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NARIAL STRUCTURES IN *ICHTHYOSAURUS* AND OTHER EARLY JURASSIC ICHTHYOSAURS AS PRECURSORS TO A COMPLETELY SUBDIVIDED NARIS

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Abstract

The Early Jurassic ichthyosaur *Ichthyosaurus* displays a variety of bony features surrounding the external naris: a small triangular process on the lacrimal protruding into the external naris; a raised edge on the posterior portion of the naris formed by the lacrimal; or an arc-shaped bone at the posterior end of the naris. These features demarcate a circular, posterior region of the external naris. Similar features also occur in the narial region of other Early Jurassic taxa, including *Temnodontosaurus*, *Leptonectes*, *Excalibosaurus*, and *Hauffiopteryx*. Additionally, *Leptonectes tenuirostris* displays a protrusion or flange on the nasal that extends over the external naris. In the more derived ophthalmosaurid ichthyosaurs, bony structures around the naris are more pronounced. Large processes on the nasal almost separate the naris into two openings in *Sveltonectes* and *Muiscasaurus*. In other taxa (e.g., *Simbirskiasaurus birjukovi, Arthropterygius thalassonotus*) the naris is completely subdivided into two openings. A subdivided naris occurred in ophthalmosaurine ophthalmosaurids as early as the Oxfordian (Late Jurassic) in *Baptanodon natans*, as described here. Recent work interprets the complete partitioning of the naris as separate openings to accommodate the functions of air exchange and salt excretion. The bony structures seen in Early Jurassic taxa are probably precursors to the complete bony subdivision of the naris and might be related to the presence of nasal salt glands.

INTRODUCTION

Recent work by Campos et al. (2020) described bony structures associated with the external naris in the ophthalmosaurids, the most derived clade of ichthyosaurs. Some taxa display bony structures that nearly subdivide the external naris, (Fischer et al., 2011; Maxwell et al., 2016) whereas in other taxa, the external naris is completely subdivided into separate anterior and posterior openings, separated by a nasomaxillary pillar (Maisch and Matzke, 2000b; Fischer et al., 2014; Campos et al., 2020). A subdivided external naris occurred earlier than has been previously known (Campos et al., 2020), in the Oxfordian (Late Jurassic) *Baptanodon natans* (see below). Campos et al. (2020) and others (e.g., Tyborowski, et al., 2018; Zverkov and Efimov, 2019) have suggested that the subdivision of the nares separated air exchange from another function. The question arises as to when and how this separation of functions occurred in the course of ichthyosaurian evolution.

We report here on narial structures in Early Jurassic ichthyosaurs, with an emphasis on *Ichthyosaurus*. In many Early Jurassic ichthyosaurs, the external naris is bordered by the nasal, lacrimal, and premaxilla. In most taxa, the dorsal portion of the maxilla underlies the lacrimal and premaxilla along the ventral margin of the external naris, although the maxilla is exposed and comprises a portion of the ventral margin in some taxa (e.g., *Stenopterygius*). Subtle bony features occur on the lacrimal or nasal along the margins of the external naris in some specimens of *Ichthyosaurus*, *Protoichthyosaurus*, *Hauffiopteryx*, *Temnodontosaurus*, *Excalibosaurus*, and *Leptonectes*. These structures likely represent precursors to the bony subdivision of the external naris in more derived ichthyosaurs. As in those derived ichthyosaurs, the narial structures are likely related to salt excretion from nasal salt glands (Wahl, 2012; Campos et al., 2020).

Institutional abbreviations—ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; **BELUM**, Ulster Museum, National Museum of Northern Ireland, Belfast, UK; **BGS**, British Geological Survey, Keyworth, Nottingham, UK; **BRLSI**, Bath Royal Literary and Scientific

Institution, Bath, UK; **BRSMG**, Bristol City Museum and Art Gallery, UK; **BRSUG**, University of Bristol, UK; **CAMSM**, Sedgwick Museum, Cambridge University, UK; **DMNH**, Denver Museum of Nature and Science, CO, USA; **GPIT**, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany; **LEICT**, Leicester Arts and Museums Service (New Walk Museum and Art Gallery), UK; **MANCH,** Manchester Museum, The University of Manchester, UK: **MBI**, Museum für Naturkunde, Berlin, Germany; **NHMUK** (formerly BMNH), The Natural History Museum, London, UK; **NMW**, National Museum of Wales, Cardiff, UK; **OUMNH**, Oxford University Museum of Natural History, UK; **PMO**, Natural History Museum, Oslo, Norway; **SMNS**, Staatliches Museum für Naturkunde (Stuttgart State Museum of Natural History), Germany; **SOMAG** (formerly AGC), Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, UK; **TTNCM**, Somerset County Museum, Taunton, UK; **UW**, University of Wyoming, Laramie, WY, USA.

BONY STRUCTURES AROUND THE EXTERNAL NARIS

Most of our observations come from examination of specimens of *Ichthyosaurus*, which show a range of narial structures. In some specimens of *I. larkini* (e.g., BRSUG 25300), *I. somersetensis* (e.g., NHMUK OR2013*), and a few other specimens of the genus not attributed to a species, a small, triangular process on the anterior process of the lacrimal projects into the external naris (Figures 1A, B, E; Table 1). It is much too small to subdivide the external naris, but instead it demarcates a nearly circular, posterior portion of the opening. A specimen of *Hauffiopteryx typicus* (BRLSI M1401) from the Toarcian of Somerset, UK, has a similar short process on the lacrimal, but also has an embayment posterior to it (Figure 2C; Table 1), again demarcating a posterior portion of the external naris.

