# On the occiput of *Megalosaurus* from Stonesfield[*].

by

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with 1 plate and 4 figures in the text.

translated by Michael Benton
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When I was in Oxford in summer 1901, to see the dinosaur remains preserved there, a skull piece struck me which belongs to the series of described *Megalosaurus* remains from the Dogger of Stonesfield, but to my knowledge hitherto not described anywhere. The specimen hitherto does not seem to have been noticed. At my request, Mr. Prof. SOLLAS was kind enough to have a cast of this specimen made which arrived at the Geological Institute of Tübingen as an exchange. The cast is so good that a description can be based easily on it. Besides I made drawings of the original in Oxford.

The occiput specimen is not only the only one of *Megalosaurus* and interesting in this respect, but it is also one of the few pieces which displays the structure of the braincase and the position of the large nerve and vessel openings in the Dinosauria in an excellent way. In this lies the great value of this otherwise so fragmentary specimen.

The occiput is preserved in a right and a left half, which still fit together exactly. They are completely free of stone. The parts bordering the braincase are present from the sella turcica and

[*] Original citation: Huene, F. v. 1906. Über das Hinterhaupt von *Megalosaurus bucklandi* aus Stonesfield. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1906(I):1-12. Typset for the Polyglot Paleontologist (http://www.uhmc.sunysb.edu/anatomicalsci/paleo) by M. Carrano, January 2001.

the orbital fissure backward to the foramen magnum. The base of the occiput is certainly damaged, while the basioccipital and basisphenoid are broken through horizontally and no longer show the lower upper surface; also the condyle is broken off in this way. Both exoccipital processes and the left squamosal are present; above, the supraoccipital and parietal form the termination.

The f o r a m e n m a g n u m has a width of 3-1/2 cm and a height of 4 cm. The lower or condylar edge projects at least 2 cm backward. Bone sutures are not recognizable in the whole piece but to conclude from other theropod skulls (e.g. *Creosaurus* and the skulls of' *Thecodontosaurus* and *Plateosaurus* to be described by me), the foramen magnum must be bordered below in a small piece by the basioccipital, indeed a part below and all the sides must be formed from the exoccipitals; whether the exoccipitals meet above as in *Creosaurus* or whether the supraoccipital extends narrowly into the foramen is not to be distinguished in the lack of visible sutures, but the former seems more likely.

The e x o c c i p i t a l p r o c e s s e s are not complete, but are only preserved in a length of 5-1/2 and 6-1/2 cm. They are in their root over 5 cm high, but thin; they extend rather downward and backward.

The o c c i p u t r o o f is directed rather steeply upward above the foramen magnum. In the middle is found a hump-like elevation, whose highest point lies 5 cm above the edge of the occiput opening. It is elevated 2 cm above its surrounding, has a length of 5 cm and a breadth of 3-12 cm, it passes backward into a short median ridge becoming lower. To both sides of the latter are found depressions, also beside the highest elevation and a single median one in front of it. This hump is in any case formed from the s u p r a o c c i p i t a l ; the bone extends scarcely further sideways and particularly forward than the elevation. The parts in front and also in the anterior half beside the hump are in any case formed from the parietals.

Beside the elevation of the supraoccipital arises the high, but narrow process of the p a r i e t a l and s q u a m o s a l . It is at its base 5 cm broad and barely 2 cm thick, later only 1/2 cm thick. The surface is backward-concave above, swollen-convex toward the opposite side. The attachment of the squamosal runs oblique from the upper end of the exoccipital upward and forward. Measured on that upper edge the process is only preserved 6 cm long, the rest of the squamosal is absent. The distal half of the process curves rather forward and shows thus the border of the u p p e r t e m p o r a l f o s s a . This was long and narrow with the longitudinal extent in a transverse direction. They cannot have measured much over 6 cm and the breadth measured 3-4

cm, for one sees the bone again swell far forward above the foramen ovale and thus the anterior border of the upper temporal fossa begins. The separate elements unfortunately cannot be sharply distinguished from each other any longer, since one sees no clear sutures; but from the foramen ovale on upward the prootic, epiotic, alisphenoid, and parietal take part in the structure of the bone wall and in the most anterior origin probably also the postfrontal. On the lest side one sees 3.2 cm above the upper edge of the foramen ovale and directly on the root of the squamosal a small round opening which I hold for the external auditory meatus (it is also found in the same place in *Plateosaurus* and *Thecodontosaurus*).

