Osteological notes on *Muraenosaurus* [*]

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translated by Richard Forrest, June 1997

Prologue

Among the many manuscripts left by Herr Professor Dr. E. Koken was a paper on the skull structure of *Muraenosaurus* almost ready for publication. As I have an ongoing interest in plesiosaurs, I was glad to take on the project of preparing this paper for publication. In doing so I have added a few footnotes, made some corrections but in the main Proff. Dr Koken's text is unchanged. I have added a short description of the first two cervical vertebrae of *Muraenosaurus*.

My thanks to Frau Professor Koken and Herr Professor Doctor Freiherr von Huene who entrusted me with the preparation of these notes, and has given much advice and guidance.

Tübingen May 1913
Dr Herman Linder

The skull structure of *Muraenosaurus*

The Geological Institute in Tübingen posses parts of four skulls as well as numerous other skeletal remains of this rare plesiosaur genus[1]. As little is known of the structure of the head, and the preservation of these bones is particularly good it is appropriate to describe the material[2]. At this stage I would like to look at only the formation of the hindskull and the base of the skull.

Basioccipital and basisphenoid
(Figs 1 to 4)

All four examples of these two important skull bones lie before me in their natural orientation. In adult animals they are well fused, in the younger example (Fig 1) there were considerable cartilaginous masses which extended on both sides deep into the body of the bone. Because of this the basisphenoid has the appearance of being split, and the basioccipital has on its anterior face a fairly deep but blind ended cavity (Fig 1b). Even in adult animals there is on both dorsal and ventral sides of both bones what appears to be the end of a channel which does not however, run through. There cannot be an intertympanic channel; here also, the cartilage has been retained. In ichthyosaurs this loosening of bone fusion is more prominent.

Seen laterally the bones are joined at an angle. If one sets the articular faces of the neuropophyses approximately horizontal, the part of the basisphenoid behind that bearing the hypophyses rises distinctly upwards.

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[*] Original citation: Koken, E and H. Linder. 1913. Osteologische Notizen über *Muraenosaurus*. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1913(1):101-115.

The strong development of the pterygoid is notable on the basioccipital, as is the vaulting of the floor between the articular positions of the exoccipitals.

The basisphenoid can be considered in two parts. The posterior portion is compact. The anterior part has the pits for the hypophyses, into which the inner carotids enter from the side. The anterior part of the basisphenoid is swallow-tailed in form; the upper side of the two processes shows the characteristics of bone covered in cartilage; one finds this in many lacertids, and it is the remains of traberculae which guided and constrained the growth of these processes. The deep hypophyseal pits are covered by a thin shell of bone. The pterygoid processes are set a little behind these pits. The prootics articulate a little higher and futher back. In the middle of the inner side are foramina through which the abduces nerves of the brain cavity pass. Small foramina further back appear to have been for blood vessels. Similar structures can be seen on the basioccipital.

The parasphenoid borders the underside of the basisphenoids. Only in young animals is it an isolated bone (Fig 1a). In older specimens in which the fusion of the elements is well advanced the posterior boundary is distinctly discernible by bulging joint and more notably by a change in surface texture. At the front, the parasphenoid lies between the pterigoids, and divides them along their whole length up to the vomer[3]. This markedly narrows the anterior end of the parasphenoid, similar to a pre-sphenoid. The pterigoids are angled at the junction with this process, smooth and straight. The posterior third of the parasphenoids is highly distinctive: it has the appearance of a large gap enclosed by curved borders, similar to those found in American plesiosaurids. The gap was never however, fully enclosed: even the thinnest rim shows signs of breakage, and therefore I believe that the opening was closed by a thin plate of bone now preserved only in the posterior part of the flat base.

I can only note the peculiar, button-like protuberance lying in the angle between the trabecular processes which are nevertheless an integral part of the parasphenoid. The dorsally oriented curve bears a shallow depression.

The existence of a distinct and well-developed parasphenoid beside an equally distinct vomer shows that both have developed separately. There is no sign of a pre-vomer. It is possible that in juveniles the unpaired vomer was paired. This cannot be distinguished in the single example I have which is fairly well-grown. It is a reasonable assumption that this was the case.