In a few specimens of *Ichthyosaurus*, the lacrimal forms a raised edge at the posterior margin of the external naris (Figure 1C; Table 1). In other specimens, the posterior portion of the naris appears to be more resistant to crushing than the rest of the naris (Figure 1D; Table 1), suggesting that it is similarly reinforced. This can even be observed on specimens where the skull is dorsoventrally crushed (e.g., BRLSI M3562). Similarly, a specimen of *Temnodontosaurus platyodon* (NHMUK R1158) also has a raised edge, formed by the lacrimal, at the posterior end of the naris.

On a couple of well-preserved specimens of *Ichthyosaurus somersetensis* (Figures 1 E, F; Table 1), a curved bone is present at the posterior end of the external naris. The bone is dislodged from its natural position in both specimens, so it is possible that it is pushed out from underneath. However, given that it occurs in a similar position on at least two specimens, and that the morphology does not match any bone that is present underneath, this is not likely.

A specimen of *Protoichthyosaurus prostaxalis* (LEICT G142.1991) possesses a broad flange that appears to connect with the anterior process of the lacrimal and extends posteromedially into the narial opening (Lomax et al., 2020:fig. 2c). In what might be a similar feature, Maisch and Matzke (2000a) reported the presence of an ossification within the posteroventral portion of the external nares in a three-dimensionally preserved skull of what was then identified as *Ichthyosaurus communis* (GPIT/RE/09728, previously GPIT 1796/1, reassigned to *P. prostaxalis* by Lomax and Massare, 2018). Following Sollas (1916), Maisch and Matzke (2000a) identified the bone as a septomaxilla. Sollas (1916) also found an ossification within the naris of a specimen that might be *Ichthyosaurus* or *Protoichthyosaurus*. The specimen was labeled as *Ichthyosaurus communis*, although Sollas (1916:63) questioned the identification.

A septomaxilla, however, has not been reported in any extant marine reptile. In extant terrestrial squamates, however, it is located in the posteroventral region of the external naris (Rieppel et al., 2008). Its morphology differs depending on its role in enclosing the Jacobson organ, which is used in chemoreception (Rieppel et al., 2008). In species with a larger Jacobson organ, the septomaxilla is larger and more curved, and can contact the maxilla and vomer (Rieppel et al., 2008). Thus the septomaxilla is an olfactory support structure, at least in extant lizards. Whether the bones identified by Sollas (1916) and Maisch and Matzke (2000a) are septomaxillae or something else, they suggest the presence of a bony structure within the external naris in *Protoichthyosaurus*.

A specimen of *Temnodontosaurus trigonodon* (SMNS 15950) has a process on the lacrimal that extends well into the external naris, more pronounced than what occurs on *Ichthyosaurus* (Figure 2B; Table 1). Other specimens of *Temnodontosaurus* have a subdued bulge on the lacrimal that extends into the external naris (Figure 2A; Table 1), which might indicate that the aforementioned process is obscured by deformation. Maisch and Hungerbühler (1997) described a specimen of *T. nuertingensis* (SMNS 13488) with a well-defined process on the lacrimal, as well as a flange on the nasal that protrudes into the dorsal margin of the naris.

Both *Leptonectes tenuirostris* (Figure 2D, Table 1) and *Excalibosaurus costini* (BRSMG Cc881) have a small process on the lacrimal which defines a small, roughly circular region at the posterior end of the naris (McGowan, 1989a:fig. 1A; McGowan, 1989b:fig. 1;

