SALT GLAND STRUCTURES IDENTIFIED IN A LATE JURASSIC ICHTHYOSAUR, *OPHTHALMOSAURUS NATANS*

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ABSTRACT

Salt glands allow marine reptiles to deal with ingested environmental salts and have been recognized on plesiosaurs and marine crocodiles. UW24816 is a large and almost complete ichthyosaur skull preserved in three dimensions, but fractured into a series of cross-sectional views. A section anterio-dorsal to the orbits revealed paired structures preserved within the sediment of the skull and these extend posterior to the external nares. The described pockets are sub-triangular, bordered by the prefrontal/lachrymal contact anteriorly and by the nasal bones dorsally and suggest preserved paired salt glands. The interior surface of the prefrontal/lachrymal contact is strongly striated in UW24816 and similar striations have been noted on the surface of the preserved casts of salt glands in marine crocodiles. The external nares are intact and display paired scoop structures of rugose, ridged bone at the posterior border, on the anterior surface of the lachrymal. These features may have facilitated the removal of excess salt via the exit point from the salt gland, through a single, short duct as has been noted in Lepidosauria. Expansion of the vomeral/nasal region anterior to the orbit in derived ichthyosaurs may have expanded the area previously occupied by the glands forward from the reduced parietal/front region.

INTRODUCTION

Reptiles that have reinvaded the marine habitat require a means to remove excess ingested salt to prevent lethal osmotic dehydration (Minnich, 1982; Miller, 1998). The need for salt removal in marine reptiles is made more efficient by use of salt glands, where it can be excreted as a concentrated solution and flushed away. Salt glands have been noted in both extinct marine crocodiles and plesiosaurs (Martin and Fernández, 2008; Gandola, et al, 2006; Fernández and Gasparini, 2000). Motani (2003) made reference to the potential support structures of possible salt glands on the skull bones of Triassic mixosaurs (McGowan and Motani, 2003). This is the first description of salt gland structures in the skull of a Jurassic ichthyosaur.

Vomeral/Nasal Glands in Reptiles—The salt gland would most likely have developed from modified Hardarian glands (Dunson, 1976). The glands occupy a space anterior to the eyes and moisten the eye in the anterior portion of the orbit at the prefrontal/orbital contact, as seen in marine turtles. (Hillenius and Rehorek, 2007). In iguanas and sea turtles, generalizations of salt glands include large ducts, numerous points of enervation, and internal structures specialized for ion transport such as deep infoldings and vascularization (Dunson, 1976). These features of extra-renal structures are similar to other vertebrates such as birds and other osmoregulatory vertebrates (Anderson, et al, 2007).

If the glands emptied into the mouth via the internal nares in marine reptiles, it would amount to a closed loop system of ingesting more salt, resulting in an increase of a lethal osmotic load on the renal system. However, if the excess salt concentrate was emptied via the external nares at the lachrymal/nasal contact, this would dump the excess salt back into the environment.

Salt glands can be extremely adaptive and are modified in response to salinity (Hilbrandt, 2001). The size and structure of salt glands in avians vary with differential contact to salinity suggesting similar responses in both size of the glands and output of salt concentrations (Hilbrandt, 2001). Likewise, equivalent salt gland structures may have occurred with an expansion of bones anterior to the orbit and may have developed along with a vomeral /nasal association in Lepidosauria.

