges. The end phalanx is present in all digits. The pes may be summarised thus:

Dig. I — 3; Dig. II — 4; Dig. III — 4; Dig. IV — 4; Dig. V — 2.

On the left side, the only parts of the hind limb showing are the digits, the rest being obscured by the vertebrae and the scutes. The metarsals and phalanges are all aligned very close together and are not well preserved; it would probably be more accurate to use the figures from the right side than to try and take measurements. Percentage ratios for some of the measures are displayed in Table IV.

The scutes (Pl. IV; Pl. V, figs. 3, 4, 6). — The scutes or dermal armour are bony plates which during life covered the animal. These have been preserved well and are abundant, and some are still in their original position.

Dorsal scutes. These have a characteristically deep honeycombed pattern on their surface and are generally square or subrectangular in shape. The size varies from the smallest (maximum length of 4.5 cm) in the cervical region, to the largest in the mid-dorsal region which are 7.0 cm long. Those of the caudal region are of similar size to those of the cervical region.

There is a slight variation in pattern: the anterior scutes have thicker inter-comb walls and the shape of the combs more circular. The posterior scutes have much larger pits and thinner adjoining walls; the shape varies from circular at the centre to a greatly elongated shape at the sides radiating outwards. The scutes from the dorsal region are intermediary.

There is one very prominent feature in all the dorsal scutes, namely, a longitudinal ridge. In the anterior scutes, this is present only as a configuration in the pattern, but posteriorly this develops into a ridge which culminates at the tail (beside caudal 15) to a ridge 1.0 cm high.

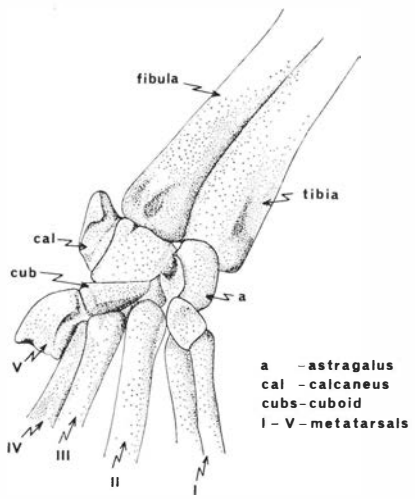

Fig. 9. The metatarsals of the right hind limb from *Steneosaurus bollensis* (R. 161). a— astragalus; cal. — calcaneus; cub. — cuboid; I—V. — metatarsals.

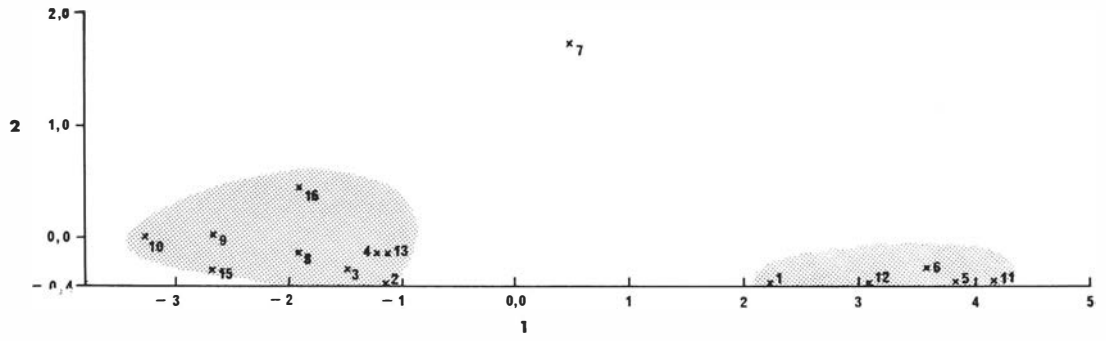

Fig. 10. A plot of the first and second transformed variables indicating size variations.