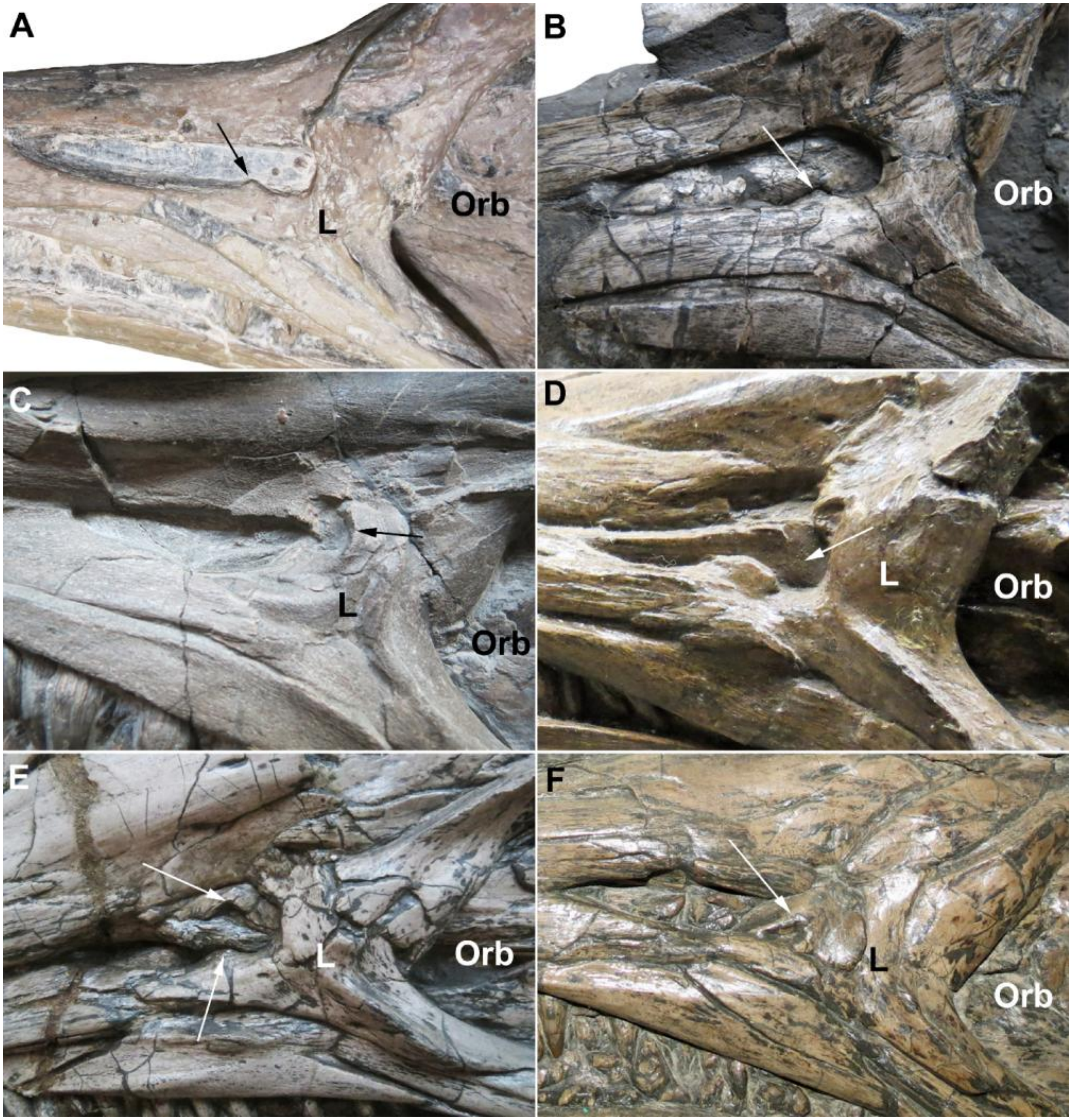

FIGURE 1: *Ichthyosaurus* specimens showing various bony structures in the external naris. Anterior to the left in all images. **A**, BRSUG 25300, holotype of *Ichthyosaurus larkini* (reversed), showing a process on the lacrimal, indicated by arrow, demarcating a circular region at the posterior end of external naris. **B**, NHMUK R1079, *Ichthyosaurus* sp. showing the same as A. **C**, NHMUK OR39492, *Ichthyosaurus* sp., showing process on lacrimal and a raised posterior edge, indicated by arrow. **D**, ANSP 17429, *Ichthyosaurus* sp. (reversed) showing flattened anterior naris and round posterior portion, suggesting that the latter was resistant to crushing. **E**, NHMUK OR2013*, *Ichthyosaurus somersetensis* (reversed), showing an arc of bone present at posterior end of the external naris (upper arrow). It also shows a process on the lacrimal that defines a circular region in the posterior naris (lower arrow). **F**, ANSP 15766, holotype of *I. somersetensis*, showing a similar arc of bone as E. The additional elements inside the external naris are dislodged teeth. **Abbreviations**: **L**, lacrimal; **Orb**, orbit.

TABLE 1. Specimens of Early Jurassic ichthyosaurs showing bony features on the margin of the external naris.

Specimen	Species	Morphology
ANSP 15766	*Ichthyosaurus somersetensis*	arc of bone at posterior naris
BELUM K28052	*Ichthyosaurus* sp.	process on lacrimal
BGS 85785	*Ichthyosaurus somersetensis*	bone at posterior naris
BRSUG 25300	*Ichthyosaurus larkini*	process on lacrimal
CAMSM J59574	*Ichthyosaurus somersetensis*	process on lacrimal
NHMUK OR2013*	*Ichthyosaurus somersetensis*	process on lacrimal; arc of bone at posterior end of naris
NHMUK OR2090	*Ichthyosaurus ?somersetensis*	process on lacrimal
NHMUK OR39492	*Ichthyosaurus* sp.	process on lacrimal; raised edge of posterior naris
NHMUK R1077	*Ichthyosaurus* sp.	process on lacrimal
NHMUK R1079	*Ichthyosaurus* sp.	process on lacrimal; raised edge of posterior naris
NHMUK R11801	*Ichthyosaurus ?conybeari*	process on lacrimal
OUMNH J.13587	*Ichthyosaurus anningae*	bone at posterior end of naris; possible process on lacrimal
SMNS 13111	*Ichthyosaurus communis*	possible process on lacrimal; differential crushing
TTNCM 8333	*?Ichthyosaurus* sp.	process on lacrimal
BRSMG Cc881	*Excalibosaurus costini*	two small processes on lacrimal
BRLSI M1401	*Hauffiopteryx typicus*	process and embayment on lacrimal
ANSP 17428	*Leptonectes ?tenuirostris*	posterior portion of naris constricted and bends dorsally
BGS 51236	*Leptonectes tenuirostris*	posterior portion of naris constricted and bends dorsally
BRLSI M3552	*Leptonectes ?tenuirostris*	flange on nasal
CAMSM J13578	*Leptonectes tenuirostris*	posterior portion of naris constricted and bends dorsally
MBI 2099	*Leptonectes* cf. *tenuirostris*	flange on nasal
OUMNH J.10305	*Leptonectes tenuirostris*	posterior portion of naris constricted and bends dorsally
SNMS 90699	*Stenopterygius aaleniensis*	flange on nasal; notch in nasal posterior to flange (Maxwell et al. 2012)
SMNS 13488	*Temnodontosaurus nuertingensis*	process on lacrimal; flange on nasal (Maisch and Hungerbühler, 1997)
NHMUK R1158	*Temnodontosaurus platyodon*	low, rounded ‘bulge’ on lacrimal raised posterior edge of naris
Hauff Museum display specimen	*Temnodontosaurus trigonodon*	prominent process on lacrimal
SMNS 13128	*Temnodontosaurus trigonodon*	low, rounded ‘bulge’ on lacrimal
SMSN 15950	*Temnodontosaurus trigonodon*	prominent process on lacrimal
	Less convincing specimens	
ANSP 17429	*Ichthyosaurus* sp.	possible process on lacrimal; differential crushing
BGS 956	*Ichthyosaurus conybeari*	bone in posterior portion of naris
BRLSI M3562	*Ichthyosaurus* sp.	differential crushing
BRLSI M3569	*Ichthyosaurus somersetensis*	differential crushing

Table 1 cont.