In lizards, the lateral nasal gland is a compound tubular gland with tubes empting into a common duct; this empties into the posterior end of the nasal sac and is enervated by the lateral ethmoidal nerve, whereas blood is supplied by the postnarial artery (Dunson, 1976). The enervations and blood supply would be in a close association to those found in the sauropsids such as Lepidosauria, although as in avians, both the size and orientation of the glands themselves are different, with some glands developing inside the nasal region then expanding to the external region of the nares (Dunson and Mazzotti, 1989).
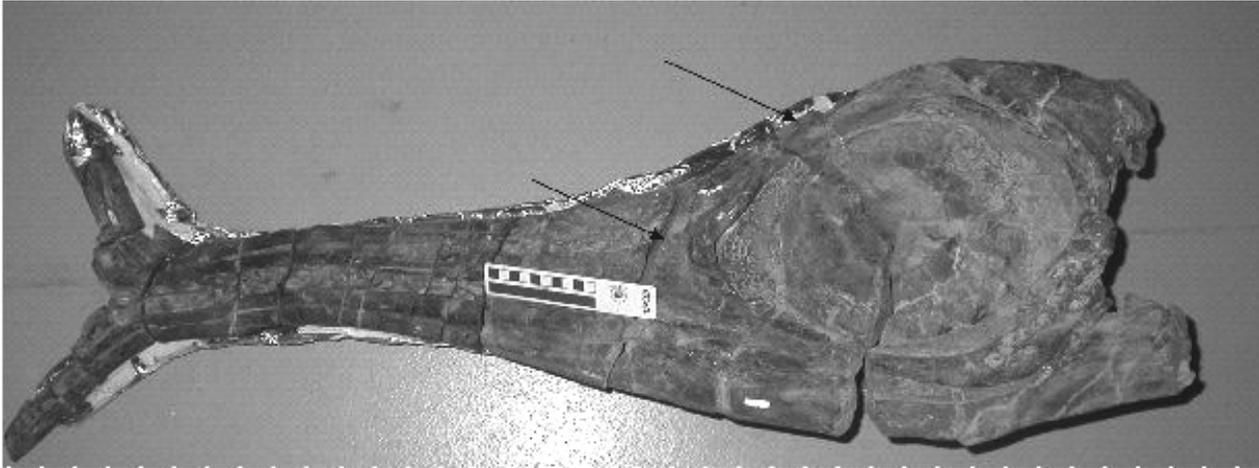
FIGURE 1.   Skull of *Opthalmosaurus natans* UW24816.   Note the breaks through the nares and orbit (arrows).   Scale bar = 10 cm.   Modified after Wahl, 2009.
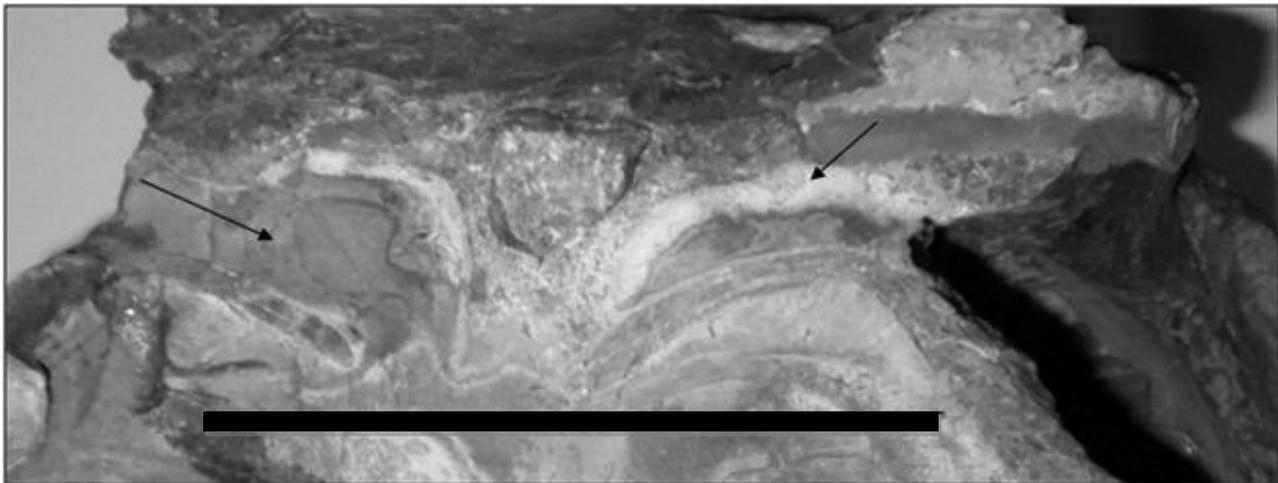
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FIGURE 2.   UW24816 cross-section of skull near the nasal/frontal contact.   Note paired sedimentary pockets defined by the sclerotic plate boundary below the nasals (arrows).   Scale bar = 10 cm.

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MATERIAL

UW 24816 consists of a partially articulated specimen of *Ophthalmosaurus natans* representing 60% of the skeleton, with an almost complete skull. The skull of UW24816 was collected in concreted blocks that display cross-sections along the long axis and this allowed examination of the specimen in serial sections, reminiscent of large CT scans. UW24816 thus represented an opportunity for study in high resolution and the ability to view the interior material in relevant cross-sections (Figure 1). The specimen was CT scanned to examine the interior of the skull but the results were inconclusive, though some surface scans were useful.

The specimen was collected from the Sundance Formation (Bajocian-Oxfordian) from the Redwater Shale Member, which records the last and most extensive transgressive sequence of the Jurassic in North America (Kvale et al., 2001). The upper Redwater Shale Member is Oxfordian in age and represents a shallow, open shelf environment dominated by silty to shaley mudstone, occasional bioturbated shale, and ripple-dominated, glauconitic,

fine-grained calcareous sandstone (Andersson, 1979; Specht and Brenner, 1979; Kvale et al., 2001).

Institutional Abbreviations—UW, University of Wyoming, Laramie, Wyoming, U.S.A.; NHMUK, Natural History Museum, London, U.K.; OUMNH, Oxford University Museum of Natural History, Oxford, U.K.
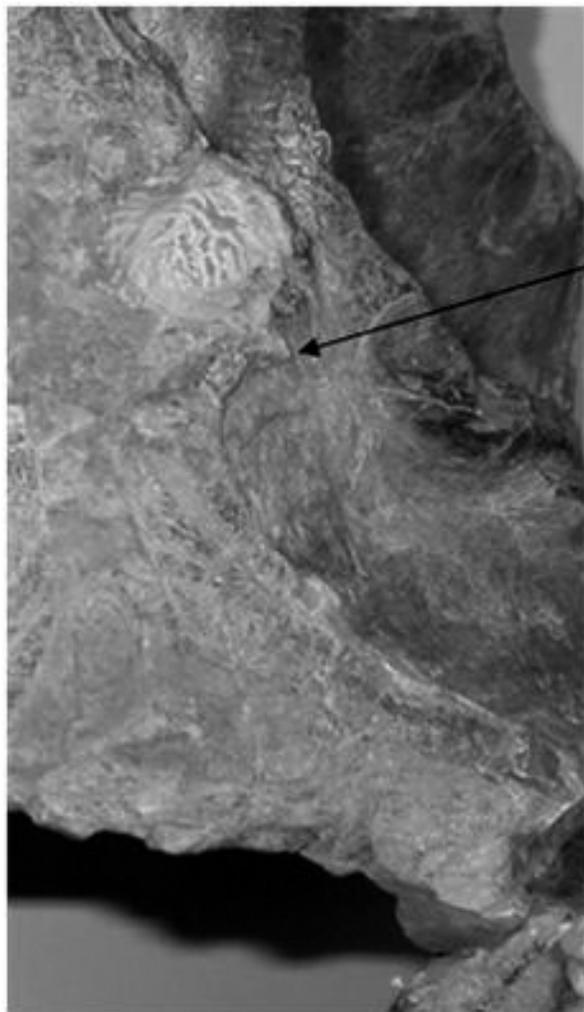
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FIGURE 3. Cross-section of the skull UW24816 posterior to the left nares. The groove in the dorsal edge of the maxilla is highlighted by arrow.

