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An external mandibular fenestra and other archosauriform character states in basal pterosaurs

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Abstract

Pterosauria, a successful clade of extinct flying vertebrates, possesses a radical body plan that offers few clues about their origin and closest relatives. Whereas most researchers hypothesize an origin within Archosauria as the sister-group to Dinosauromorpha, others favor a position among non-archosauriform archosauromorphs. Here we present evidence that supports a placement within Archosauriformes: the presence of an external mandibular fenestra in two basal pterosaur taxa, *Dimorphodon macronyx* and a specimen referred to *Eudimorphodon* cf. *ranzii* (= 'Seefeld *Eudimorphodon*'; BSP 1994 I 51). Furthermore, the arrangement of the mandibular bones surrounding the mandibular fenestra and the presence of a posterior process of the dentary that laterally overlaps the angular in the mandible of *Dimorphodon* and BSP 1994 I 51 are identical to those of *Erythrosuchus*, *Euparkeria*, and Archosauria. When mapped on a cladogram, presence or absence of an external mandibular fenestra in basal pterosaurs possibly indicates that the feature is primitive for Pterosauria but later lost. The presence of an external mandibular fenestra, along with morphological evidence elsewhere in the body of pterosaurs (serrated teeth, antorbital fossa present, fourth trochanter on the femur present), supports a placement of Pterosauria within Archosauriformes and is consistent with a position within Archosauria.

Keywords: Pterosauria, archosaur, dinosauromorph, phylogeny.

Zusammenfassung

Der Bauplan der Pterosaurier liefert nur wenige Hinweise auf den Ursprung und die nächsten Verwandten dieser erfolgreichen Gruppe ausgestorbener fliegender Wirbeltiere. Während die meisten Forscher einen Ursprung innerhalb der Archosaurier als Schwestergruppe der Dinosauromorpha annehmen, favorisieren andere eine Stellung innerhalb nicht-archosauriformer Archosauromorpha. Wir präsentieren hier Hinweise, die eine Stellung innerhalb der Archosauriformen stützen: Dies ist zum einen die Existenz eines externen Mandibularfensters bei zwei basalen Pterosaurier-Taxa, *Dimorphodon macronyx* und einem als *Eudimorphodon* cf. *ranzii* (= 'Seefeld *Eudimorphodon*'; BSP 1994 I 51) bezeichnetem Exemplar. Zum anderen entsprechen die Anordnung der Knochen, die das Mandibularfenster umgrenzen, sowie die Existenz eines hinteren Fortsatzes des Dentales, der das Angulare in der Mandibel von *Dimorphodon* und BSP 1994 I 51 überlappt, der Situation bei *Erythrosuchus*, *Euparkeria* und den Archosauria. Die Verteilung der Merkmalszustände des externen Mandibularfensters deutet darauf hin, dass die Existenz dieses Fensters ein ursprüngliches Merkmal der Pterosaurier ist, das später verloren gegangen ist. Die Existenz eines externen Mandibularfensters sowie weitere morphologische Merkmale an anderen Körperteilen der Pterosaurier (Zähne mit gezackten Schneiden, antorbitale Grube vorhanden, vierter Trochanter am Femur vorhanden) unterstützen deren Stellung innerhalb der Archosauriformes und stehen im Einklang mit einer Position innerhalb der Archosauria.

Contents

1. Introduction

Despite over 200 years of research on the anatomy and relationships of pterosaurs, their origins and the identity of their closest relatives remain an outstanding problem. Pterosaurs first appear in the fossil record in the Late Triassic (Norian) from localities across Europe and Greenland (Wild 1978; Jenkins et al. 2001; Dalla Vecchia 2003; Barrett et al. 2008). At least six different species-level taxa have been named from the Triassic (Dalla Vecchia 2003) and recent revisions of specimens once referred to *Eudimorphodon* have turned out to be new lineages (Dalla Vecchia 2009a), revealing a radiation of early pterosaurs unparalleled in their evolutionary history. Many Triassic pterosaur specimens are represented by superbly preserved and articulated material (although generally compressed into two dimensions). Yet all Triassic pterosaurs, despite being the earliest members of Pterosauria, share a divergent morphology of the skull, axial column, forelimbs, and hindlimbs that characterizes Pterosauria as a unique group of vertebrates. Hence, there is a paucity of morphological clues linking pterosaurs to their closest reptilian relatives.