The pterygoids[4] are widely spaced in the middle. They start with a point at the vomer, gradually broaden to form a flat plate on the underside, become narrower but thicker adjacent to the pterygoideous process, curve outwards, then back to the basioccipital where they extend an hook-like process towards the inside. At the pterygoideus process the basioccipital stops the horizontal palatal surface of the bone which is here curved at an angle and joined by an angled seam to the quadrate. The roller joint of the quadrate is very well marked (Fig 4).

The epipterygoid, whose insertion point in the pterygoid in Fig 3 (just in front of the basisphenoid) is well marked is preserved only as formless fragments.

Hindskull and ocular region

(Figs 5-7, Plate X, figs 1-4)

The basioccipital is already described. Fig 5 shows the associated occipitalia of a juvenile *Muraenosaurus* which are undistorted and fit together precisely. The paroccipital processes are broken off the exoccipitals apart from the fragments of the ophistoticum; they are however perfectly preserved in many other specimens.

The exoccipitals are pierced by three holes, of which two are taken as foramina praecondyloria (for hypoglossus and glossopharyngeous) and one as foramen lacerum posterius (for vagus group and cervical veins). The supraoccipital is a very characteristic bone: it is deeply indented, and a distinct, thick extension extends deep into the gap which appears to offset the foramen magnum dorsally. The small bones forming the surround of the labyrinths and semi-circular canals are supraoccipital, exoccipital (or at least the ophisthoticum) and a prootic (or otosphenoid). The ocular cavities are exceptionally well-preserved, though I will not dwell at this point on the fine detail[5]. Only the important junction between exoccipitals and prootics is described here.

The prootic is a distinctively formed bone, laterally thickened and with a granular surface, posteriorly drawn out in a handle-like extension. This connects to the basisphenoid on the upper rim, and the wide upper surface with the supraoccipital. The contact with the exoccipital is relatively short. On the inside the prootic is deeply hollowed, with the cavity widening medially.

The prootic is distinctly smaller than the exoccipital. It can articulate with the basisphenoid in spite of the fact that it connects in the same place to the exoccipital because basioccipital and basisphenoid meet at an angle, and the basisphenoid is angled sharply upwards.

The large opening bounded by exoccipital, basisphenoid and prootic could also be used by the venous blood vessels of the neck: the penetrations of the exoccipitals are hardly large enough for these. The path of the carotis interna ran deep in a channel in the basisphenoid.

The supraoccipital (Fig 5) sits as a curved keystone onto the two exoccipitals and forms the upper rim of the foramen magnum. Undoubtedly this upper part of the hole in the back of the skull bounded by the supraoccipital is not the entry point of the medula oblongata, but a separate segment distinct from the foramen magnum. The narrowing of the lower part indicates this.

The distinct plug-like projection formed by the division of the opening is primarily formed by the insertion of the nuchal ligament, which in ichthyosaurs with their massive skull and narrow neck must have been well developed. The plug shows all the characteristics of such an insertion: therefore its existence is evidence for the cause of the partitioning of the upper foramen. More conspicuous is the increase in height of the foramen magnum caused by the gap in the supraoccipital in plesiosaurs. One can compare the undeveloped supraoccipital of a juvenile *Muraeonosaurus*. Here also an insertion point on the upper rim projects downwards and narrows to form a double rim. This can have nothing to do with the arteries as the entry position for these is well defined. The supraoccipital forms part of the rim of this foramen. In ichthyosaurs it leads from here into the supraocciptial itself. A part of the labyrinth is always enclosed within the lateral part of the supraoccipital. There is no sign of a separate epioticum, not even in juveniles. The concept of the epioticum is purely theoretical and is not supported by any physical evidence.

The rim adjacent to the parietals is thick and hollowed, and with evidence of ample cartilage covering. Nothing can be said of the suture with the parietals.