In front of the foramen ovale and at the same time on the anterior edge of the preserved skull part is found the (left) orbital fissure; it lacks the lower and the anterior edge except for a small piece above. The strip extends to 3 cm high above the sella turcica and is very narrow; for entirely above where the anterior edge is still preserved it is only 3 mm broad. The orbital fissure is intended for the passage of the optic nerve, but usually also the oculomotor and the first branch of the trigeminal pass through (ramus ophthalmicus), further perhaps the trochlear and the ophthalmic artery and vein[(1)]. The bone wall has on the posterior edge of the fissure a thickness of 2 cm; but the thickness of this septum between the fissure and the foramen ovale measures only 1 cm. Downward the fissure does not seem to be closed by bone (as also in *Plateosaurus*). It could be that the connective tissue lower closing was found 1 cm above the sella turcica, for here the bone is rough and elevated.

The foramen ovale is, as the name suggests, a perforation oval on the inside, 9 mm high and 8 mm broad, which serves as passage for the 2nd and 3rd branches of the trigeminus. Toward the outside the foramen expands more, particularly upward. Caudally from here still follow 6 larger and smaller foramina.

On the inside one sees only ca. 3 mm from the foramen ovale a small elongated opening; this is the fallopian canal, which lets the facial through; certainly on the outside the corresponding opening is obscure. It is either very small or not exposed or again it opens together with the succeeding jugular foramen; the latter is not at all unlikely, for in *Plateosaurus* both these openings are very close together on the outside.

Now two very large perforations close behind the inner entrance of the fallopian canal follow, namely the jugular foramen and the foramen lacerum; both are separated only by a thin

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(1) But these could also exit through another canal above the foramen ovale (see below).

bone column and pass through the wall directed obliquely backward. The jugular foramen opens on the outside with oval opening 5 mm broad and 10 mm high. The inner entrance lies right below the pyramid of the inner ear and cuts rather far into it above. The inner opening has the form of an oblique triangle with one edge directed downward, one upward, and one backward. The perforation is found only in the lower edge of this triangle. The internal auditory meatus is directed upward toward the pyramid, which is 12 mm broad above. Here a portion of the acoustic nerve ends, and probably also the eustachian tube passes through, coming from below from the bone, above this wide outer orifice of the inner ear. The jugular vein appears through the jugular foramen from the braincase outward.

The foramen lacerum is the largest of these foramina; it also enters deepest downward, i.e. into the region of the midline. Its form inside are outside is that of a right angle with rather irregularly curved sides, it is placed obliquely backward and upward so that an angle points right upward. The height of the foramen (diagonal direction of the right angle) measures 16 mm, the breadth 7 mm. The vagus, glossopharyngeus, and accessorius exit through the foramen lacerum.

Behind the foramen lacerum follow still three small foramina. One of these lies below at the top of the lower angle of the foramen lacerum, the second, also small, lies above beside the upper angle of the foramen lacerum, and the third, largest and placed furthest back, lies at the top between both and is only 1 cm from the edge of the foramen magnum. These are the openings on the inside. On the outside particularly the largest of these openings is clearly obvious, the canal runs rather upward and at the same time a little forward. This outer opening is visible particularly on the left side; it lies below the exoccipital process and extends on it for a short distance as a groove (XII' on the figure). On the right side one recognizes above this opening still a smaller one that ends on the posterior side of the exoccipital process; this becomes the upper canal of the inside. These two I hold for exit places of the two parts of the hypoglossus; the larger of the two foramina corresponds to the hypoglossus canal of most reptiles (XII'). Usually the hypoglossus has only a single exit place, but in Lacertilia two occur, e.g. in *Agama colonorum* DAUD.[1]; these two openings are present in *Plateosaurus* also. Now the third opening still remains, there seem to me to be two possibilities for its function; either the hypoglossus has three branches, which exit separated, or again—and this is the more probable case—the internal carotid enters by

[1] SIEBENROCK, *Sitz.-Ber. Akad. Wiss. Wien*. 104 I 1895, pl. I, 2.

this way and not through the canal of the vagus group (foramen lacerum). The outer opening is found below the large hypoglossus opening and close behind the posterior angle of the foramen lacerum. Indeed the opening is rather small for the carotid, but it may have belonged to it. If the carotid enters here, this displays a great approach to the characteristics in the Crocodilia, where the carotid also enters so deep and separates; also in many lizards the foramina of the hypoglossus, vagus, and carotid lie similarly close together.