Table IV. Some significant ratios from *Steneosaurus bollensis*:

I. Skull length — 75.0 cm. Humerus length — 17.5 cm:

$$\frac{17.5}{75.0} \cdot 100 = 23.3\ \%.$$

II. Skull length as percentage of the femur length (31.0 cm):

$$\frac{31.0}{75.0} \cdot 100 = 41.3\ \%.$$

III. Skull length as a percentage of the ulna length (11.5 cm):

$$\frac{11.5}{75.0} \cdot 100 = 15.3\ \%.$$

IV. Skull length as a percentage of the tibia length (17.0 cm):

$$\frac{17.0}{75.0} \cdot 100 = 22.6\ \%.$$

and ulna length as a percentage of the tibia length:

$$\frac{11.5}{75.0} \cdot 100 = 68.2\ \%.$$

V. Skull length as a percentage of the cervical and dorsal vertebrae (156.0 cm):

$$\frac{75.0}{156.0} \cdot 100 = 48.2\ \%.$$

VI. Femur length as a percentage of the humerus length:

$$\frac{17.5}{31.0} \cdot 100 = 56.5\ \%.$$

VII. Tibia length as a percentage of the fibia length (17.0 cm):

$$\frac{17.0}{17.0} \cdot 100 = 100\ \%.$$

All the dorsal scutes lie to the left of the specimen except for 15 which lie to the right of the tail in perfect line.

Ventral scutes. These have a totally different form and have no pattern on their surface to speak of. They are rectangular in shape with curving sides, and are attached by sutures which can be clearly seen. These remain only between the limbs and lie to the right of the specimen.

STATISTICAL ANALYSIS

Westphal (1962) gave a great deal of information about a number of specimens of *Steneosaurus bollensis* which were used to compare similar measurements from the Uppsala specimen. Having assimilated all Westphal's information in one table, measurements that were regarded as being significant for all species involved were then subjected to a statistical analysis which would indicate any variation in vectors of size and shape. The statistical procedure used was a multivariate one, and although in theory it is ideal, in practice this procedure may be subjected to many factors which are maximal in paleontology (differential changes in the specimens during diagenesis for example). However, seven variables in the body dimensions were taken as follows: x_1 = skull length, x_2 = length of backbone (cervical and thoracic-lumbar), x_3 = length of the orbit, x_4 = width of the orbit, x_5 = length of the humerus, x_6 = length of the

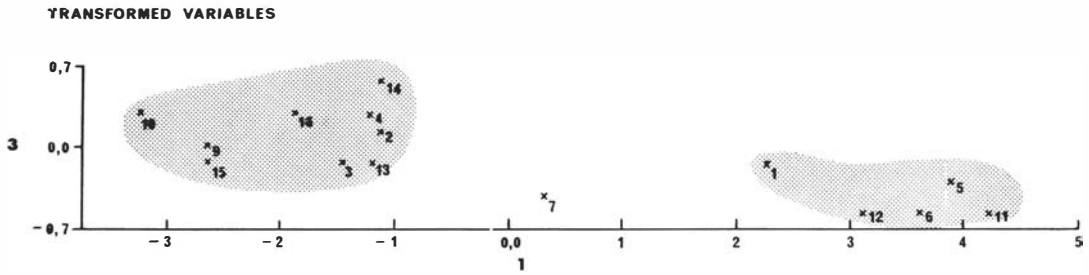

Fig. 11. A similar plot to fig. 10 using the first and third transformed variables indicating different size variations.

femur, and x_7 = the length of the rostrum (distance from the tip of the snout to the line across the skull at the anterior of the orbits). Sixteen specimens were taken including the Uppsala specimen (see appendix), and the relevant statistics calculated. From this a correlation matrix was obtained. The correlations are clearly very high, and they are highly significant. Using the variances and covariances, the three principal components shown in Table V were separated out.

The first principal component represents a pure size variation vector; here there is an almost equal contribution of all variables. The second principal component represents a shape variation vector; the variables x_3 and x_4 vary together against the rest. The third principal component represents another shape variation vector, and in this case variables x_3 and x_4 are in a negative association.

These eigenvectors were then transformed into variables shown in Table VI which the computer then plotted (Figs. 10, 11, 12). Plot 1 is a plot of transformed variable 1 against transformed variable 2, which indicates largely variation in size. Plot 2 was formed using transformed variables 1 and 3, and Plot 3 was made using transformed variables 2 and 3. Plot 2 is another plot of size, but Plot 3 shows the variation in shape.