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DESCRIPTION

Taphonomy—The skull of UW24816 was found partially buried at an angle of almost 90º to the bedding plane, suggesting that the skull was driven into the sediment (a "nose-dive") and partially buried. The body appears to have flopped back onto the sea floor after the head penetrated the sediment by the impact of the carcass sinking through the water column (Wahl, 2009). The skull was upside down and partially laying on the right side, whereas the vertebral column appeared to be lying on its left side. This suggests that the body may have "corkscrewed" slightly at the sediment contact.

Ironstone and pyrite occur on the edges of foramina on both lower and upper jaws, with more material occurring at the contact of the upper maxilla and premaxilla (Wahl, 2009). Ironstone and pyrite do not occur in the vacuities of the vertebral column where some calcite crystallization has occurred. There was no ironstone accreted within the spaces between bones or the enervations of the rostrum. As the skull was buried at an extreme angle to the bedding, the semi-hollow structure of the jaws may have provided a conduit for mineralization in the fossa (Wahl, 2009). This allowed the accretion of alternating ironstone cementation around the surface of the distal portions of the bone. The very ends of the jaws may have rotted away from iron-mineral accretion as evidenced by the splintered bone (Wahl, 2009).   No evidence of boring, burrows, or infaunal disturbance could be found on the middle and distal portions of the skull, again suggesting that it had been driven into the sediment possibly below the infaunal interaction level, thus removing it from exposure (Wahl, 2009).

The skull is fractured into sections from just posterior to the external nares to the distal end of the rostrum. Although large open spaces within a skull are typically susceptible to sediment crushing, spaces exposing the thinner, more fragile bones were not similarly crushed. For example, sclerotic rings on either side of the skull were not damaged by the distortion of the bones that make up the orbit. As with the larger openings in the back of the skull, the vacuities anterior to the orbits contained no shell hash material that was similar to that packed around the intact teeth in the distal rostrum. It also appeared that the mineral accretion displaced the shell hash that was packed around the distal portion of the skull. The shell hash was in the sea floor sediment and collected around the rostrum when the skull went through the sediment during deposition   (Wahl, 2009).   There was no ironstone accreted, nor crystal growth, within the spaces below the displaced skull in contact with several skull bones. As the skull was deposited upside down, fine-grained sediment could have settled as layers within the vacuities of the posterior and middle portion of the skull. This may have also provided resistance to crushing and retention of the void space within the skull. The layering of the sediments may have allowed for limited mineralization in the vacuities resulting in alternating cementation and preservation of casts of soft, organic structures normally lost. (Figure 2).
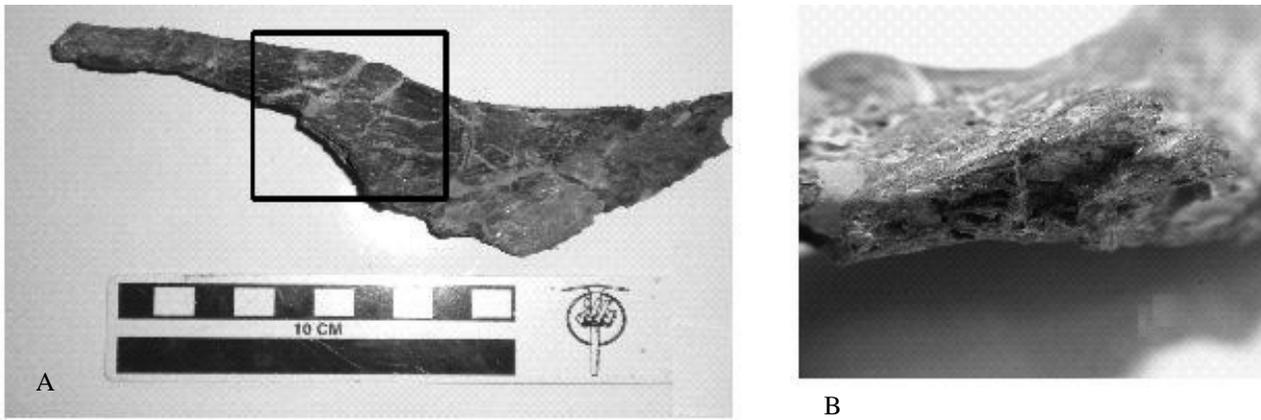
FIGURE 4. A. UW24804 left maxilla (black rectangle). B. Note the raised groove (foramen) on the dorsal ridge in contact with the nasal.
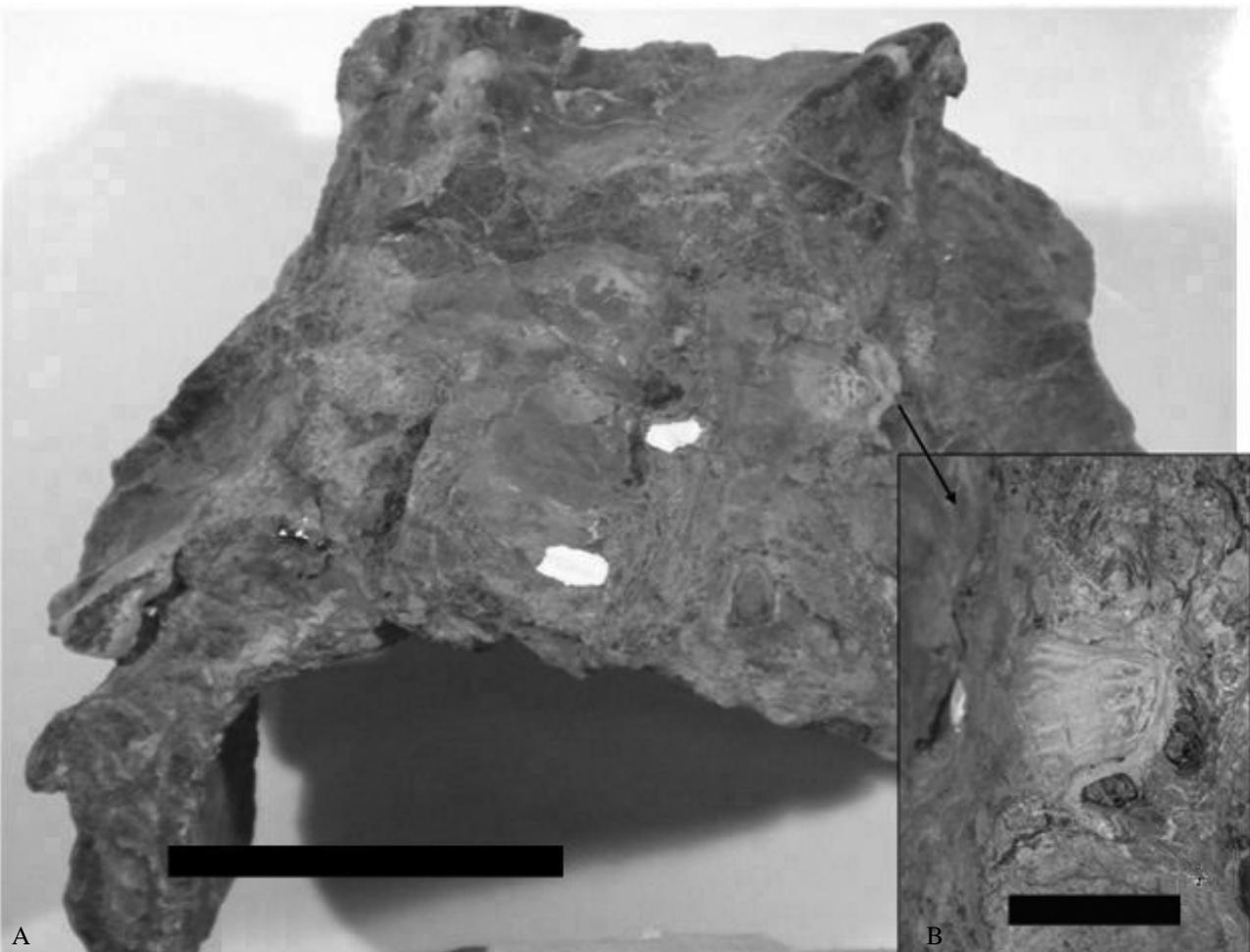