These are the large nerve and vessel openings which lead out from the braincase toward the sides. But there is still a pair of foramina to be mentioned which are found on the floor of the braincase behind the sella turcica close together and on the same line with the internal aperture of the fallopian canal, which are the exit places of the abducens pair. There are small round openings 2 cm below the dorsum sellae turcicae; they run obliquely downward and end in the hypophyseal cavity 1/2 cm deeper than on the inside. The hypophyseal cavity is no longer preserved as a cavity, since its lateral and lower boundary is broken off, also nothing more of the presphenoid is preserved.

The lumen of the braincase above the sella turcica is 5.5 cm high and in the upper half 5 cm broad. In front of the auditory pyramid the upper part is the broader. From the pyramid on the skull roof falls off steeply to the foramen magnum and there the pyramid itself arises rather wide in the lumen of the braincase, so that from here on the upper part is constricted and only remains preserved below the width of the foramen magnum.

The floor of the braincase is smooth and quite level; no, median longitudinal ridge is to be observed as in *Plateosaurus*. The sides and roof of the braincase display more interesting details.

On the right side (i.e. only clearly preserved here) one sees on the upper edge of the inner entrance to the fallopian canal a small pore open from above; this I hold for the internal acoustic pore, in which a part of the acoustic enters; SIEBENROCK has described similar characteristics for *Lacerta simonyi* STEIND[1]; there a part of the cochlear ramus and a part of the vestibular ramus enter the auditory pyramid close above the facial opening, while one branch of each of these 2 rami also enters the vestibulum through the internal auditory meatus. Entirely similar features also seem to be present here in *Megalosaurus*. Above the entrance of the fallopian canal and the internal auditory meatus several very small pores are still visible on the right side. BRÜHL has observed the same in Crocodilia and suggests that they admitted smaller blood vessels

[1] *Sitz.-Ber. Akad. Wiss. Wien*. 103 1894, pl. III, 18.

into the vestibulum. About 10 mm from here on the anterior and lower edge of the pyramid is found a deep broad cavity with a steep posterior edge, which forms a curve open forward and arises sharp at the deepest place (right side) and thus probably also indicates an opening of the vestibulum. If one compares the descriptions of BRÜHL on Crocodilia and of SIEBENROCK on Lacertilia, it is probable that here the lagenal ramus of the acoustic and a third part of the cochlear ramus and of the vestibular ramus reach into the inner ear.

About 12-13 mm above the anterior edge of the foramen ovale (inside) begins a clearly depressed groove which in a length of 27 mm runs in flat curve obliquely upward and backward and on both ends, but particularly on the upper cuts deep into the upper surface; here again is clearly the opening of a canal. From its position I hold the groove for a trace of the endolymphatic sac sunk into dura mater, in which from the inner ear the endolymphatic duct opens; the opening through which the latter opens is the external aperture of the vestibular aqueduct. In contrast to the lower end of the groove, a small opening is found on the outside close above the foramen ovale (visible on the left side). Thus it is probable that a canal perforates the skull wall here; from its position it was possible that either the trochlear or at least blood vessels for the eye appear through it.

In the skull roof one sees from the inside a deep irregular double cavity which really gives the impression of being weathered out in the bone material; it lies in the anterior half of the supraoccipital hump. But in Crocodilia right in this place are found air-bearing cells which according to BRÜHL communicate with the upper part of the tympanic opening toward both sides. Thus, the idea is suggested that also here such air-bearing cells were present, in which weathering could easily occur. The ear of Crocodilia and of Theropoda seems generally to be built very similarly; I hope to be able to come back to this point in the description of the Triassic theropod skull in more detail and with more material.

The delimitation of the bones is exactly carried out neither inside nor outside since, as already said, the sutures are not to be observed; but however they may be approximately established.