The results are clearly very significant. Plots 1 and 2 show two distinct clusters of specimens with one on its own between them. The Uppsala specimen lies in the cluster to the left, the one which in both cases indicates a larger size (for the parameters taken) than the cluster to the right. One would infer, that this is some indication of sexual dimorphism — those on the right being females, and those on the left being males. How-

Table V. The first three principal components of the covariance matrix:

	Eigenvectors		
	1.	2.	3.
x_1	0.372	0.241	0.296
x_2	0.364	0.289	−0.158
x_3	0.292	−0.380	0.693
x_4	0.465	−0.742	−0.393
x_5	0.359	0.207	−0.203
x_6	0.392	0.264	−0.316
x_7	0.376	0.219	0.330

Table VI. *Transformed variables:*

2.330	−0.310	−0.093
−1.076	−0.054	0.174
−1.421	−0.146	−0.056
−1.176	−0.054	0.281
3.926	−0.374	−0.186
3.682	−0.255	−0.421
0.413	1.554	−0.351
−1.797	−0.000	0.303
−2.591	0.059	0.010
−3.152	−0.106	0.326
4.218	−0.369	−0.429
3.184	−0.277	−0.451
−1.149	−0.000	−0.136
−1.034	−0.263	0.686
−2.534	0.141	−0.008
−1.820	0.529	0.353

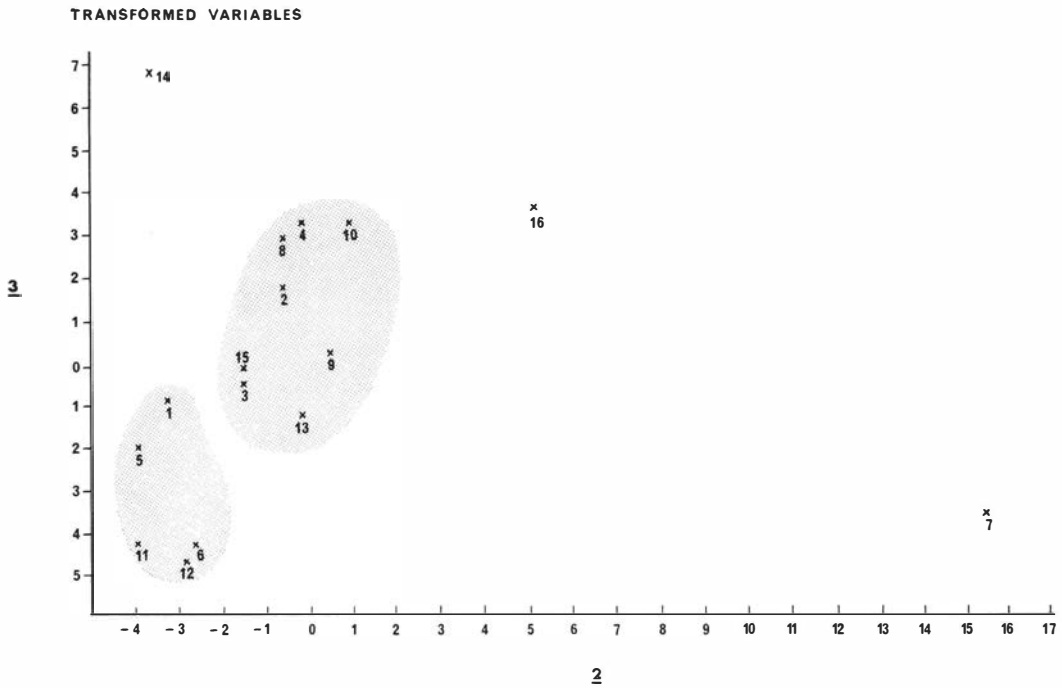

Fig.12. A plot of the second and third transformed variables of principal components indicating shape variations.

ever, one must not forget that this (and other) types of statistical analysis purely represent information in such a way as to show any significances more clearly that in any other way. So it is a pure assumption, but a reasonable one, that these distinct clusters are due to sexual differences. The individual that is lying in between is a problem: it may be a juvenile male, which seems most likely, but it may be a separate species (or genus). Plot 3 is an indication of shape variation, and here again two clusters are seen although not so distinctly: the females here are in the bottom left corner and the males to the upper right. Our juvenile is again very different from the rest, lying over to the far right. The Uppsala specimen does not fit in here so well and appears to have a shape tending a little towards that of a juvenile. This is an interesting case, where shape acts as an independent variable of size. This is the only evidence that the specimen may not in fact belong to *Steneosaurus*, but *Mystriosaurus*, but it is insufficient to be regarded as decisive.