FIGURE 5. A. UW24816 cross-section at the external nares/internal nares. Note the "scoop" posterior to the nasal capsule. Scale bar = 10cm. B. Enlargement of the "scoop" posterior to the nasal capsule (arrow). Note the odd feathering on the anterior edge of the lachrymal. These paired structures are not taphonomically distorted. Scale bar = 2 cm.
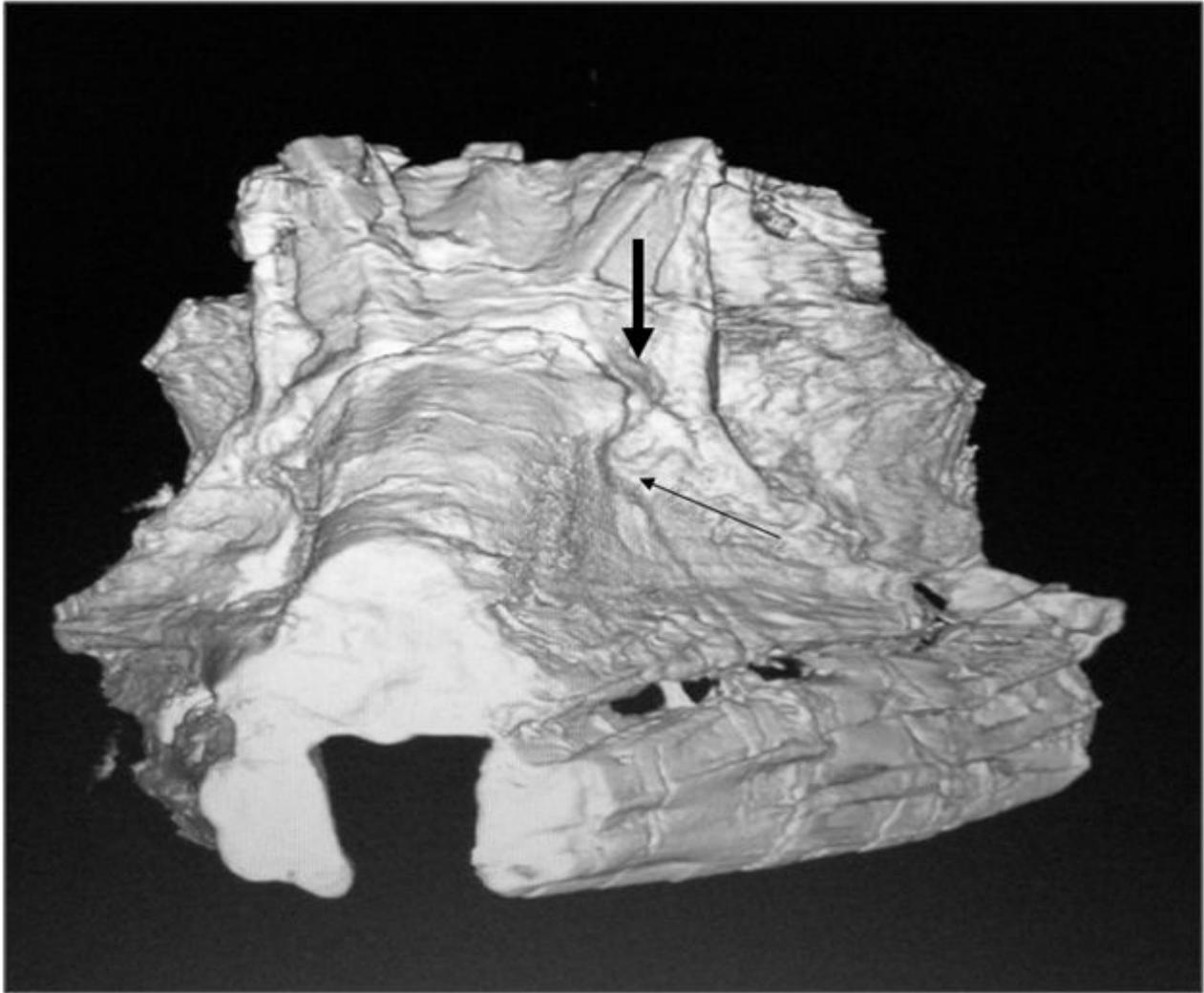
FIGURE 6. 3-D surface scan of partial skull UW24816 in rostral view illustrating the external nares (arrow). Note the "scoop" opening posterior to the nasal capsule (bold arrow). Scale bar = 10 cm