Particular mention must be made of the channel which always joins the supraoccipital to a point close to the ocular region. In juvenile bones it is only a slit. I can find no other explanation than that it corresponds to the channel found, for example, in crocodiles between supraoccipital and squamosal leading from the back to the upper temporal fenestra. In Liassic forms the supraoccipital is only has a rim where this slit lies in young ophthalmosaurs. In this character Liassic forms can hardly be distinguished from ophthalmosaurs.

The first two cervical vertebrae of *Muraenosaurus*

The atlas and epistropheus of a very young *Muraenosaurus* was found among the material used by Herr Proff. Koken in his description above. This fortunately complements my research[6] into the first two cervical vertebrae of plesiosaurs and I would therefore like to describe then briefly and figure (Fig 9-11).

The single parts which comprise the vertebrae are completely unfused; basal pieces, neural arches and ribs have fallen off and are lost, so that I can deal only with the centra of the as yet unfused epistropheus and atlas.

The body of the atlas (or odontoideum) is almost as large as the epistropheus. It forms the base and side borders of the articular socket of the occipital condyle and separates widely base and neural arch. The later forms the upper rim of the articular surface, and the base widens to the front so that the base of the neural canal appears to be triangular. On the underside the odontoideum shows two contiguous facets of which the larger is oriented to the front so that it forms the articular surface for the basal pieces of the atlas. The other facet is oriented to the back and forms, with an butting and similarly sized facet on the base of the epistropheus, a facet for the attachment of basal pieces of the epistropheus. Above these but touching both facets narrow grooves show where the atlas ribs were attached to the odontoideum.

Atlas and epistropheus join with more or less flat surfaces. On the underside of the epistropheus is the above mentioned facet for the articulation of the basal piece, and on the sides two large facets for the ribs of the epistropheus abutting the atlas rib facets.

What makes this piece especially interesting is that beside the basal piece of the atlas separate basal piece of the epistropheus is discernible, a feature which cannot be seen on mature animals[7]. My assumption that a separate basal piece of the epistropheus was formed in all plesiosaurs is confirmed by this evidence. The odontoideum and epistropheus grow together and fuse in such a way that the basal piece of the epistropheus is fused completely at a certain age with the corresponding bone.

This is also evidence of distinct atlas ribs in *Muraenosaurus*.

A comparison of these first two cervical vertebrae with those of *Cimoliosaurus* shows a developmental tendency in growth. Unfortunately it cannot be determined if the basal piece of *Muraenosaurus* was also laid down as a pair. The articular surfaces give no clue.

Legend to Plates

Plate X

Fig. 1. *Muraenosaurus*. Exoccipitals (+opisthoticum) from behind. A little over natural size
Fig. 2. *Muraenosaurus*. Exoccipitals (+opisthoticum) from front. A little over natural size. C.S.II - hole for horizontal semicircular canal. A.P. - ampula posterior.
Fig. 3. *Muraenosaurus*. Exoccipitals (+opisthoticum) from inside. A little over natural size
Fig. 4. *Muraenosaurus*, Prootic; 4a from outside, 4b from inside. A little over natural size
Fig. 5. Exoccipitals (+opisthoticum) of a very young *Muraenosaurus*, from front. Natural size.
Fig. 6. *Muraenosaurus*. Exoccipitals (+opisthoticum) and prootic from inside. Natural size.

The bones illustrated originate from the Oxford Clay of Peterborough, England.

Notes

1. The skull remains as well as the cervical vertebrae described below originate from the Oxford Clay of Peterborough, England.

2. Since this was written a catalogue written by Andrews and published by the British Museum has been issued in which also the genus *Muraenosaurus* is described. [H. Linder, by whom all other footnotes have been added.]

3. This description must be modified. The pterygoids meet at the anterior end of this so-called interpterygoideal break, and form a sharply pointed anterior extension which inserts into the vomer. The posterior end of the break is similar to that of the Cretaceous *Trinacromerum bentonianum* in which the forked ends of the parasphenoid do not reach the vomer as one would believe from the above description, but stop at about the middle of the break.