DISCUSSION

All these specimens have been well preserved and have been valuable in supplying additional details of these two crocodilian families. The Metriorhynchides have, however, only been of use as regards their anatomical detail which is already well known, but little can be deduced as regards their environment. We can derive a mode of living from a study of functional morphology (relative size and strength of the girdles and limbs, and the downward flexure of the tail as adaptations for an aquatic life) but the conditions of the environment have left no evidence in these specimens. The *Steneosaurus* however, being preserved and mounted in the original rock matrix in which it was deposited, allows something of prevailing conditions to be seen. Firstly, the most striking feature is the contorted position of the crocodile, which becomes more striking the closer one looks. This position may be seen as the result of post-mortem contractions of the muscles and ligaments,

but the positioning of the limbs and the fact that the neural spines of the vertebral column are all leaning over to one side along with the general position makes me think this is not the only reason. I see this as a deposition in a medium speed current (a fast current would wash the specimen away, while a slow current would show no effect) originating from the top right of the specimen (unfortunately, the orientation was not recorded when excavated). The sediments are shown to be definitely marine by the presence of a perisphinctid ammonite (Pl. VI, fig. 4), although confirmation by a geochemical analysis might be more satisfactory. A small bivalve is also present, but is insignificant, except that it is on the right side and is probably allochthonous.

The statistical analysis shows clearly the synonymy between *Steneosaurus bollensis* and *Mystriosaurus bollensis* (a synonymy which probably includes eleven species) that was set up by enthusiastic workers during the latter part of the nineteenth century. Hence the name *Steneosaurus bollensis* has been retained in favour of *Mystriosaurus bollensis*, as it has priority.

Clearly, more research is required to elucidate the detailed taxonomy of the teleosaurs (using a similar treatment to that used above) before work can begin on investigating the phylogeny of the Crocodilia.

APPENDIX

Information on specimens extracted from Westphal (1962) used in the statistical analysis for comparison with the Uppsala specimen:

1. Tübingen Re 1193/12. 2. Freiburg, Geologisches Landesamt. 3. London R. 3937. 4. Tübingen Re 1193/1. 5. Stuttgart 10000. 6. Holzmaden 38a. 7. Winterthur A. 8. Frankfurt SMF R 454. 9. Berlin 1921 Nr 1. 10. Tübingen Re 1193/3. 11. Berlin 1931 Nr 4. 12. Stuttgart 15391. 13. Holzmaden 68. 14. London 14792. 15. Tübingen 1193/2.

The numbers by the side correspond to the numbers by the plots in figures 10, 11, and 12.

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PLATES

Plate I

Metriorhynchus superciliosum (R. 165).

1. Dorsal surface of entire skull. (× 0.3)
2. Posterior right mandible — interior surface. (× 0.4)
3. Posterior left mandible — interior surface. (× 0.4)
4. Palatal view of the posterior part of the skull. (× 0.75)

Plate II

Metriorhynchus superciliosum (R. 170).

1. Dorsal surface of entire skull. (× 0.2)
2. A close up of the dorsal surface of the frontals. (× 0.5)
3. The interior surface of the left and right mandibles. (× 0.3)
4. The exterior surface of the left and right mandibles. (× 0.3)

Plate III

Metriorhynchus superciliosum (R. 170).

1. A stereopair of the interior facet of the articular of the left mandible.
2. A stereopair of the interior facet of the articular of right mandible.
3. A stereopair of a tooth of the left mandible.
4. Showing the cervical vertebrae and the pectoral girdle (× 0.3)
5. Showing the flexure in the tail at the 24th to the 29th caudal vertebrae. (× 0.5)
6. The right coracoid. (× 0.75)

Plate IV

Steneosaurus bollensis (R. 161).

Showing the entire specimen. (× 0.1)

Plate V

Steneosaurus bollensis (R. 161).