Some portions of the skull are preserved intact. The anterio-orbital portion of the skull of the UW24816 displays sedimentary structures within the cross-section of the skull associated with the nares. The skeletal elements in contact with the nasals are visible and not damaged below the frontal/nasal contact. The interior and exterior posterior portion of the external, laterally-oriented nares are intact and not damaged, and the contacts of all bones associated with the nares, including the anterior surface of the lachrymal are well preserved.   The facets of the skeletal elements in contact with the nasals are visible and not overlapping below the frontal/nasal contact. The skull bones show some taphonomic distortion resulting in dorsal sections of the nasals displaced over the anterior portion of the frontal region, and portions of the dorsal rostrum seen in cross-section exhibit a rippling of the bone within the open space of the nasal maxilla channel (Wahl, 2009).

Morphology—The interior surface of the lachrymal is strongly striated in ophthalmosaurs as is seen in the prefrontal/lachrymal contact of this specimen. Striations have been noted on the surface of the preserved casts of salt glands in marine crocodiles (Fernández and Gasparini, 2008). The interior surface of prefrontal/nasal contact of UW24816 is blunt at the contact, suggesting the salt gland structure did not extend internally to the nasal region. The interior and exterior portion of the external nares display paired structures of rugose, ridged bone at the posterior border
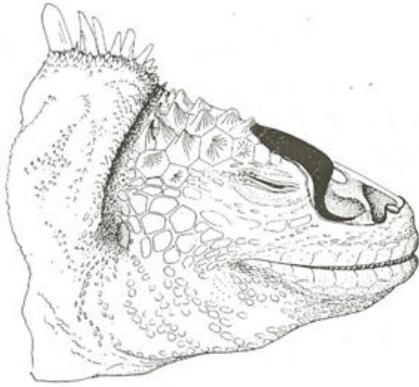
FIGURE 7. Illustrations of salt glands in the marine iguana, *Amblyrhynchus*. Note the position of glands dorsal and anterior to the eye orbit. Modified after Dunson, 1976.

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of the external nares, on the anterior surface of the lachrymal. The funnel-shaped structures face anteriorly and are probably not involved in breathing nor as a support of a vascular valve. These features would increase drag on the streamline skull of an ichthyosaur and facilitate the removal of excess salt as a concentrated solution via a laterally oriented, post-nares structure that can be flushed with water. The exit point from the gland would have been through a single, short duct as seen in Lepidosauria (Dunson, 1976). These ducts can be seen on the dorsal edge of the maxilla at the contact with the nasal on the intact skull of UW24816 (Figure 3), as well as on the dorsal edge of the isolated maxilla of a disarticulated skull from a second *Ophthalmosaurus natans* specimen, UW24804 (Figure 4).

The interior and exterior portion of the external nares display paired structures at the posterior border. Removal of matrix on the skull of UW24816 revealed a rugose surface facing lateral and posterior to the nares. These structures are on the anterior surface of the lachrymal (Figure 5). This surface presents an odd feathering of the posterior border of the external nares and would interfere with water moving past the skull. This feature was initially thought to be a paired distorted portion of bone that was taphonomically displaced during the nose dive or subsequent movement of the skull through sediment. However, it occurs in other specimens, including both articulated and disarticulated ophthalmosaurs (e.g., NHMUK R3893), suggesting the feature was present on the skulls before deposition. Both funnel-shaped structures face anterior to the orbit but open posterior to the nares (Figure 6). The structures were probably not involved in breathing although similar suggestions have been made about the internal and external nares of other marine reptiles (Cruickshank, et al., 1991).