Within Archosauromorpha (taxa closer to Aves than to Squamata), Pterosauria has been linked with 'prolacertiforms' (Wild 1978, 1983, 1984; Peters 2000), a likely paraphyletic or polyphyletic clade (Müller 2003); the enigmatic drepanosaurids (Renesto & Binelli 2006); the non-archosaurian archosauriforms (Bennett 1996); and nested within crown-group Archosauria as the sister-taxon of Dinosauromorpha (Padian 1984; Gauthier 1986; Sereno 1991a; Juul 1994; Bennett 1996; Benton 1999; Irmis et al. 2007; Nesbitt in press). The archosaurian hypothesis is supported by numerical phylogenetic analyses, though typically with few cladistic characters supporting the node that joins the pterosaurs to other clades. However, a number of character states (e. g., the lack of serrated teeth and a fourth trochanter) in Pterosauria are cited (Bennett 1996; Peters 2000) as being incompatible with archosaurian ancestry.

One of the most commonly cited contradictions in the archosaurian-Pterosauria hypothesis for pterosaur origins is the apparent absence of an external mandibular fenestra (EMF) in pterosaurs (Wild 1978, 1983, 1984; Benton 1990; Bennett 1996; Peters 2000). This fenestra has long been used to diagnose *Erythrosuchus* + crowngroup Archosauria (e. g., Benton 1985; Juul 1994; Bennett 1996) and persists in a majority of clades of Archosauria. Richard Owen (1870) tentatively identified an EMF in *Dimorphodon* stating that the mandible had a "vacuity, if it be natural and not due to the abrasion of the thin outer wall" (Owen 1870: 59) and this was later followed by the independent reconstruction of Arthaber (1919). Romer (1956) also noted a mandibular fenestra in *Dimorphodon*, but his reconstruction was copied from Arthaber (1919). Later descriptions and reconstructions of *Dimorphodon* simply show no EMF (e. g., fig. 9 of Young 1964; fig. 2 of Wellnhoffer 1978; fig. 6 of Padian 1983a; fig. 3 of Kellner 2003; fig. 8 of Unwin 2003) with the exception of Padian (1983a, fig. 29; 1983b; 1984) or state that pterosaurs lack one (e. g., Bennett 1996). Thus, pterosaurs are widely regarded as lacking an EMF – a key character for diagnosing *Erythrosuchus* + Archosauria. Nevertheless, a clear EMF is present in two basal pterosaur taxa, *Dimorphodon macronyx* (Buckland 1829 sensu Owen 1870), and BSP 1994 I 51, a specimen referred to *Eudimorphodon* cf. *ranzii*, upon a recent examination.

Here, we fully describe the morphology of the EMF and adjacent mandible elements in two basal pterosaurs. We discuss the distribution of the EMF within the clade, and illuminate the implications of an EMF. The presence of an EMF adds to a growing list of other emerging evidence for an archosaurian ancestry for pterosaurs.