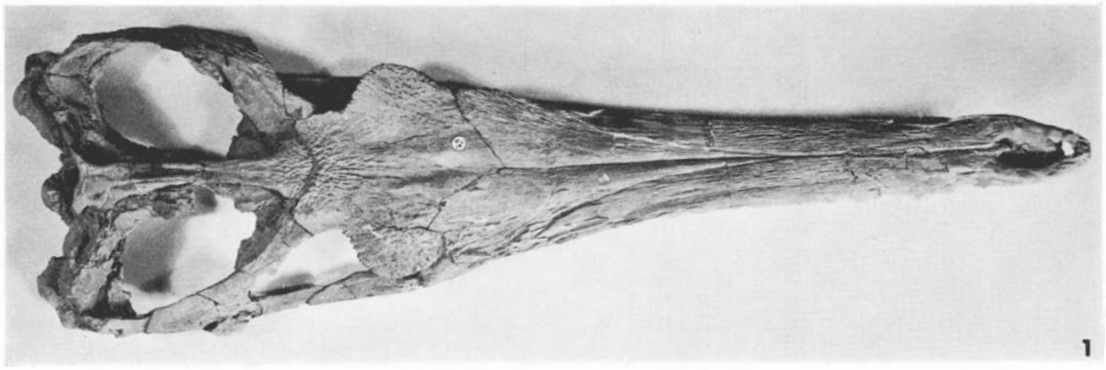
1. Anterior tip of the snout showing the nasal pit. (× 1.0)
2. Posterior of the skull and the cervical vertebrae. (× 0.3)
3. The right forelimb also showing the dorsal and ventral scutes and the ribs. (× 0.3)
4. The dorsal vertebrae with the dorsal and ventral scutes, also showing the preserved stomach contents. (× 0.3)
5. The first sacral vertebrae also showing an impression of a bivalve shell in the top right corner. (× 0.75)
6. The caudal vertebrae with chevrons. (× 1.0)

Plate VI

Steneosaurus bollensis (R. 161).

1. The femur, tibia and fibular of the right hind limb. (× 0.4)
2. The pes of the right hind limb. (× 0.4)
3. Left manus. (× 1.0)
4. A perisphinctid ammonite found with the specimen. (× 1.0)

Plate I



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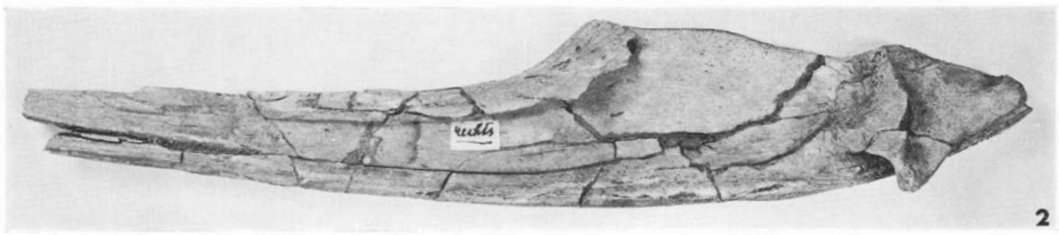

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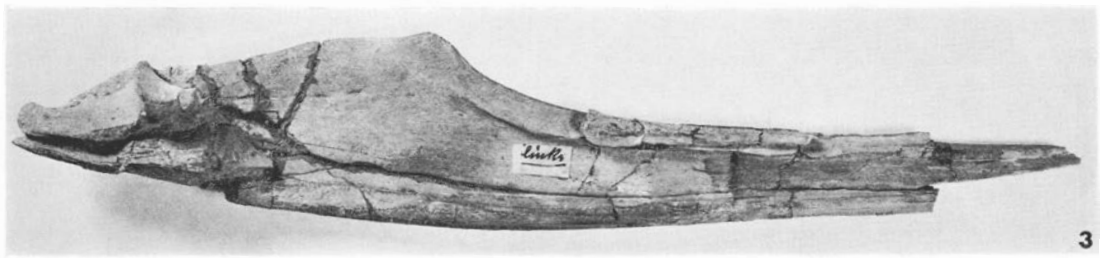

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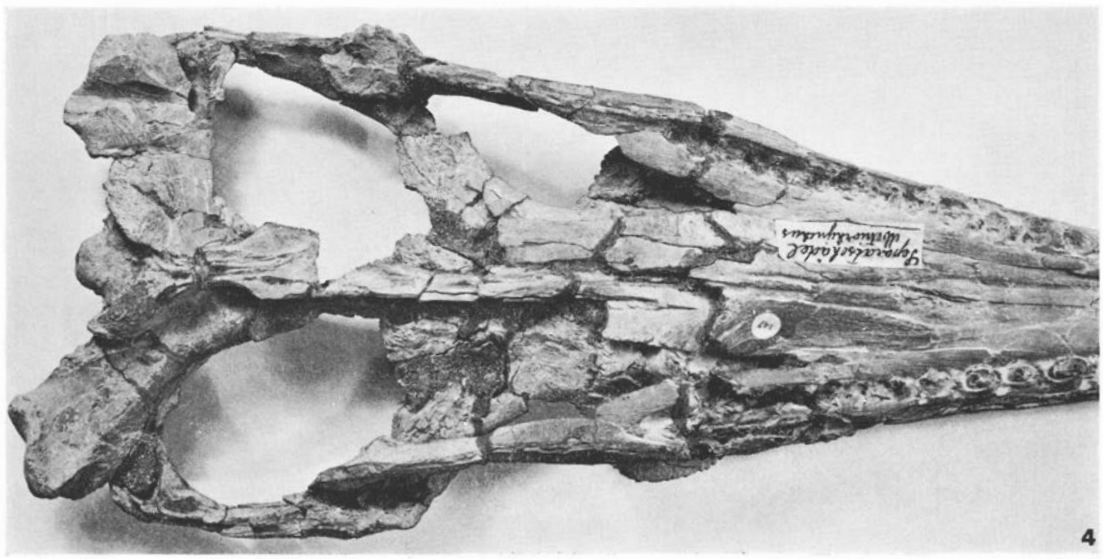

