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SALT GLANDS IN THE FOSSIL CROCODILE METRIORHYNCHUS

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The Metriorhynchidae, marine mesosuchian crocodiles from the Jurassic and early Cretaceous, must have possessed an extra-renal mechanism for processing salt just like all living marine reptiles (including some birds). Metriorhynchus superciliosus, a species known from all over Europe, was presumably no different—its other morphological specializations (enlarged paddle-like appendages, fin on the tail) demonstrate that it was well adapted to a marine lifestyle. However, unlike living marine mammals that excrete salt via their kidneys, the comparatively inefficient reptilian renal system necessitates extra-renal salt glands (Schmidt-Nielsen and Fange, 1958). All extant marine reptiles and many marine birds have evolved cranial salt glands to remove excessive electrolytes (Schmidt-Nielsen and Fange, 1958; Bentley, 1976; Dunson, 1976; Minich, 1982) as marine turtles, for example, salt is excreted via lacrimal glands located in the corner of the eye (Dunson, 1976; Reina et al., 2002).

The skull of Metriorhynchus superciliosus is anatomically well known (Andrews, 1913; Wenz, 1968, 1970; Adams-Tresman, 1987) but as yet no direct fossil evidence for the position and shape of extra-renal salt glands has been found (Fernández and Gasparini, 2000). The presence of a pocket in the antorbital region of metriorhynchid skulls has been noted by several authors (Witmer, 1997), including Fernández and Gasparini (2000) who described a natural cast of the gland itself in this area of the snout in the metriorhynchid Geosaurus araucanensis (Fernández and Gasparini, 2000; figs. 2, 4).

Consistent with Fernández and Gasparini’s (2000) study of Geosaurus, we present the first direct fossil evidence for salt gland morphology in Metriorhynchus superciliosus. We describe two well-preserved skulls of M. superciliosus, from the mid-late Jurassic Oxford Clay Formation of Huntingdonshire, England. Not only do these skulls preserve a well-defined space that could have accommodated a nasal salt gland, but they also preserve a duct leading from this region into the antorbital fenestra. The presence of this duct shows that the nasal gland discharged via the antorbital fenestra, corroborating its function for excretion, most likely for salt. We discuss the presence of a salt gland in Metriorhynchus and comment on its physiological significance.

FOSSIL MATERIAL

The two skulls of Metriorhynchus superciliosus, which are the subject of this article, are held in the geological collections of the National Museum of Ireland (NMING). Each was purchased from Alfred Nicholson Leeds in 1893, along with assorted post-cranial elements.

Institutional Abbreviations—NMING. National Museum of Ireland (Division of Natural History), Dublin, Ireland; GFCL, Laboratoire de Paléontologie stratigraphique de l’Université Catholique de Lille, Lille, France.

DESCRIPTION

Of the two skulls, one (NMING F21731) comprises a series of broken skull elements, including the braincase, frontal-prefrontal, and rostrum (Fig. 1A). The second specimen, NMING F16892, consists of a largely intact cranium and rostrum, including an almost complete palate (minus the choana; skull not shown). On both sides of the cranium in NMING F21731, the prefrontal wall is thin and high (at least on the left hand side), separating the orbit from the antorbital cavity. This creates a pair of concave depressions in this area of the rostrum that could accommodate the posterior regions of nasal glands similar in size to those described in Geosaurus by Fernández and Gasparini (2000). In NMING F21731, small semicircular pits project into the overlying prefrontal, again concurrent with Fernández and Gasparini’s (2000) proposal that the nasal salt glands in metriorhynchid crocodiles were lobate in shape (Fig. 1B). A similar teardrop-shaped depression is seen in another Metriorhynchus skull (GFCL 491) from the Callovian of Le Waast, northern France (Dubar, 1957; Deville, 2004). In all likelihood, all sufficiently well preserved specimens of these crocodiles will have these depressions. NMING F21731 and NMING F16892 also exhibit symmetrical swellings on both sides of their palates ventral to the area where the salt gland was positioned. Numerous foramina are visible on the ventral surface of these swellings, perhaps for the supply of blood to the overlying gland.

Visible in NMING F21731, on the ventral side of the skull roof, narrow grooves lead away from these depressions in an anterolateral direction towards the margin of the snout (Fig. 1A). Most clearly seen on the right side of this skull, these grooves form the dorsal margin of ducts that open into the posterior end of the antorbital fossa (Fig. 1D, E). The morphology of these openings agrees with Wenz (1968, 1970) who described a small fenestra opening into the antorbital fossa in Metriorhynchus (Wenz, 1968). The presence of ducts leading away from the nasal glands was inferred in Geosaurus araucanensis by Fernández and Gasparini (2000) even though they are not visible on the natural casts of this specimen (Fernández and Gasparini, 2000; fig. 2). These workers proposed that these ducts emptied either via the nares or into the antorbital fossa in Geosaurus; evidence from the Dublin specimens demonstrates that the latter interpretation is correct.

DISCUSSION

The prefrontal region in Metriorhynchus was almost certainly not a site for muscle insertion or attachment. The marked depressions seen in this part of the skull in the Dublin specimens either housed glands or some kind of air space. The presence of anterolateral grooves opening into the antorbital fossa by way of the antorbital fenestra indicate that glands were likely present in this region of the Metriorhynchus cranium. Our evidence is further consistent with natural casts of just such glands described in the closely related Geosaurus from the Jurassic of Patagonia (Fernández and Gasparini, 2000). The fact that the canals preserved in the Dublin specimens open into the antorbital fossa on both sides of the skulls suggests that these glands functioned for excretion into the external marine environment. Salt glands are thus the most parsimonious explanation for the presence of these structures.

The function and evolution of the antorbital fenestra in archosaurs is much debated; our result does not imply that this fenestra functioned as the site for salt excretion in all, or even most, archosaurs (see Witmer, 1997: pp. 12–40). In extant Crocodylus, for example, salt excretion is achieved via a lingual gland on the tongue (Mazzotti, 1989). The evolution of this characteristic in extant crocodilians was discussed by Fernández and Gasparini (2000); differences in the position of the salt gland between taxa suggest that they are likely non-homologous across crocodyliforms. The emplacement of this gland within the antorbital cavity raises one possible explanation for its appearance within archosaurs.
Both Witmer (1997) and Fernández and Gasparini (2000) suggest that nasal salt glands in *Metriorhynchus* were likely modified from the more primitive generalized nasal glands found across all major clades of archosaurs (Witmer, 1997). Thus, these basal marine crocodilians retained the nasal positioning for this gland inherent in their ancestral precursors. This positioning is not seen in the lineage giving rise to extant taxa, which suggests independent evolution of lingual salt glands.

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**LITERATURE CITED**


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