Institutional abbreviations

BMNH/NHM	Natural History Museum, London, United Kingdom
BNM	Bündner Naturmuseum of Chur, Grisons, Switzerland
BP	Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
MCSNB	Museo Civico di Scienze Naturali di Bergamo, Italy
MFSN	Museo Friulano di Storia Naturale, Udine, Italy
MGUH	Geological Museum, University of Copenhagen, Denmark
PVSJ	Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina
SC	Italian State collections, Italy
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany

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2. Materials and methods

We studied the remains of two basal pterosaurs, the Early Jurassic *Dimorphodon macronyx* (BMNH 41212, 43486, R 1035) and a Triassic pterosaur specimen referred to *Eudimorphodon* cf. *ranzii* (BSP 1994 I 51; Wellnhofer 2003). Of the *Dimorphodon* specimens with mandibles, the posterior portions of the mandibles of BMNH 41212 and BMNH 43486 are exposed whereas the posterior portions of the mandibles of BMNH R 1035 are covered by forelimb elements.

BSP 1994 I 51 (= 'Seefeld *Eudimorphodon*') was originally assigned to *Eudimorphodon* cf. *ranzii* by Wellnhofer (2003). However, Dalla Vecchia (2009a) noted that BSP 1994 I 51 did not share any apomorphies of *Eudimorphodon ranzii*, differed in morphology on many elements, and did not find BSP 1994 I 51 as the sister-taxon of *Eudimorphodon ranzii* in an extensive phylogenetic analysis. BSP 1994 I 51 was found as one of the most basal pterosaurs in the analysis of Dalla Vecchia (2009a, b) but not tested in the phylogeny of Andres et al. (2010) or in previous analyses. We identify the nearly complete mandible of BSP 1994 I 51 (fig. 5B of Wellnhofer 2003) as a right element (contra Wellnhofer 2003; see below).

3. Description

The complete, left mandible of *Dimorphodon* (BMNH 41212) is well-preserved and exposed in lateral view (Fig. 1a–c). A large fenestra is present in the posterior portion of the mandible, slightly obscured posteriorly by the jugal. The substantial oval opening is surrounded by the posterior portion of the dentary anteroventrally and anterodorsally, the angular ventrally, and possibly a small piece of the surangular dorsally. Although parts of the mandible elements are broken around portions of the opening (Fig. 1), a close inspection reveals that unbroken bone frames all sides of the opening. The participation and positions of the dentary, angular, and possibly the surangular to the