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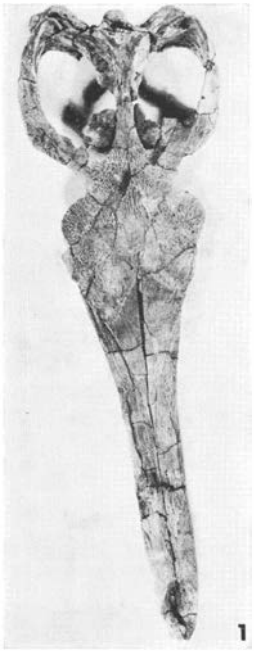

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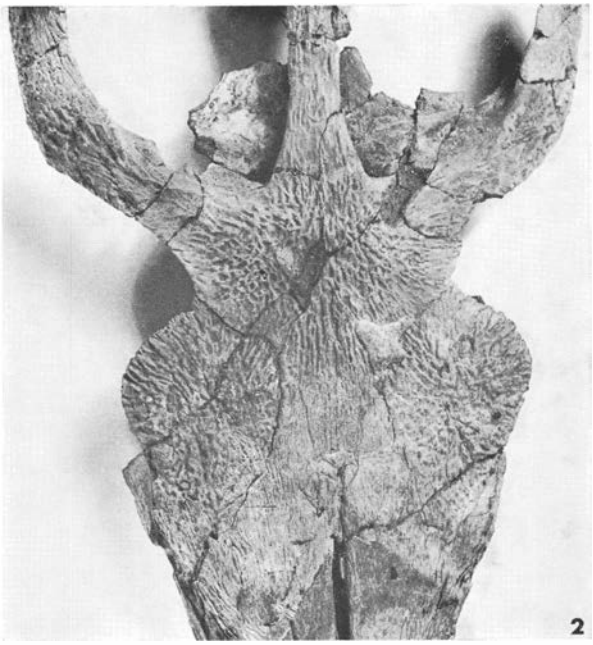

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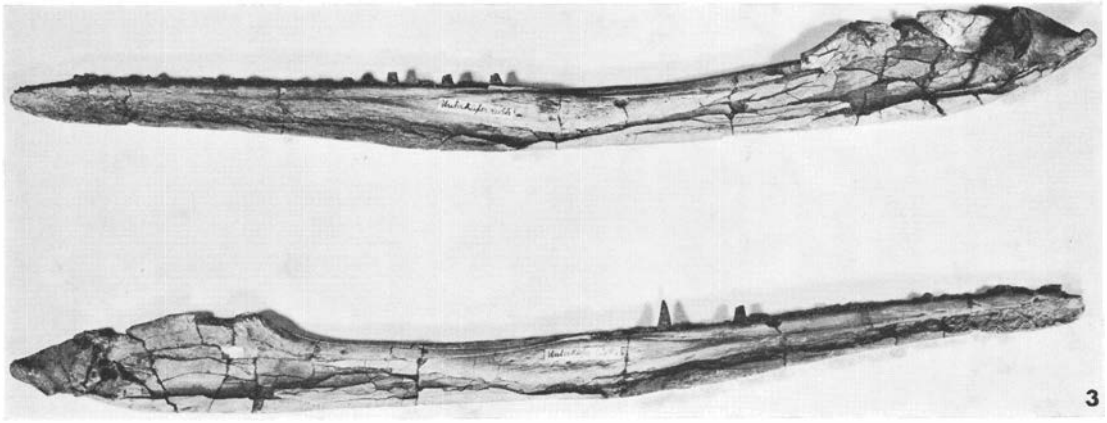