CAMSM TN4194	*Ichthyosaurus* sp.	differential crushing
NMW G1553	*Ichthyosaurus ?somersetensis*	possible process on lacrimal; differential crushing
SOMAG/3	*Ichthyosaurus* sp.	possible process on lacrimal; bone inside posterior external naris
SOMAG/11	*Ichthyosaurus larkini*	possible process on lacrimal
TTNCM 8373	*Ichthyosaurus somersetensis*	possible process on lacrimal
GPIT 1796/1	*Protoichthyosaurus prostaxalis*	bone at posterior end of naris
LEICT G141.1991	*Protoichthyosaurus prostaxalis*	possible raised posterior edge of naris
DMNH 2729	*Stenopterygius* sp.	possible embayment on lacrimal

also see reconstructions in McGowan and Motani, 2003:figs. 72, 75). The posterior portion of the naris curves slightly dorsally compared to the rest of the naris, further isolating the region from the rest of the naris. Both taxa also show a small bulge on the nasal. In the case of *Leptonectes*, it is likely due to deformation of a flange on the nasal that overhangs the external naris, as occurs in MBI 2099 (Figure 3A; referred to as MBI 007.11 in Maisch and Matzke, 2003:fig.2). Another *L. ?tenuirostris* specimen (BRLSI M3552) illustrates how taphonomic compaction can push the flange into the external narial opening (Fig. 3B). Maxwell et al. (2012:4) found a similar structure on the nasals in a Middle Jurassic species, *Stenopterygius aaleniensis*, which they described as “a thin shelf overhanging the naris”. Posterior to the overhang, at the dorsoposterior edge of the naris, is a notch and a thickened ridge (Maxwell et al. 2012:fig. 3), the latter being reminiscent of the raised edge on the lacrimal on the posterior margin of the naris described above for *Ichthyosaurus*. The result is that a portion of the naris margin projects outward from the streamlined contour of the rostrum in these taxa (Figure 3A).

NARIAL STRUCTURES IN MORE DERIVED ICHTHYOSAURS

Maisch and Matzke (2000b:91) suggested that processes on the nasal and lacrimal in Early Jurassic taxa were probably precursors to the complete subdivision of the external naris seen in some ophthalmosaurids. Even in taxa where the naris is not completely subdivided, bony narial structures are much more prominent in ophthalmosaurids than in Early Jurassic species. In the Middle-Late Jurassic species *Ophthalmosaurus icenicus,* the posterior portion of the naris is somewhat constricted, caused by small processes on the nasal and lacrimal, and a portion of the nasal overhangs the external naris, sometimes with a posterior notch in the nasal (Moon and Kirton, 2016:22, text-fig. 4, Pl. 1). Gasparini (1988:fig. 2) described an ophthalmosaurid with a projection from the nasal that extends into the external naris, dividing the narial opening into two lobes. A narrower descending process of the nasal occurs in the Early Cretaceous ichthyosaur *Sveltonectes insolitus* (Fischer et al., 2011:fig. 1). The Early Cretaceous species *Muiscasaurus catheti* has an even longer descending process that nearly contacts a small, triangular process on the lacrimal, almost completely dividing the external naris (Maxwell et al., 2016). The position of the projections produce a well-defined oval shape at the posterior portion of the naris (Maxwell et al., 2016:fig. 2b,d).

Many authors have recognized that the two openings in the narial region of some ophthalmosaurids are the result of the subdivision of the external naris (e.g., Maisch and Matzke, 2000b; Fischer et al. 2014; Maxwell et al., 2016). Some Late Jurassic taxa, the Oxfordian species *Baptanodon natans* (UW 24866; Figure 4; see below) and the Tithonian species *Arthropterygius thalassonotus* (Campos et al., 2020) have two openings in the narial region. What Zverkov and Efimov (2019, fig. 3C) interpreted as a nasal foramen on *Undorosaurus gorodischensis* (= *Cryopterygius kristiansenae* in Druckenmiller et al, 2012, fig. 5A) could also be interpreted as a small, round posterior narial opening bounded anteriorly by a very narrow nasomaxillary pillar. Posterior and anterior narial openings have also been reported in the Early Cretaceous ichthyosaurs *Simbirskiasaurus birjukovi* from the Barremian, *Platypterygius australis* (=*P. longmani* of Kear, 2005) from the Albian (Fischer et al., 2014), *Platypterygius sachicarum* from the Barremian-Aptian (Maxwell, 2016:65, 2019), and possibly in the Late Cretaceous species *Pervushovisaurus bannovkensis* from the Cenomanian (Maisch and Matzke, 2000b :92). Significantly, the completely subdivided naris occurs not only in the Cretaceous

