

A Rebuttal to Nesbitt & Hone's "An external mandibular fenestra and other archosauriform characters in basal pterosaurs"

BENNETT, S. Christopher

Nesbitt & Hone (2010) identified what they interpreted as external mandibular fenestrae in two specimens of *Dimorphodon macronyx* and in *Eudimorphodon cf. ranzii* (BSP 1994 I 51; Wellnhofer, 2003), identified what they interpreted as antorbital fossae in one specimen of *Dimorphodon macronyx*, in *Raeticodactylus filisurensis* (Stecher, 2008), and in unspecified specimens of *Pterodactylus*, and despite their title argued that the presence of external mandibular fenestrae and antorbital fossae in pterosaurs plus the shared absence of fourth trochanters in *Dimorphodon macronyx* and *Dromomeron romeri* supported inclusion of the Pterosauria within the clade *Erythrosuchus* + Archosauria. Suspecting that Nesbitt & Hone (2010) had made several errors of interpretation, I examined available specimens of *Dimorphodon macronyx*, *Eudimorphodon cf. ranzii*, *Raeticodactylus filisurensis*, and *Dromomeron romeri*, and here report on the results of those examinations.

Nesbitt & Hone (2010) described and illustrated large holes anterior to the articular region of the mandible of *Dimorphodon* in a large skull exposed in left lateral view (NHMUK OR 41212) and an isolated mandibular ramus exposed in medial view (NHMUK R 43486), and interpreted the holes as external mandibular fenestrae. They made no mention of another isolated mandibular ramus exposed in medial view (NHMUK R 43487) that also exhibits a hole, and dismissed NHMUK R 1035, which includes a skull and disarticulated mandibular rami exposed in right lateral view, as uninformative because forelimb bones cover the posterior part of the mandible. The holes in the mandible are bounded by the angular and surangular, and the splenial lies nearby, but the dentary cannot be seen on the isolated rami. Regarding NHMUK OR 41212, Nesbitt & Hone (2010, p. 227) stated that "unbroken bone frames all sides of the opening;" however the dentary, while not overlapping the hole, overlaps the angular, surangular, and splenial and has broken edges above, below, and anterior to the hole and so provides no evidence that the hole was not sheathed laterally by the dentary. In

Department of Biological
Sciences, Fort Hays State
University, Hays, KS 67601
U.S.A.



NHMUK R 1035, a hole is visible on the medial aspect of the left mandibular ramus whereas the lateral aspect of the right ramus exhibits an imperforate dentary extending posteriorly to the overlapping forelimb elements. Comparison of the right and left rami shows that the dentary covered at least 60% of the hole, and there is no reason to think that the sheathing did not continue posteriorly under the forelimb bones to cover all of the hole. Thus, there is no evidence that *Dimorphodon* had external mandibular fenestrae, and evidence to suggest that it did not.

Nesbitt & Hone (2010) reinterpreted the larger mandibular fragment of BSP 1994 I 51, which Wellnhofer (2003) had interpreted as a left ramus in medial view with a large adductor fossa, as a right ramus in lateral view with an external mandibular fenestra. Although they failed to identify the splenial and argued incorrectly that much of the medial aspect of the ramus would have been sheathed by the splenial, I concur with their reinterpretation. Thus, BSP 1994 I 51 demonstrates that some pterosaurs had external mandibular fenestrae.

Nesbitt & Hone (2010) briefly described and illustrated what they interpreted as an antorbital fossa at the anteroinferior corner of the antorbital fenestra of the large skull of *Dimorphodon* (NHMUK OR 41212), but did not find a fossa in NHMUK R 1035 even though that specimen also preserves the anteroinferior corner of the antorbital fenestra. An isolated right maxilla of *Dimorphodon* exposed in medial view (NHMUK R 590) demonstrates that the ascending and posterior rami were roughly tubular struts connected at the anteroinferior corner of the antorbital fenestra by a thin plate of compact bone that presumably functioned as a gusset to reinforce the joint between the two rami. The plate of bone was continuous with the lateral surfaces of the rami and formed the lateral wall of an internal pneumatic fossa with curving margins. The supposed antorbital fossa of Nesbitt & Hone (2010) is on the lateral surface of the gusset plate, which is gently bowed inward but does not exhibit even the slightest curving margin around the depressed surface, and in NHMUK R 590 and NHMUK R 1035 the gusset plates are not bowed inward to even the slight extent seen in NHMUK OR 41212. Therefore, we must conclude that the supposed antorbital fossa is merely an artifact of crushing and compression and that *Dimorphodon* did not have antorbital fossae.