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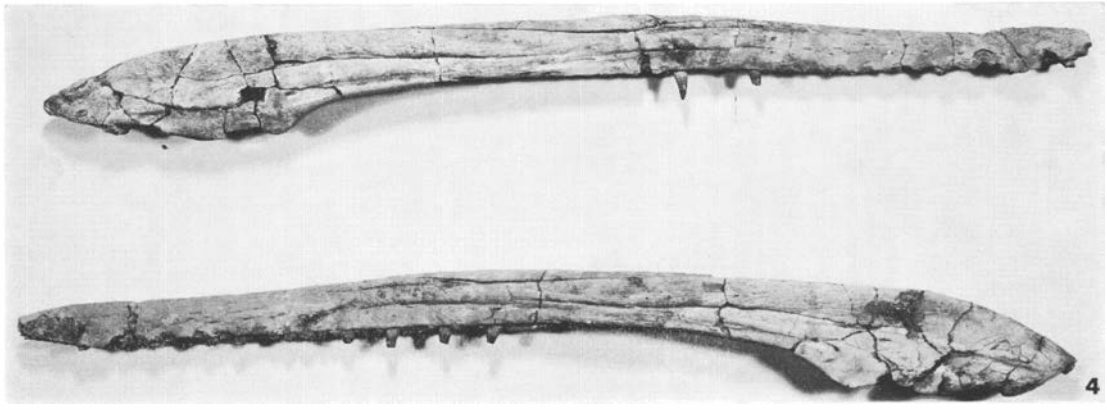