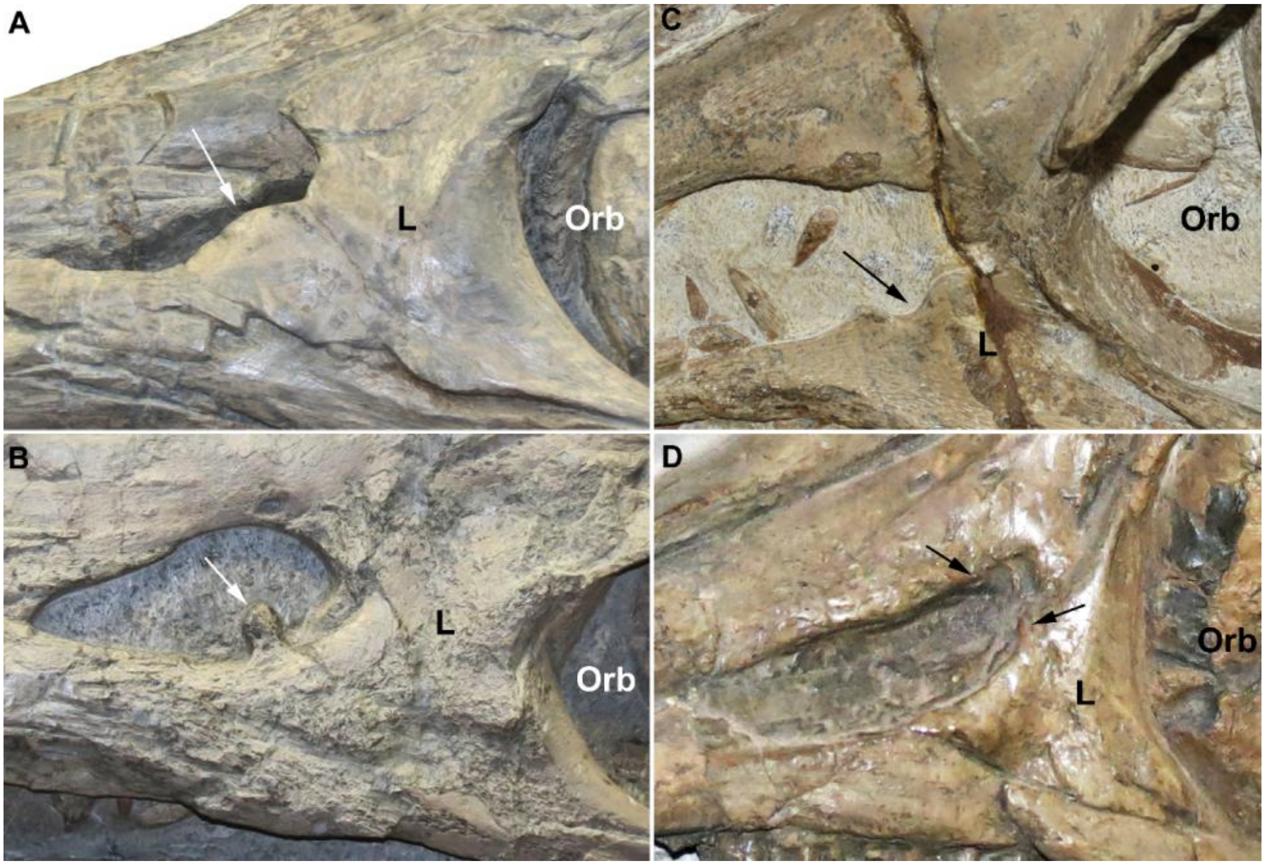

FIGURE 2: Some Lower Jurassic taxa showing bony features of the external naris. Anterior to the left on all images. **A**, SMNS 13128, *Temnodontosaurus trigonodon* showing rounded 'bulge' on the lacrimal, indicated by arrow. **B**, SMNS 15950, *Temnodontosaurus trigonodon* showing prominent process on lacrimal, indicated by arrow. **C**, BRLSI M1401 (reversed), *Hauffiopteryx typicus* showing process on lacrimal and an embayment, indicated by the arrow. **D**, ANSP 17428, *Leptonectes ?tenuirostris*, showing dorsal bend of posterior naris and distinct processes on lacrimal and nasal (arrows). **Abbreviations**: **L**, lacrimal; **Orb**, orbit.

platypterygiines (e.g., *S. birjukovi*, *P. australis*), but also in Jurassic ophthalmosaurines (e.g., *B. natans*, *A. thalassonotus*). Campos et al. (2020) hypothesized that the phylogenetic distribution of the subdivided naris suggested that subdivision occurred more than once within the ophthalmosaurids.

Additionally, Kear (2005) reported a raised edge of the naris and a portion of the nasal overhanging the external naris in *P. australis*. The latter sounds similar to narial structures in *Leptonectes tenuirostris*.

EARLIEST OCCURRENCE OF A SUBDIVIDED NARIS

Campos et al (2020) described a subdivided naris in the Late Jurassic (Tithonian) ophthalmosaurid, *Arthropterygius thalassonotus*, at the time thought to be the earliest occurrence of a subdivided naris in ichthyosaurs. We report here on an earlier occurrence, in a specimen from the Late Jurassic (Oxfordian) Redwater Shale Member of the Sundance Formation from northwestern Natrona County, Wyoming.

The specimen, UW24816, is *Baptanodon natans*, the only ichthyosaur species reported from the Sundance Formation (Massare et al., 2014). The nearly complete, ~1 m long skull was preserved in three dimensions, oriented at a right angle to the anterior skeleton, which was lying along bedding. The carcass had evidently descended to the seafloor head first, with the skull sinking into the soft substrate and the broader postcranial portion resting on the substrate (Wahl, 2009). The most anterior ~15 cm of the rostrum was split open, with the premaxillary and dentary portions at nearly right angles to each other, perhaps because the rostrum hit something hard in the substrate (Wahl, 2009, fig. 1). The tip of the rostrum is missing.