The nares in basal ichthyosaurs are dorsally situated, but on derived forms are laterally oriented and split. The orbits are more reduced in basal ichthyosaurs and it has been suggested that salt glands were situated at the parietal/frontal contact external to the nares (McGowan and Motani, 2003). Expansion of the nasals and their subsequent contact with associated bones is seen in derived forms such as ophthalmosaurs. This expansion may have moved the glands forward to the vomeral/nasal region anterior to the orbit but posterior to the nasal capsule (McGowan and Motani, 2003).

DISCUSSION

The presence of salt glands is overemphasized and the role simplified in the study of extant marine reptiles (Dunson and Mazzotti, 1989). However its presence in some marine sauropsids, such as birds and some lizards, is so large as to extend posterior and dorsal to the orbit outside the interior of the vomeral/nasal region of the rostrum (Dunson and Mazzotti, 1989). The marine iguana *Amblyrhynchus* is an extreme example of this condition (Dunson, 1976; Dunson and Mazzotti, 1989; Figure 7). The position in the ichthyosaur skull of the paired sedimentary casts at the posterior external nares, the sub-lobate shape of the structures, and the rugose contact on the internal and external skull bones suggest salt glands such as those of *Amblyrhynchus*. Within the posterior rostrum of UW24816, these nasal capsules were covered dorsally by the nasals, prefrontals, lachrymals, and probably portions of the anterior frontals (Figure 8).

The interior surface of the lachrymal is strongly striated as described by Andrews (1910) in an *Ophthalmosaurus icenius* specimen (NHMUK R3893), and this feature is present in UW24816; however, the anterior edge of the lachrymal in NHMUK R3893 is described as "rounded and reflected inwards" (Andrews, 1910), but this is not what is observed in UW24816 (Figure 9). Also, the prefrontal/lachrymal contacts of UW24816 and UW24804 are strongly striated as well. (Figure 10). The required blood flow to the glands may have left rugose surfaces on the sedimentary material that filled the vacuities during deposition. Striations have been noted on the surface of the preserved casts of salt glands in marine crocodiles (Gandola, et al, 2006; Fernández, and Gasparini, 2008). The interior surface of the prefrontal/nasal contact of UW24816 are partially rugose at the contact suggesting the salt gland structure did not extend very far internally into the nasal region.

Relationship of Diet and Salt Gland Function— The development of salt glands is in direct response to ingested salts. For example, the Diamond backed terrapin, *Malaclemys terrapin,* which spends a
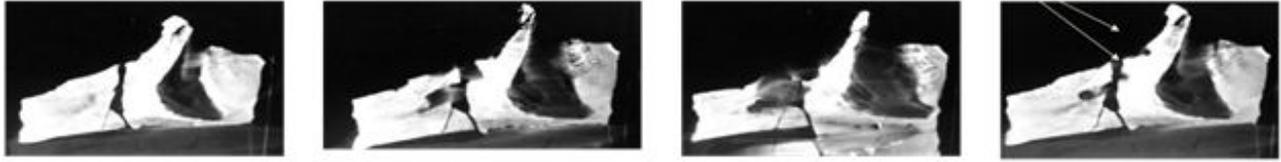
FIGURE 8. UW24816 skull lateral CT scan image in series with a view of the nasal capsule and interior surface of the nasal/maxilla/lachrymal contact. Note the open space posterior to the nasal capsule and the foramen at the nasal/lachrymal posterior to the nares (arrows). CT "slices" are in 2mm. Scale Bar = 10 cm.

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considerable amount of time in sea water feeding on invertebrates with a high salt content, relies on the salt gland for the removal of salt (Dunson, 1976; Dunson and Mazzotti, 1989). Salt glands lateral and dorsal to the nasal orifices are found in members of several recent lizard families (Dunson, 1976; Dunson and Mazzotti, 1989). Some are herbivorous such as the marine iguana, *Amblyrhynchus*; others are insectivorous lizards such as *Uta encantada* and *U. loweii,* with a diet high in environmental salts from such prey items as marine tidal isopods (Hazard, et al 1998). It would be expected that higher sodium secretion would reflect higher dietary salinity, and although there are no extant pelagic lepidosaurs, the salt glands are variable in size in other extant marine reptiles, influenced by the quantity of ingested salts (Dunson and Mazzotti, 1989). "Gulp" feeders, animals which use mastication or suction feeding such that incidental salt water is ingested with prey (such as in leatherback turtles *Dermochelys coriacea)*, versus animals that feed on large whole prey (such as some sea snakes *Hydrophis)*, possess a range of large and small salt gland sizes, respectively (Dunson and Mazzotti, 1989).

Ichthyosaurs such as *Ichthyosaurus* and *Ophthalmosaurus* have been noted with cephalopod remains in preserved gastric contents (Massare and Young, 2005). The presence of large hyoids in both toothed and toothless forms of ichthyosaurs may suggest a form of suction feeding in which the prey is gulped in to the gullet (Wahl, 2011). The salt content of coleoids is not known, however, most recent cephalopods are high in water content (2-3% denser than seawater) and achieve neutral buoancy by forcing dense salts out of kidneys into the body cavity. Presumably any excess salt from ingesting the salt in the prey or from suction feeding would have to be dealt with in a marine diet (Clarke, 1988; Anderson and Demont, 2000).

Salt removal—Use of osteological correlates to suggest nasal glands, let alone salt glands, in extant

sauropsids is subtle and the inference would be more so in extinct forms (Witmer, 1991; Fernández and
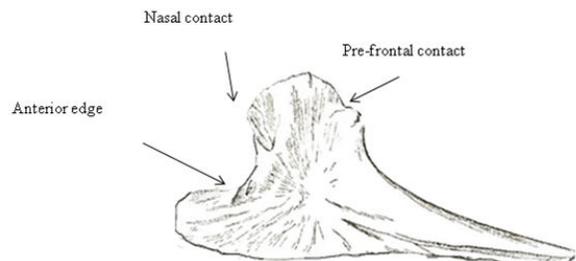

FIGURE 9. Lachrymal of *Ophthalmosarus icenius* NHM R3893. Andrews (1910) described the striated interior surface at the nasal contact and pre-frontal contact. Modified illustration of right lachrymal after Andrews, 1910.