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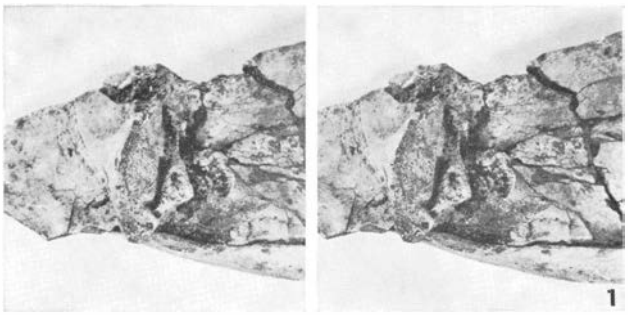
Plate III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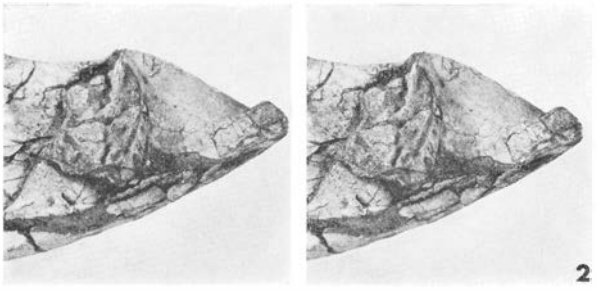
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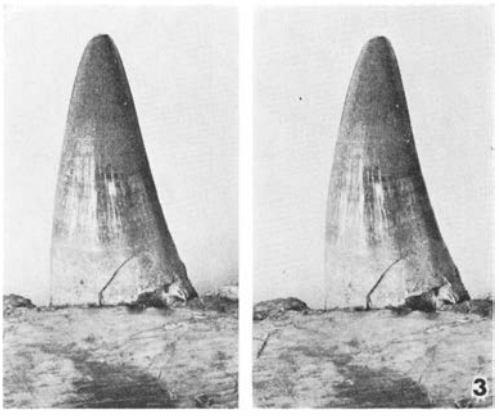
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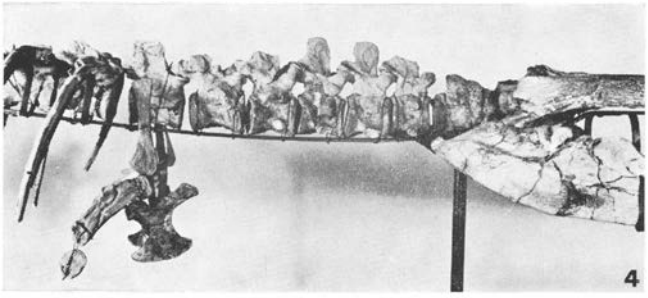
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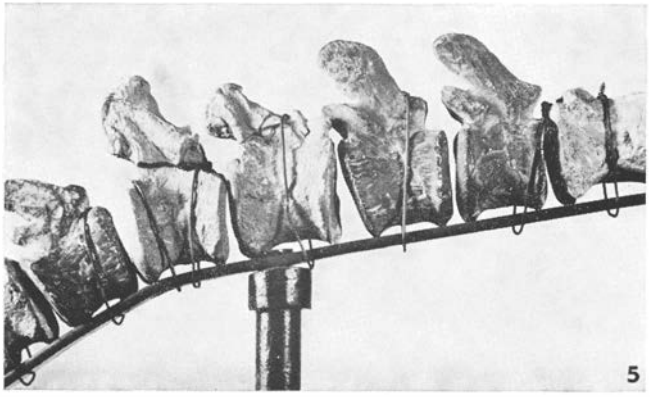
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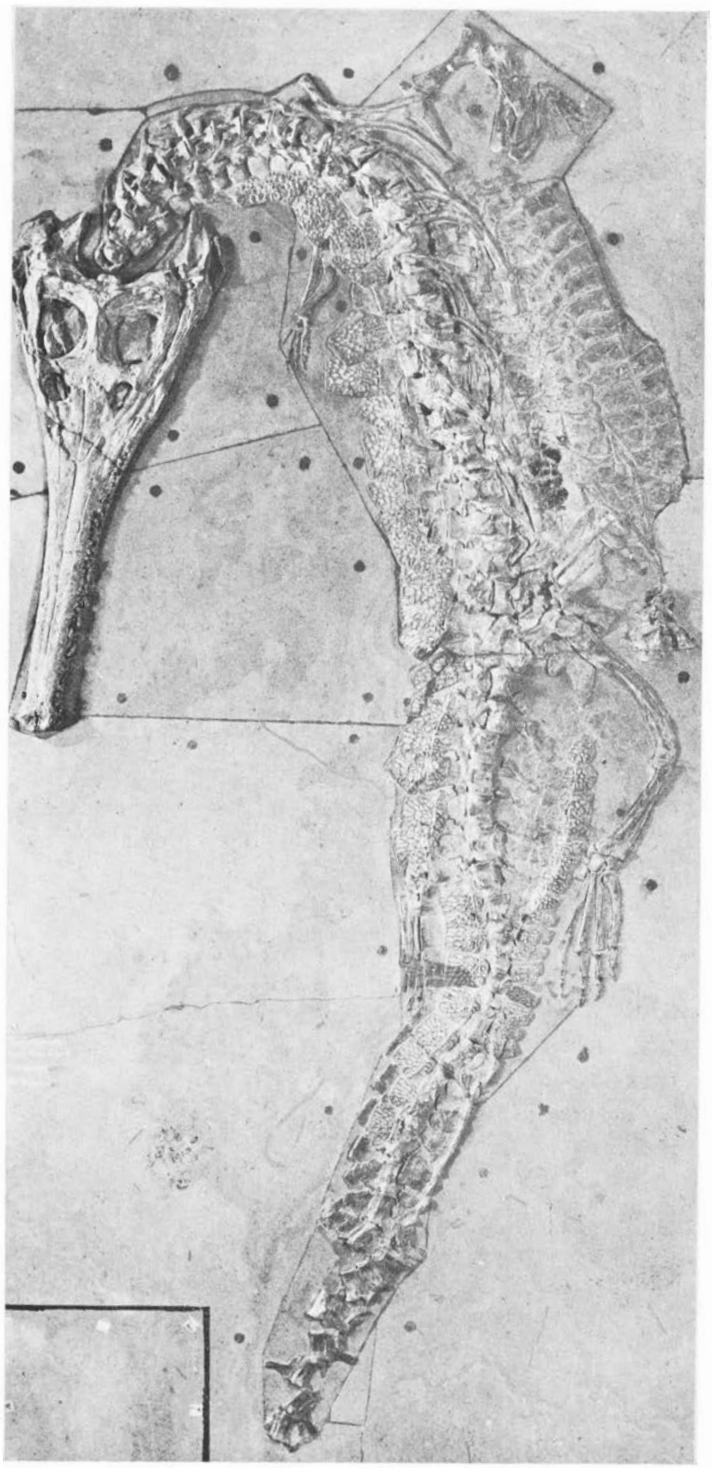

Plate V