The narial region in UW24816 has an anterior and posterior opening, separated by a broad nasomaxillary pillar (Figure 4A). The anterior opening is antero-posteriorly elongated and bordered by the nasal,

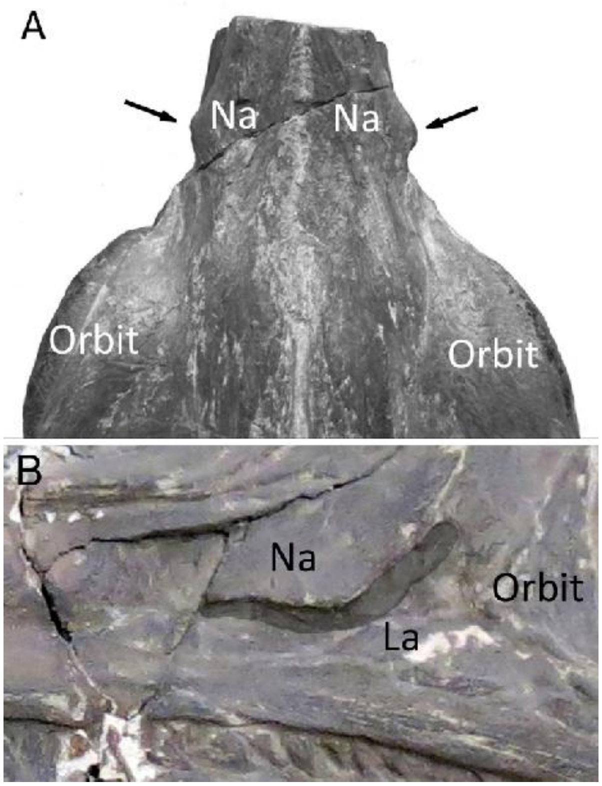

FIGURE 3: **A**, Dorsal view of three-dimensional partial skull BMI 2099, *Leptonectes* cf. *tenuirostris.* Arrow indicates a flange on the nasal that overhangs the external naris. Anterior towards the top. **B**, Left lateral view of BRLSI M3552, *Leptonectes* ?*tenuirostris*, showing the flange on the nasal covering part of the external naris because of deformation. Anterior to the left. The external naris has been shaded to better show the extent of the nasal flange. Abbreviations: **La**, lacrimal; **Na**, nasal.

premaxilla, and maxilla. The posterior opening is almost circular and is bordered by the nasal, maxilla, and lacrimal. It is located more dorsally than the anterior opening. The posterior opening has raised edges that show rugosity or 'sculpting', especially on the posterior margin (Figure 4A).

The rostrum was fractured perpendicular to its length, from just posterior to the external nares to the anterior end, revealing a series of cross-sectional views along nearly the entire length of the rostrum. Wahl (2012) described a pair of lobate infillings posterior to the external naris, seen in the cross-section, and a groove on the interior of the maxilla. Appleby (1961), after studying Sollas' (1916) serial sections of an ichthyosaur skull, concluded that a pair of 'hollows' occur posterodorsal to the external naris in *Ichthyosaurus* (or more likely *Protoichthyosaurus*, see above) and *Ophthalmosaurus*. He interpreted these voids as space for an anterior extension of the brain. The lobate infillings reported in *Baptanodon natans* (UW24816) are approximately in this position, and Wahl (2012) suggested instead that this was the location of nasal salt glands.

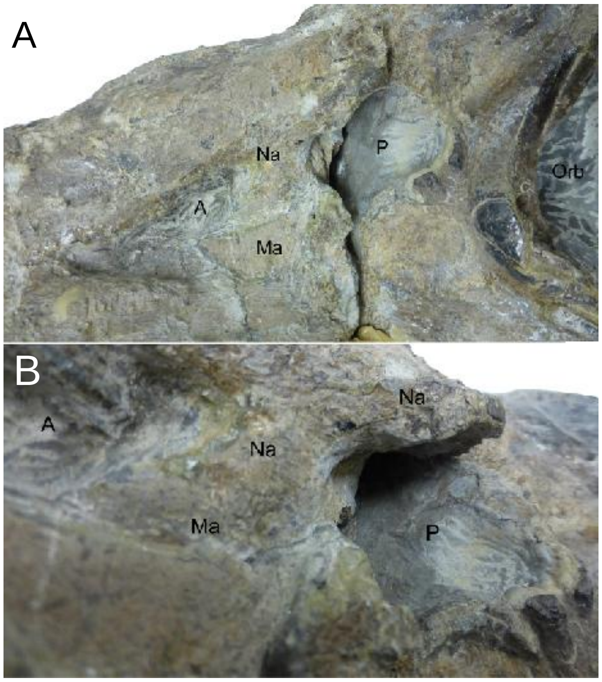

FIGURE 4: Completely divided naris on UW24816 *Baptanodon natans*. **A**, lateral view, (anterior to the left) showing two narial openings separated by nasomaxillary pillar. Note the raised, irregular edge of the posterior opening. **B**, oblique view, left side, showing flange on nasal overhanging the posterior narial opening. **Abbreviations**: **A**, anterior narial opening, **L**, lacrimal; **M**, maxilla; **Na**, nasal; **P**, posterior narial opening.

TAPHONOMIC ISSUES

Considering the large number of specimens known of Early Jurassic ichthyosaurs, especially *Ichthyosaurus*, the number showing the features of the external naris described above is fairly small (Table 1). Recognizing the bony features described here requires a lateral orientation or three dimensional preservation of the skull. And, of course, the external naris must be intact. However, the external naris is crushed or deformed in many specimens (e.g. Figures 1C, 3B). Thus the preservation of narial structures might be controlled by the quality of preservation, specifically the amount of crushing and the direction of compression. In fact, in one specimen of *Ichthyosaurus* (BELUM K28052), the right external naris is well preserved and a small, well-defined process is present at the anterior end of the lacrimal (Figure 5A). The left side of the specimen is not as well preserved and the small process is missing (Figure 5B).