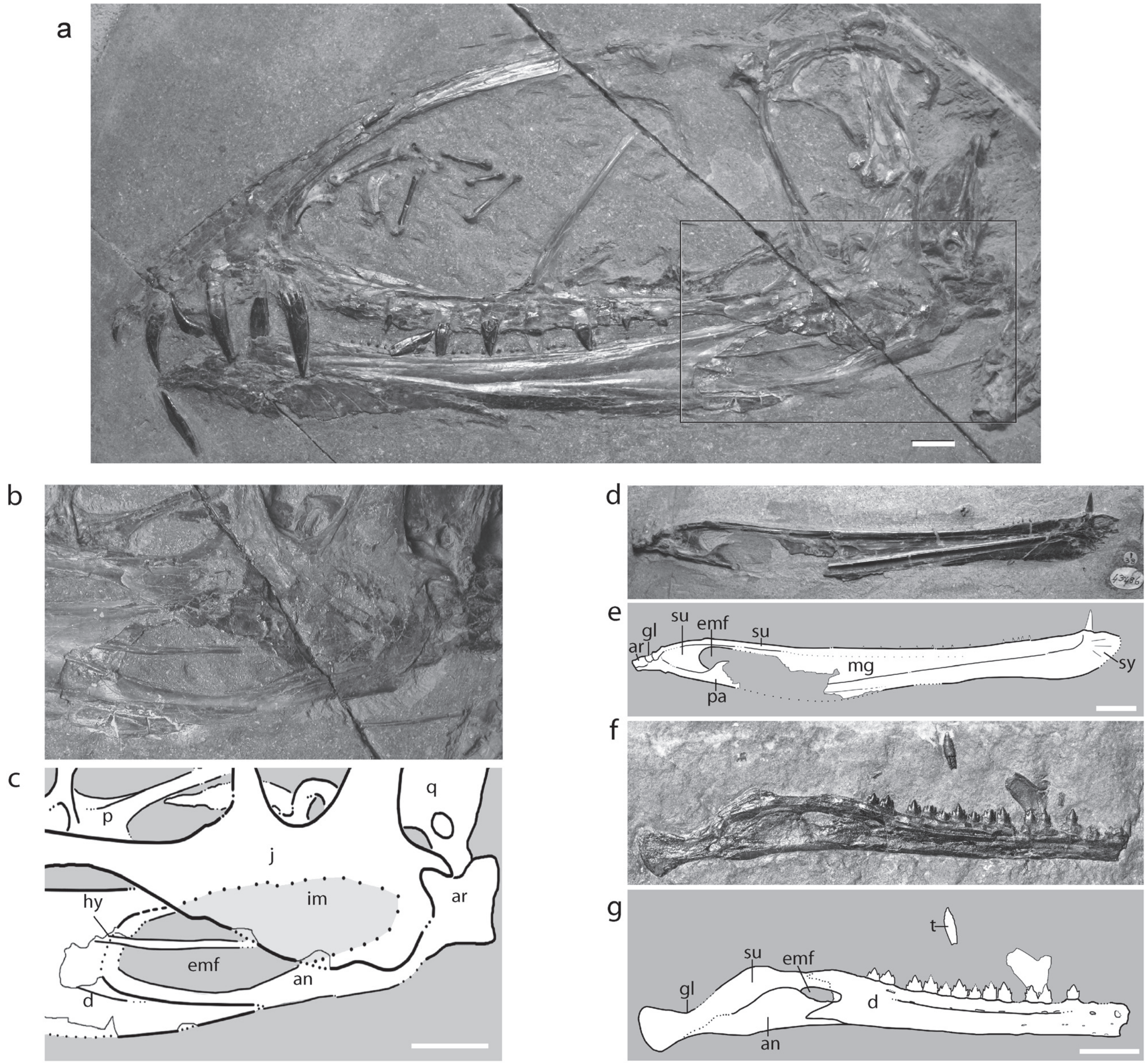

Fig. 1. Mandibular fenestrae in *Dimorphodon macronyx* (a–e) and BSP 1994 I 51 (f–g). – **a**. The skull of BMNH 41212 in left lateral view. The box highlights figure parts b and c. **b**. The posterior portion of the mandible of BMNH 41212 in lateral view. **c**. Drawing of the posterior portion of the mandible of BMNH 41212 in lateral view. **d**. The left mandible of BMNH 43486 in medial view. **e**. Drawing of the left mandible of BMNH 43486 in medial view. **f**. The right mandible of BSP 1994 I 51 in lateral view. **g**. Drawing of the right mandible of BSP 1994 I 51 in lateral view. – Abbreviations: an, angular; ar, articular; d, dentary; emf, external mandibular fenestra; gl, glenoid; hy, hyoid; im, impression of the external mandibular fenestra; j, jugal; mg, Meckelian groove; p, palatine; pa, prearticular; q, quadrate; su, surangular; sy, symphysis; t, tooth. – Scales: 1 cm.