Nesbitt & Hone (2010) stated that *Raeticodactylus* had an antorbital fossa on the lacrimal and ascending ramus of the maxilla, but did not describe or illustrate the feature, and Stecher (2008), who first described *Raeticodactylus*, did not comment on it. The skull of *Raeticodactylus* is preserved in three dimensions, exposed in left lateral view, and has been expertly prepared to show the open spaces within. The antorbital fenestra is subtriangular with a straight vertical posterior margin, a gently curving convex inferior margin, and a gently curving convex anterosuperior margin. At the superior corner of the fenestra, the lacrimal has a depressed area surrounding a pneumatic foramen. The body and posterior ramus of the maxilla present a flat surface that forms part of the lateral surface of the skull. The ascending ramus of the maxilla is more robust than in *Dimorphodon* and has a suboval cross-section with the long axis of the oval directed anterolaterally such that the anterior part of the ramus forms part of the lateral surface of the skull and the posterior part lies deep to the plane of the lateral surface of the skull. The anteroinferior corner of the antorbital fenestra has a thin gusset plate of compact bone between the ascending and posterior rami of the maxilla just as in *Dimorphodon*. The superior end of the gusset plate is continuous with a narrow flange of bone that extends posteriorly from the lateral surface of the ascending ramus. I assume that the flange is the anterolateral boundary of what Nesbitt & Hone (2010) interpreted as an antorbital fossa on the ascending ramus of the maxilla. However, the flange is rugose and its margin is irregular, which suggest that the flange was not a normal part of the maxilla but instead resulted from the ossification of the margin of the fibrous connective tissue sheet covering the antorbital fenestra. As such it probably was



ossified only because the specimen is fully mature and perhaps old, and would not have been ossified in immature individuals. The space behind the flange may be termed an antorbital fossa, but its morphology is such that homology with the antorbital fossae of erythrosuchids and aetosaurus is doubtful.

Although it has long been known that pterosaurs lacked fourth trochanters, Nesbitt & Hone (2010) identified a 'distinct muscle scar' in *Dimorphodon* in 'the same position where the fourth trochanter is' in archosaurs, and seemed to suggest that the muscle scar was somehow phylogenetically equivalent to a fourth trochanter while noting that the fourth trochanter was also absent in *Dromomeron romeri*. Because the presence of *m. caudofemoralis* is a symplesiomorphy of the Amniota, and muscle scars, trochanters, and other such processes that we find on fossils are merely the osteological components of the tendon-bone attachment in the living organism, the presence of a *m. caudofemoralis* muscle scar in *Dimorphodon*, though phylogenetically informative, would merely inform us that pterosaurs are amniotes. However, in the case of *Dromomeron romeri*, the absence of a fourth trochanter is not phylogenetically informative. The *m. caudofemoralis* muscle scar on the holotype femur of *Dromomeron romeri* (GR 218) is on a depressed fracture and so appears lower than it was, and it and the articular ends of the bone exhibit the incomplete ossification of a small juvenile. GR 218 and femora assigned to *Tawa hallae* (e.g., GR 155, GR 235) form a clear growth series, and the morphological differences between the femora reflect their differing ontogenetic ages. The supposed diagnostic characters of *Dromomeron romeri* (Nesbitt et al., 2009) merely reflect the immaturity of the holotype and referred specimens, and mature individuals of *Dromomeron romeri* had aliform fourth trochanters and were conspecific with *Tawa hallae*. Failure to correctly interpret the ontogenetic age of specimens meant that juveniles were considered basal dinosauromorphs whereas adults are clearly theropods.

To sum up, *Dimorphodon* had neither external mandibular fenestrae nor antorbital fossae whereas BSP 1994 I 51 had external mandibular fenestrae and *Raeticodactylus* had antorbital fossae on its maxillae. Mapping the presence/absence of external mandibular fenestrae onto Dalla Vecchia's (2009) cladogram of pterosaurs suggests that BSP 1994 I 51 and other basalmost pterosaurs (e.g., *Austriadactylus*, *Peteinosaurus*, '*E. cromptonellus*') had external mandibular fenestrae, whereas the fenestrae were lost in later pterosaurs (e.g., *Dimorphodon*, *Campylognathoides*) by posterior extension of the dentary to strengthen the mandible while keeping it light. Interestingly, there is a faint oval depression on the lateral surface of the mandible of *Raeticodactylus*, which probably resulted from compression of the sheathing dentary into an internal hole between the angular and surangular. The ancestor of pterosaurs presumably had external mandibular fenestrae, but because *Proterosuchus* and its close relatives had the fenestrae, their possession by pterosaurs only supports inclusion of the Pterosauria within the Archosauriformes, not within the clade *Erythrosuchus* + Archosauria. Mapping the presence/absence of antorbital fossae on the maxillae onto the same cladogram shows that they are absent in the basal pterosaurs *Austriadactylus*, *Peteinosaurus*, '*E. cromptonellus*', *Dimorphodon*, *Campylognathoides*, and *Eudimorphodon*, and so it is most parsimonious to interpret the fossae of *Raeticodactylus* as convergent with those of archosaurs, whereas their absence in basal pterosaurs supports exclusion of the Pterosauria from the clade *Erythrosuchus* + Archosauria. Similarly, the absence of fourth trochanters in pterosaurs supports exclusion of the Pterosauria from the clade *Erythrosuchus* + Archosauria.

Institutional Abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GR, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico; and NHMUK, Natural History Museum, London, England (Formerly BMNH).



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