However, preservation is not the only factor because a small number of fairly well-preserved specimens (e.g., USNM V4967, CAMSM J47057, TTNCM 8341) do not seem to show any of the features described. Another possible explanation is that the process on the lacrimal might be visible only from a certain angle because it projects downward into the naris, below the level of the dermal skull bones. This was the case in a skull of *Protoichthyosaurus prostaxalis* (LEICT G142.1991), where additional preparation was required to expose a bone that extended from the lacrimal into the external naris (Lomax et al., 2020).

Additionally, over preparation, especially on historical specimens, can easily result in any of these minor features being unintentionally removed. A *Baptanodon natans* skull (CM 878) figured by Gilmore (1906: pl. 8) seems to have an elongated external naris that bends sharply dorsally at the posterior end. It is quite possible that the nasomaxillary pillar was inadvertently removed during preparation because, at the time, a subdivided naris was not expected.

INTERPRETATION

The bony structures associated with the external naris in *Ichthyosaurus* and other Early Jurassic taxa separate a posterior region of the external naris from a larger anterior portion. This suggests that even in Early Jurassic taxa, the external naris was not simply an opening for air exchange. A dual function for the external naris has been suggested before, mainly for ophthalmosaurids, but the nature of the second function has still not been resolved.

Moon and Kirton (2016: 22, text-fig. 4) recognized bony processes on the nasal of *Ophthalmosaurus icenicus* and suggested that they were for soft tissue valvular structures, presumably to open and close the external naris. Tyborowski et al. (2018) argued that the external naris functioned for both air exchange and olfaction, with seawater being taken in through the naris and expelled through the mouth. Zverkov and Efimov (2019:fig. 3) suggested that a small posterodorsal opening on *Undorosaurus gorodischensis* (=*Cryopterygius kristiansenae*), was for the passage of blood vessels and/or nerves. Campos et al. (2020) argued that the subdivision of the external naris separated salt excretion from air intake. The latter interpretation is consistent with the position of salt gland ducts in the extant marine iguana.

In *Baptanodon natan*, the bones around the posterior narial opening protrude outward, in contrast to the otherwise streamlined shape of the rostrum and skull (Figure 4B). *Leptonectes tenuirostris* (Figure 2; Maisch and Matzke, 2003:fig.2) and *Stenopterygius aaleniensis* (Maxwell et al., 2012:fig.3) have a flange on the nasal that extends outward over the external naris. A similar, although less prominent, protrusion occurs in *Ichthyosaurus* in the form of a raised edge of the lacrimal at the posterior end of the naris. These features could alter the flow of water along the rostrum, perhaps creating turbulence that could flush out the posterior portion of the naris. Thus salt glands emptying into the external naris could be in a position for passive removal of a concentrated salt solution. Of course, these protruding features could be enhanced or subdued by soft tissue/skin. It is also possible that the salt solution could be expelled with seawater when an ichthyosaur surfaced to breathe.

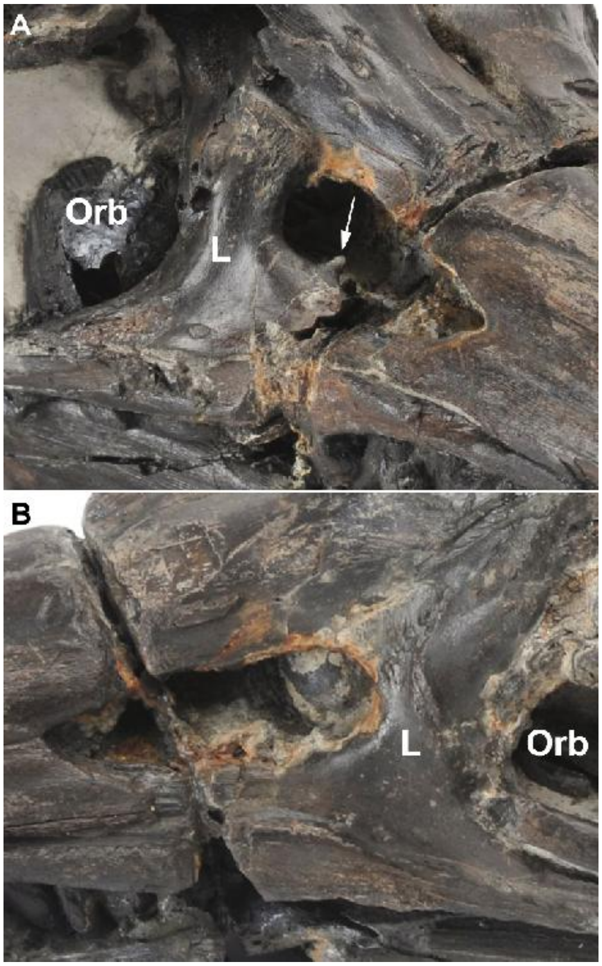

FIGURE 5: BELUM K28052, *Ichthyosaurus* sp. showing differences in preservation on a single specimen. **A**, Right side with arrow pointing to the distinct process on the lacrimal that is angled slightly medially. Anterior to the right. **B**, Left side with no process on the ventral margin of the naris. Anterior to the left. **Abbreviations**: **L**, lacrimal; **Orb**, orbit.