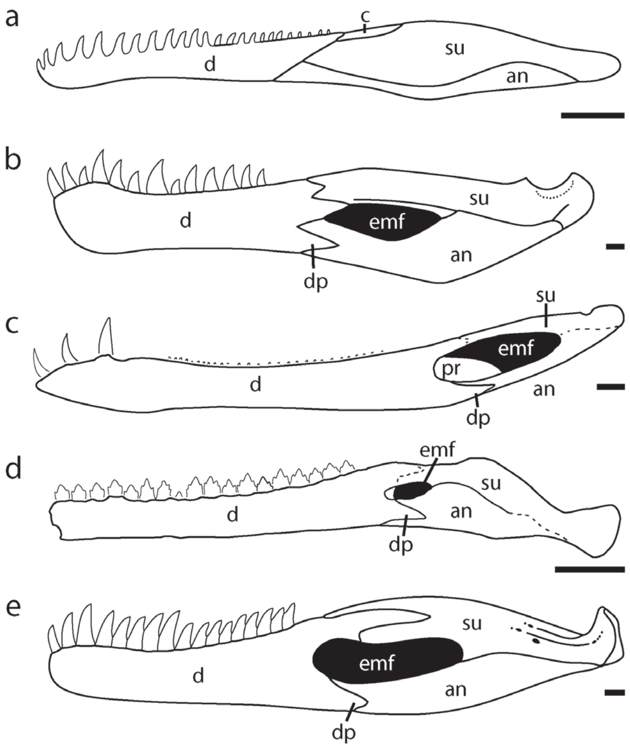

Fig. 2. Reconstructions of the mandibles of archosauromorphs in lateral view. – **a**. *Prolacerta broomi* (from Nesbitt in press). **b**. *Erythrosuchus africanus* (from Gower 2003). **c**. *Dimorphodon macronyx* (based from BMNH 41212). **d**. BSP 1994 I 51. **e**. *Herrerasaurus ischigualastensis* (from Sereno & Novas 1994). – Abbreviations: see Figure 1 for most; c, coronoid; dp, posterior process of the dentary. – Scales: 1 cm.

opening are identical to that of other archosauriforms with mandibular fenestrae (e. g., the stem archosaur *Erythrosuchus* BP/1/5207, the dinosaur *Herrerasaurus* PVSJ 407). Furthermore, the tapering posteroventral portion of the dentary overlaps the angular laterally, a character state present in archosauriforms with external mandibular fenestrae (Nesbitt et al. 2009b: character 18). The posterior portion of the EMF is covered by the jugal. However, crushing of the jugal into the mandibular fenestra demonstrates that the mandibular fenestra of *Dimorphodon* extended posteriorly to nearly the articular region.

A second nearly complete mandible of *Dimorphodon* (BMNH 43486) exposed in medial view (Fig. 1d, e), preserves an opening in the same area of the mandible as BMNH 41212. This specimen has a complete posterior border of the opening, which is formed by the surangular. This observation confirms that the surangular contributes to the EMF as in other archosauriforms (Fig. 2). The prearticular, surangular, and articular of BMNH 43486 shows that *Dimorphodon* also had an extensive internal mandibular fenestra.

In combination, both mandibles of *Dimorphodon* illustrate that the EMF was: 1) large and located at the posterior portion of the mandible, 2) framed by the dentary anteriorly, angular ventrally, and surangular dorsally and posteriorly, and 3) similar to that of archosauriforms. The reconstruction presented in Figure 2c incorporates these details.

The nearly complete, well-preserved right mandible of BSP 1994 I 51 is exposed in lateral view (Fig. 1f, g). Wellnhofer (2003) identified a mandibular fenestra in this specimen (fig. 5 of Wellnhofer 2003) but given that he identified the element as a left mandible in medial view, he presumably identified the opening as an internal mandibular fenestra (though without specifying this). We reinterpret the specimen as in lateral view because 1) the glenoid of the articular is not exposed and the surface near the articular region is undamaged, 2) the splenial would be exposed in medial view and it would cover much more of the surface of the mandible if in medial view, and 3) the surface ventral to the tooth row bears grooves and foramina typical of the lateral surface of the dentary in tetrapods.

Given that the anterior portion of the dentary is missing, the oval EMF is presumably located in the posterior third of the mandible. Although proportionally smaller than that of *Dimorphodon*, the EMF shares a similar arrangement of mandibular elements surrounding it with *Dimorphodon* and other archosauriforms; the dentary forms the anterior margin, the angular forms the ventral and part of the posterior margin, and the surangular forms part of the posterior and dorsal portions of the opening. The matrix visible through the EMF may indicate that BSP 1994 I 51 also possesses a large internal mandibular fenestra. Similarly, the posteroventral portion of the dentary laterally overlaps the angular as in *Dimorphodon* and in *Erythrosuchus* + Archosauria. The angular of BSP 1994 I 51 is well preserved and the posterior portion of the angular arcs dorsally posterior to the EMF. The dorsal arcing of the angular is present in a variety of archosauriforms with an EMF.