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Herrera, 2009). The current study on ichthyosaurs was modeled in part on the report of salt glands in metriorhynchid crocodiles (Fernández and Herrera, 2009). The homology of such structures was based on facial structures described in extant crocodiles that allowed for the reconstructions of soft organs, the resulting natural casts in the skull, and the contact of the skull bones that cover them (Witmer, 1991; Fernández and Herrera, 2009). Analogies to the anteorbital fenestra and the spaces in the archosaur skull that support salt glands are hypothesized in UW24816. Based on morphological evidence, the positions in the archosaur skull, and topological equivalence, the hypothesis that requires the least ad-hoc assumptions to explain observations is preferred (Witmer, 1995; Fernández and Herrera, 2009). For this study, osteological analogous correlates between lepidosaurs and archosaurs would suggest an open space to house the salt gland structure within or near the optic area above the narial region. Likewise the structural supports that allow for a salt gland to be utilized efficiently in a marine environment by either crocodiles or ichthyosaurs would be similar.

Encrustations of salts from the salt glands must be removed to avoid blockage. The salt glands in birds

drain into the nasal cavity then drip out externally. Marine turtles flush the salt concentrations out with the
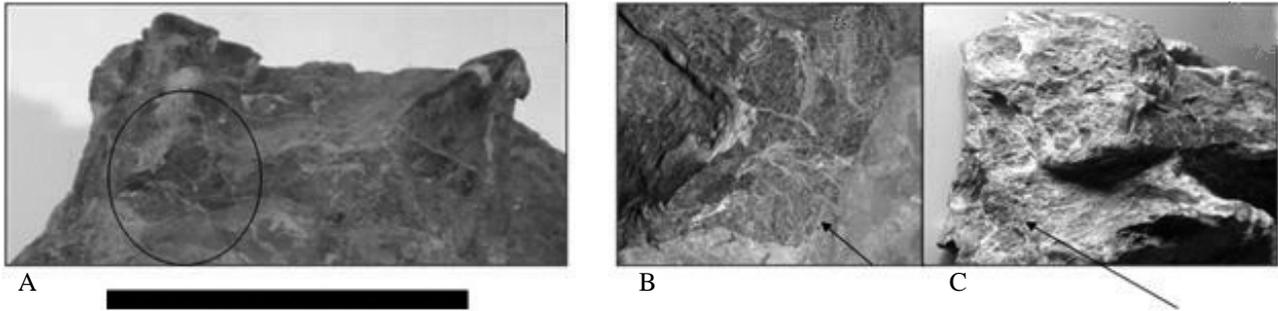

FIGURE 10. A. The interior surface of the lachrymal and nasal is strongly striated in UW24816 (circle). B. Close up of this structure (arrow). C. The interior of the lachrymal of UW24804 (arrow). Scale bar = 10 cm.

turbulence of the redirected water across the eye (Dunson, 1976; Dunson and Mazzotti, 1989). Marine iguanas "sneeze" the salt out thus clearing the nares (Miller, 1998). However, in an animal with a long skull, an extended, recessed duct maybe inefficient to flush salt out of the narial area. The long skull of some marine crocodiles provides a useful analogy. The short duct of the marine crocodile inferred by Fernández and Gasparini (2000) and described by Gandola, et al, (2006), suggests a short surface area channeled to flush with water, which in turn removes the salt encrustations (Fernández and Gasparini, 2000; Gandola, et al, 2006). The long skull shape of ichthyosaurs would suggest an analogous short duct associated at the maxillary contact with the posterior nasal that would allow for a flush. Such a structure is seen on the intact skull of the ophthalmosaur UW24816 and the dorsal edge of the isolated maxilla of the ophthalmosaur UW24804.

Function of Post-narial Lachrymal Flares— The scoop-like structures of the post-narial flares are an interesting feature in the skull of UW24816. Cruickshank, et al., (1991) suggested a form of "ramjet" olfaction in pliosaurs by mapping the flow of water through the scoop-like internal nares, through to a groove to the external nares. However, the water flow through ichthyosaur nares, if it occurred, would have been different as the internal nares are not anterior to the external nares as in pliosaurs, and the post-nares "scoop-like" structures in *Ophthalmosaurus* face anteriorly and lie dorsal and posterior to the canal or foramen on the dorsal process of the maxilla. Air flow through the internal and external nares would not have been inhibited by the external structure (Figure 11).

The structures also do not suggest a support of a vascular valve as the external nasal opening presents no bone sculpting or rugosity as evidence for a valve. Such valve structures are suggested in some Triassic reptiles as *Lystrosaurus*, which may have developed

then within the active burrowing niche, but these are usually anterior to the exposed nares. However a valve, external to and at the posterior point of the nares, is not structurally sound on a hydrodynamic surface. The scoop-like feature may instead increase hydrodynamic drag and facilitate the removal of excess salt at the short duct through the dorsal process of the maxilla.