All extant marine reptiles and marine birds, as well as some reptiles living in salt-stressed environments, have salt glands, although the position varies (Babonis and Brischoux, 2012). Preying upon marine organisms results in ingesting large amounts of salt, but reptilian and avian kidneys cannot excrete it in sufficient concentrations (Babonis and Brischoux, 2012). Preserved gut contents of ichthyosaurs often contain numerous cephalopod hooklets (e.g., Pollard, 1968; Buchy et al., 2004; Brinkmann, 2004; Massare and Young, 2005; Lomax, 2010; Dick et al., 2016), indicating that cephalopods were frequent prey for many different species. Cephalopods are isotonic with seawater, and thus ichthyosaurs would have ingested high concentrations of salt. A salt gland for excreting extra salt would be required.

Fernández and Gasparini (2000) described a pair of lobate casts at the base of the rostrum between the orbits and external naris in *Geosaurus* (now *Cricosaurus*) *araucanensis* from the Late Jurassic (see also Fernández and Gasparini, 2008). Fernández and Herrera (2009) recognized a bony signature of a salt gland, a depression on the inner surface of the lacrimal and prefrontal, on the Middle Jurassic metriorhynchid *Metriorhynchus westermanni*. Herrera et al. (2013) subsequently found that a lacrimal-prefrontal depression on *Cricosaurus araucanensis* perfectly fit a lobate endocast of what was probably a salt gland. Gandola et al. (2006) also interpreted a depression on the inner surface of the prefrontal of another metriorhynchid, *M. superciliosus*, as the position of a salt gland. Recently, an expansion of the nasal cavity anterior to the orbits was interpreted as the position of salt glands in the Early Jurassic teleosauroid *Pelagosaurus typus*, suggesting that nasal salt glands were present early in the evolution of marine crocodylomorphs (Pierce et al., 2017).

Nasal salt glands have also been suggested in other extinct marine reptiles. Martin and Fernández (2009) argued that the paired infilling in the narial region of the Late Cretaceous polycotylid plesiosaur, *Pahasapasaurus haasi* (Schumacher, 2007:fig. 4), are actually casts of salt glands. The ‘botryoidal surfaces’ of the infillings, described by Schumacher (2007:137), seem similar to the lobate structure described for metriorhynchid crocodyliforms (e.g., Fernández and Gasparini, 2008; Herrera et al., 2013). Konishi (2015) has also hypothesized that mosasaurs had a nasal salt gland in the antorbital region, posterior to the choana.

Wahl (2012) argued that the lobate infillings posterior to the external naris in *Baptanodon natans* (UW 24816) were casts of salt glands. Kear (2005) described a similar lobate depression on the inner surface of the lacrimal and a groove leading to the external naris in *Platypterygius australis* (Kear, 2005). In both cases, the lobate structure and its location seem similar to casts attributed to salt glands in metriorhynchid crocodyliforms (e. g., Fernández and Gasparini, 2000, 2008; Herrera et al., 2013). Thus the presence of nasal salt glands in ichthyosaurs would be consistent with what has been found in other Mesozoic marine reptiles.

CONCLUSION

In *Ichthyosaurus* and other Early Jurassic ichthyosaurs, bony structures are present at the posterior end of the external naris. The degree of expression of structures around the naris varies among taxa, but the structures are subtle and easily overlooked or removed during preparation (especially on historic specimens). Some features, such as a bony projection on the lacrimal that extends into the naris, or a dorsal bend in the posterior region of the external naris, or both, demarcate a posterior region of the external naris. These structures are probably related to the presence of nasal salt glands. The difference in these structures among Early Jurassic taxa is not stratigraphically or phylogenetically controlled, i.e. the most derived taxa do not display the most prominent structures.

The narial structures in Early Jurassic ichthyosaurs are likely precursors to more prominent structures in ophthalmosaurids (see Campos et al. 2020), the most derived parvipelvian clade. *Sveltonectes birjukovi* and *Muiscasaurus catheti*, for example, have a long, descending process on the nasal that almost fully subdivides the external naris (Fischer et al., 2011; Maxwell et al., 2016). In other taxa (e.g., *Platypterygius australis*, *Simbirskiasaurus birjukovi*, *P. sachicarum*, *Arthropterygius thalassontotus*, *Undorosaurus gorodischensis*; Kear, 2005; Fischer et al., 2014; Maxwell, 2016; Zverkov and Efimov, 2019; Campos et al. 2020) the external naris is completely divided into two separate openings by a nasomaxillary pillar (Fischer et al., 2014). Interestingly, in some species the anterior opening is the larger one, whereas in other species the reverse occurs (Campos, 2020). As with the Early Jurassic forms, the most derived naris morphology does not necessarily occur in the most derived taxa. The fully subdivided external naris occurs in both ophthalmosaurines and platypterygiines, and was present as early as the Oxfordian stage (Late Jurassic), in *Baptanodon natans* as discussed herein. We agree with Campos et al. (2020) that the subdivision probably served to isolate the function of air exchange from excretion of a concentrated salt solution from nasal salt glands.

Ichthyosaurs, like all extant marine reptiles, needed salt glands. The extant marine iguana, which spends most of its time on land but eats marine plants, has a salt gland for osmoregulation (Dunson, 1969; Wikelski and Trillmich, 1994). It is more amphibious than marine, with few adaptations for aquatic locomotion compared to Mesozoic marine reptiles (Dawson et al., 1977; Miles et al., 1995), yet it has large salt glands. Similarly, marine turtles and crocodylomorphs developed salt glands very early in their history, the former even before acquiring adaptations for swimming (Hirayama, 1998; Pierce et al., 2017). Thus ichthyosaurs must have evolved salt glands early in their evolutionary history, probably soon after their terrestrial ancestors began taking marine prey.

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