The exoccipital extends on the inside from the condyle, whose lateral part also belongs in its region, up to the foramen lacerum, which lies in the Crocodilia in the suture between exoccipital and opisthotic. The basioccipital extends up to the jugular foramen, but it only occupies a narrow strip in the midline; the foramina of the carotid and hypoglossus lie entirely in

the exoccipital. The pyramid of the inner ear is known to be formed from the opisthotic, prootic, and epiotic; the former occupies the posterior descent, the second the anterior in its lower half, and the latter the upper part of it and its anterior border. The o p i s t h o t i c and p r o o t i c meet on the crest of the pyramid, the wide cavity in front of the pyramid and above the foramen ovale belongs to the e p i o t i c . In front of the latter is found the a l i s p h e n o i d , it reaches into the foramen ovale and forms its anterior edge; also the orbital fissure belongs in its region. The base of the braincase is formed from the foramen lacerum up to the sella turcica (inclusive), also the border of the hypophyseal cavity as far as it is preserved here.

The p r o o t i c and e p i o t i c appear also most probably on the outside of the skull. If the prootic forms the posterior and upper, perhaps also lower edge, of the foramen ovale, it must also appear in these places outward and there at least borders the foramen ovale for a small bit. It is very likely that the epiotic forms the outer surface from the upper edge of the prootic up to the outer ear opening and also occupies a part of the anterior wall of the exoccipital process. Therefore the outer ear opening lay approximately on the boundary of epiotic, parietal, and squamosal, but probably still belongs in the region of the epiotic. In several places it even seems as if one can see something of the sutures. It is suggested that a small bit of the p o s t f r o n t a l lies in front above on the anterior border of the upper temporal fossa which meets the parietal and the alisphenoid.

The just-described occiput specimen of *Megalosaurus* shows the characteristics of the ear and the position of the large nerve and vessel openings uncommonly well. This part of the skull has also to my knowledge never been described from Theropoda or other Dinosauria in specimens that show these features so well. Thus the occiput preserved in Oxford is of the greatest interest. I will soon describe similar and partly even better preserved skull parts also from the Triassic and then also I will attempt to carry out a comparison with other reptiles, which remains omitted here.

# Figure Captions.

Fig. 1. Occiput of *Megalosaurus bucklandi* from Stonesfield, view from behind, c. 1/2 nat. size. The condyle and the left exoccipital process are badly damaged; the left, upper process consists of parietal and squamosal, the right is the same broken off. Above the foramen magnum one sees the supraoccipital hump. Within the foramen magnum one sees the ear pyramids and on the right beside the outer edge the foramina XII' and XII" (see Fig. 2), beside the root of the exoccipital process the outer opening of XII".

Figs. 2 and 3. Occiput of *Megalosaurus bucklandi* from Stonesfield, left half in c. 2/3 nat. size. Line drawings of the photographs on Pl. I. Fig. 2 inner view. Fig. 3 outer view obliquely from below. Explanation of the terms: Al. = alisphenoid; A. v. = external aperture of the vestibular aqueduct, in which the groove of the endolymphatic sac ends; Car. = probable passage of the internal carotid; Cond. = broken off upper half of the occipital condyle; Eo. = epiotic; Ex. = exoccipital; Fis. orb. = orbital fissure; F. j. = jugular foramen (see text); F. l. = foramen lacerum (see text); F. m. = foramen magnum; F. ov. = foramen ovale for the trigeminal; M. a. = external auditory meatus; P. = pyramid of the inner ear; P. a. = acoustic pore; Par. = parietal; Pfr. = postfrontal; R. l. c. v. = entrance place of a part of the lagenal, cochlear, and vestibular rami acoustici into the inner ear; So. = supraoccipital; Sq. = squamosal; S. t. = sella turcica; T.? = possible exit place of the trochlear and of blood vessels for the eye; VI = passage place of the left abducens; VII = passage place of the facial (fallopian canal), outer opening doubtful (Fig. 3); XII' and XII" = the two hypoglossal foramina.

Fig. 4. Occiput of *Megalosaurus bucklandi* from Stonesfield, view from front, c. 1/2 nat. size. Above in the middle one sees the supraoccipital hump, on the right and left below the damaged exoccipital processes, on the right above the process of the parietal and squamosal, in front on the right the orbital fissure covered by a part of the alisphenoid. In the braincase one recognizes the auditory pyramids; it is closed below at the sella turcica, below one sees the 2 openings for VI (see Fig. 2).

# Plate Explanation.

**Plate I.**

Fig. 1. *Megalosaurus bucklandi* from the Dogger of Stonesfield, left half seen from inside. The same specimen as text-fig. 2. See there for explanation.

Fig. 2. Ditto. The same specimen seen obliquely from below and outside. For explanation see text-fig. 3. Original in Oxford, University Collection.