4. It should be noted than the pterygoid bears weakly developed lateral extensions to join with the transversum. In this respect they differ from the description from Andrews reconstruction of the skull of *Muraenosaurus*.

5. I would like to add at this point a description of the inner ear (Plate X, Fig 5 and 6 as well as 1-4). The labyrinth is enclosed by a capsule of bone formed of the prootics and exoccipitals, and the semi-circular canals are set deeply into the above mentioned bones and the supraoccipital (Plate.X, Fig. 6).

On the posterior rim of the exoccipital (+ ophistoticular) there is a hole from which channels run from above and to the outside. It is assumed that this is for the ampulla posterior. A ridge on the inner side of the bone above the foramen lacerum posterius indicates the point at which a branch of the nervus acusticius leaves the brain case. A horizontal branch of the channel runs from deep inside the ocular cavity to the outside. In younger animals this is not completely enclosed by bone, but must in part have run through cartilage. The layer of bone which covers the outside in older animals is proportionally thin. It bends posteriorly and anteriorly into the prootic where it leads into a large cavity for the ampula superior. This is the horizontal semicircular canal. A further canal, which can be distinguished clearly only in the juvenile animal shows as a further cavity rising to the boundary with the supraoccipital and is assigned as sinus utriculi superior. It runs as far as the joint between exoccipital and prootic, and is similarly bounded by these two bones in adult animals. A thin branch of this channel bends suddenly inwards at the joint between exoccipitals and supraoccipitals, rises close to the inner side of the supraoccipitals, and turns again to the outside. It appears to be bounded at the front by the prootics, following the projecting part closely and forms the rear semicircular canal. A shallow channel on the upper back of the cavity for the ampula superior in the prootic of the older examples indicates the entry into the sacculus which must have been positioned between the prootic and exocciptals and surrounded by cartilage. The layout of the anterior semicircular canals cannot be clearly discerned. They must have lain a little further forward, with the posterior bend running into the supraoccipitals, and then entering the prootics where it entered the anterior upper inner wall of the cavity for the ampula superior. A hole in the prootic facet of the supraoccipital shows the point of entry into the prootic. The shell-like part of the ear, the cochlea, is not enclosed by other bones, but is separated from the other skull bones as in *Nothosaurus* (KOKEN, *Beiträge zur Kenntnis der Gattung* Nothosaurus *(Contributions to the recognition of the genus* Nothosaurus*) Zeitschr. d. deutsch. geol. Ges*. 45 p.337 ff. 1893). In this case the pyramidal parts of the prootic, opisthotics (as exoccipitals) and supraoccipital bones remain cartilaginous throughout life. It is noteworthy that in plesiosaurs the prootic is ossified at a early age, in contrast to *Nothosaurus* where it occurs only late in life. The inner part of the middle ear is enclosed ventrally by the basisphenoid, and to front and back by prootics and exoccipitals. It forms a circular and notably large cavity, open to the skull in the inside and opening onto the temporal fenestra externally. This opening, as KOKEN assumes, also forms a passage for blood vessels serving the temporal fenestra, in a similar manner to *Nothosaurus*. No conclusions can be formed on the details of the tympanum, the eustachian tubes and the cavum tympani. It is notable that in the juvenile specimen the cavities and channels have roughly the same dimensions as those in adult specimens, although the overall dimensions of the bones are hardly half as much. The growth of bone occurs mainly on the outer surface of the skull so that a gradual sinking of the ear into the bone occurs. If we compare these details with those of *Ophthalmosaurus* the location of the curved canals is and cavities corresponds closely, though they are not as well defined in this later case. Both anterior and posterior parts of the otic capsule in these ichthyosaurs lie within the opistoticum, which is completely separated from the exoccipital and allows the conclusion to be formed that various parts of the exocciptal of plesiosaurs belong to the associated opisthoticum, such that the exocciptal has no contact with the ear.

6. *Geolog. u. Paläontolog. Abhandl*. 1913. N.F. XI (the whole of row XV) Published 1913. Vol 5, pp 402 ff.

7. see Andrew, *Catalogue of the fossil Reptiles* etc. 1910. p. 92