4. Character distribution of the mandibular fenestra within Pterosauria

Few basal pterosaurs possess an unambiguous mandibular fenestra. The preservation of most basal pterosaurs does not allow the absence or presence of the feature to be confirmed. Triassic pterosaur skulls are usually crushed at an oblique angle so that the posterior portion of the mandible is hidden, cracked, and partially or fully disarticulated. Furthermore, all Triassic pterosaur skulls possess thin and fragile skull bones that are subject to loss when the specimen is discovered and/or prepared. For example, the only known specimen of *Preondactylus buffarini* is preserved as an impression in the matrix and the holotype of *Austri-*

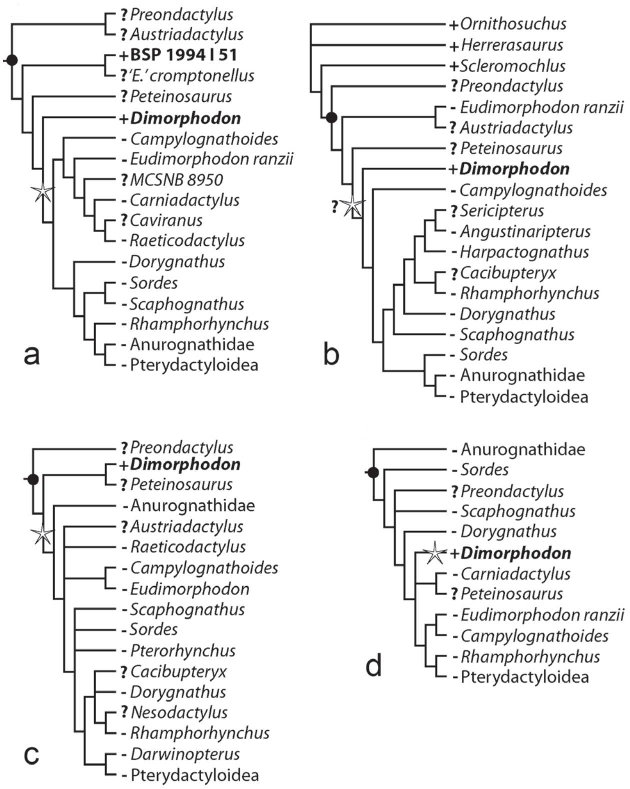

Fig. 3. Hypotheses of the relationships of basal pterosaurs with the presence of an external mandibular fenestra mapped onto the tree. – **a**. Dalla Vecchia (2009a, b). **b**. Andres et al. (2010). **c**. Lü et al. (2009). **d**. Kellner (2003). – Taxa in Pterodactyloidea and Anurognathidae have been collapsed to clade level. Plus signs indicated pterosaurs with an external mandibular fenestra, negative signs indicate taxa without an external mandibular fenestra and question marks indicate uncertainty. The star indicates hypothesized changes of the presence of an external mandibular fenestra. The black circles represent the node Pterosauria.