The shape of the ophthalmosaur skull is sleek (low draft coefficient around .05) clearly adapted for low flow resistance. However, an external feature, namely the anterior facing flare, would have increased the drag coefficient. Such a feature of the skull surface at the water contact may have been useful to remove excess salt excreted via the duct above the maxilla. Surface friction passing over this flare would increase drag on the streamline shaped skull of an ichthyosaur and facilitate formation of a riffle of water. It would remove excess salt as a concentrated solution via a laterally oriented, post-narial structure that can be flushed with water. This would coincide with the exit point from the gland which then would have been through a single, short duct as seen in Lepidosauria such as iguanas (Dunson, 1976). However, though the feature of a short channelization to flush the duct to the salt gland was also seen in marine crocodiles, the riffle producing structure is not (Fernández and Gasparini, 2000; Gandola, et al, 2006). However, this channel feature as an efficient mode of salt removal does not suggest an archosaur ancestor for ichthyosaurs but merely an analogous structure supported by the flare.

Evolution of the Salt Glands in the Ichthyosaur Skull—Dorsally situated nares have been noted on the more basal ichthyosaurs such as *Utatsusaurus*, although less so on mixosaurs (McGowan and Motani, 2003). On derived forms such as the paripelvans *Ichthyosaurus* and *Ophthalmosaurus,* the nares are laterally oriented (McGowan and Motani, 2003; Figure 12). The space in between the nares of the derived

forms such as *Ophthalmosaurus* appears to have expanded in relation to the forward extension of the nasal bones and the medial reduction of the frontal bones (McGowan and Motani, 2003). The salt gland in

FIGURE 11. The illustration above describes the hypothetical flow of water the across the ichthyosaur nares. The post-nares "scoop-like" structures (crescent) face anteriorly and lie dorsal and posterior to the canal or foramen on the dorsal process of the maxilla. The feature may increase hydrodynamic drag and facilitate the removal of excess salt (curved arrow) at the short duct through the dorsal process of the maxilla. Air flow through the internal and external nares (light arrows) would not have been inhibited by the external structure. Modified from Appleby, (1961).
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FIGURE 12. Illustrations of ichthyosaur skulls all represented at the same size. A. *Utatsusaurus*, B. *Mixosaurus*, C. *Ichthyosaurus* Modified from McGowan and Motani. (2003).
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the derived paripelvan ichthyosaurs may have followed the nasal expansion forward from dorsal to the orbit to anterior to the orbit, moving as the bones involved in the cheek region expanded in response to the orbital expansion (McGowan and Motani, 2003). It is likely that the salt glands may have been retained within the same spaces but moved anterior to the frontal/nasal contact as the orbit increased in size, and would then

have occupied the space at the frontal/prefrontal contact with the nasals inside the skull. The nasals in paripelvans are described as thickened and elevated displacing the nares to sides of the skull (McGowan and Motani, 2003). However, the bone thickness of the nasals as noted in UW24816 and UW24804 at the prefrontal contact is thin possibly to accommodate the expanded salt gland.

Likewise, The nasal glands undoubtedly evolved within the vomeral/nasal region as the ducts that support the associated glands do not extend beyond the nasal capsule. However, as mentioned before, individual glands are notoriously hard to identify within sauropsids, and there is dependence on homologous structure and analogous interpretation (Witmer, 1995). The ontogenetic path of the salt gland would suggest that in both archosaurs (birds) and lepidosaurs (marine iguanas) the salt gland would expand to the external spaces anterior/dorsal to the orbits as noted in some earlier ichthyosaurs (Marple, 1932; McGowan and Motani, 2003). This has been noted in extant tetrapods in 'extreme' situations such as the marine iguana and sea birds such as gulls (Dunson and Mazzotti, 1989).

As such, the bone terraces that support the enlarged salt glands in the marine iguana have been suggested as analogous supports for the glands in some ichthyosaurs (McGowan and Motani, 2003). The terraces occur in Triassic mixosaurs in a groove on the skull at the frontal/post-frontal parietal contact. These terraces appear to have been lost in the most of the more derived paripelvans such as ophthalmosaurs (McGowan and Motani, 2003). The sculpting of the UW24816 skull at this point is a mildly rugose surface and may have supported the salt gland and its corresponding blood flow and channelization. The space is bordered by the lateral edge of the nasals to the side and forms a deep valley posterior to the nares. As mentioned previously, the draft coefficient of the *Ophthalmosaurus* skull is low and adapted for low flow resistance so as to be hydrodynamically efficient. The increased drag caused by the large scoop-shaped structure would be improved if the space between the eyes was filled in with the external salt glands.

Curiously, Appleby's description of the nasal capsule in an *Ichthyosaurus communis* skull (Appleby, 1961, Figure 12, p. 346) illustrated area (delimited by a dotted line) posterior of the nares for an open space labeled as "brain". This is significant in that it is doubtful that the brain would be forward of the orbit. Appleby (1961) may have actually noted the open space which was occupied by the salt gland instead. Although this was a graphical interpretation of the of the vomeral/nasal region of *Ichthyosaurus communis* (OUMNH 2239), the space described is the same as that of the vomeral/nasal region of *Ophthalmosaurus natans* UW24816.

CONCLUSION

UW24816 is an opportunity for study of features preserved as sedimentary structures in cross-sections of the anterior-orbital region of a Jurassic ichthyosaur skull. These features and auxiliary support structures are displayed both internally and externally, and are here identified as salt glands. The open spaces of the skull would suggest a potential weak space to be distorted by compacting sediment. However the "salt gland" spaces are intact suggesting some resistance to the taphonomic deformation because there may have been some organic material inside that space preventing collapse. Coping with excess salt is a constant problem for secondarily adapted marine vertebrates and require a means to remove the excess of salt and flush it out of the body. Salt glands have been found in marine crocodiles and in plesiosaurs and had been expected in ichthyosaurs.

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