adactylus cristatus (SMNS 56342) is heavily crushed so it is not clear if an EMF is present but cannot be seen given the compression of the thin skull bones (i. e., an EMF could be 'filled in' by other flat bones) and the poor surface preservation. With these biases in mind, we were unable to determine if a mandibular fenestra was present in *Preondactylus buffarini* (MFSN 1770), *Austriadactylus cristatus* (SC 332466 and SMNS 56342), *Peteinosaurus zambellii* (MCSNB 2886), and '*Eudimorphodon*' *cromptonellus* (MGUH VP 3393). The posteriorly disarticulated mandibles of *Peteinosaurus zambellii* (MCSNB 2886) and *Austriadactylus cristatus* (SC 332466) may suggest that a mandibular fenestra was present as evidenced by the loose connections of the dentary bones. On the other hand, a mandibular fenestra is clearly not present in *Dorygnathus banthensis* (SMNS 55886; Padian 2008a), *Campylognathoides liasicus* (SMNS 50735; Padian 2008b), *Eudimorphodon ranzii* (MCSNB 2888), *Carniadactylus rosenfeldi* (MFSN 1797), *Raeticodactylus filisurensis* (BNM 14524; Stecher 2008), or any members of the Pterodactyloidea. All of these taxa have mandibular elements that meet to form a solid lateral wall to the mandible.

Using the distribution data described above, we mapped the presence of a mandibular fenestra in basal pterosaurs onto recent phylogenies of pterosaur relationships. We chose the phylogenetic analyses of Kellner (2003) and Lü et al. (2009) and the best sampled basal pterosaur matrices of Dalla Vecchia (2009a, b) and Andres et al. (2010) (Fig. 3a–d). These four analyses differ in the phylogenetic position of basal pterosaurs including anurognathids, *Eudimorphodon*, and *Dimorphodon*. *Dimorphodon* is consistently found in a basal position in Pterosauria (Fig. 3), always outside a clade containing *Dorygnathus banthensis* and Pterodactyloidea (Unwin 2003; Dalla Vecchia 2009a, b; Andres et al. 2010). We focus on the work of Dalla Vecchia (2009a, b) and Andres et al. (2010) because 1) they include the most Triassic and basal pterosaur taxa, 2) their results differ from one another particularly with the position of *Dimorphodon*, a specifically targeted taxon, and 3) they use specimen-level terminal taxa for some of the Triassic pterosaurs (see the effect of specimen-level scoring of *Eudimorphodon* in Dalla Vecchia 2009a). Nevertheless, the relationship among *Dimorphodon*, *Eudimorphodon ranzii*, and other pterosaurs differs among the most complete pterosaur phylogenies incorporating abundant Triassic taxa. Andres et al. (2010) found *Dimorphodon* more closely related to Pterodactyloidea than to *Eudimorphodon ranzii* whereas Dalla Vecchia (2009a, b) found *Eudimorphodon ranzii* more closely related to pterodactyloids (represented by species-level taxa) than to *Dimorphodon*.

5. Discussion

Phylogenetic analyses of pterosaur ingroup relationships (e. g., Kellner 2003; Unwin 2003; Dalla Vecchia 2009a, b; Lü et al. 2009; Andres et al. 2010) have produced a variety of results with occasionally highly variable positions for some clades or genera. As such, making definitive statements about the optimization of the EMF on phylogenies of basal pterosaurs is contentious. Phylogenetic analyses (or reanalyses) of basal pterosaurs are beyond the scope of this paper; however, we have mapped the presence of an EMF onto a variety of phylogenetic hypotheses for basal pterosaurs (see Figure 3). This exercise illustrates that an EMF is present only in basal members of Pterosauria and absent in more derived members of the clade.

The EMF cannot be scored in most Triassic pterosaurs and disagreements concerning the phylogenetic position of some taxa inhibit a clear picture of evolution of the EMF among pterosaurs. Among Triassic taxa, the phylogenetic position of *Eudimorphodon ranzii* is critical to the understanding of the evolution of the EMF. In the phylogenetic hypothesis of Dalla Vecchia (2009a, b), an EMF optimizes as a plesiomorphic character in Pterosauria (Fig. 3a) and is absent in a number of "stem" Breviquartossa (sensu Unwin 2003), and is lost only once. This is also a possibility in the hypotheses of Lü et al. (2009) (Fig. 3c). In the hypothesis of Andres et al. (2010), it is not clear if an EMF was lost in *Eudimorphodon ranzii* independently or is an autapomorphy of *Dimorphodon* (Fig. 3b). Finally, in the hypothesis of Kellner (2003), it is not clear whether an EMF was plesiomorphic for Pterosauria and then lost in *Eudimorphodon* and *Campylognathoides* + Pterodactyloidea or if an EMF represents an autapomorphy of *Dimorphodon*. The distribution of this character can be more confidently accessed with the addition of more basal pterosaurs or specimens into the phylogeny or the discovery of new Triassic or basal pterosaur taxa, or better preserved specimens (e. g., *Preondactylus*). Nonetheless, we urge pterosaur workers to include the following two phylogenetic characters when accessing pterosaur relationships, both within Pterosauria and among diapsid reptiles:

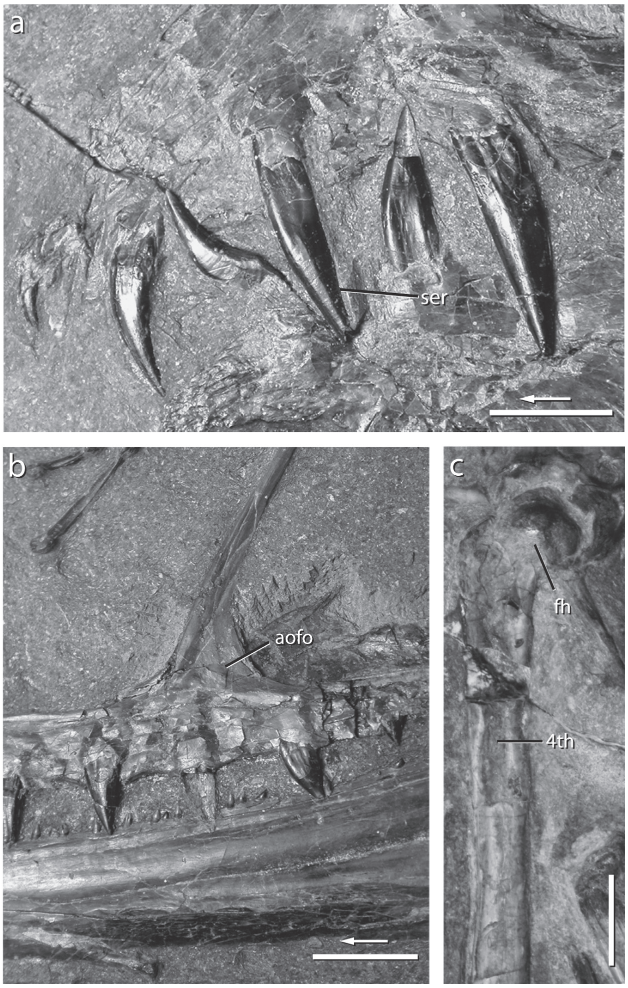

Fig. 4. Features of the skeleton of *Dimorphodon macronyx* that are present in archosauriforms and archosaurs. – **a**. The anterior portion of the skull of BMNH R 41212 in lateral view highlighting the third premaxillary tooth with serrations. **b**. The left maxilla of BMNH R 41212 in lateral view highlighting the antorbital fossa. **c**. The proximal half of the right femur of BMNH R 41212 in medial view highlighting the depression for the attachment of the caudifemoralis musculature (= 4th trochanter). – Abbreviations: 4th, fourth trochanter; aofo, antorbital fossa; fh, femoral head; ser, serrations. – Scale: 1 cm. Arrows indicate the anterior direction.

1) External mandibular fenestra: present (0) or absent (1). (Gauthier 1984; Benton 1985, 1990; Benton & Clark 1988; Juul 1994; Bennett 1996)

2) Dentary, posteroventral portion: just meets the angular (0) or laterally overlaps the anteroventral portion of the angular (1). (Modified from Nesbitt et al. 2009b, angular previously incorrectly referred to as 'surangular')

The presence of an EMF and similar arrangement of mandibular elements between some basal pterosaurs and *Erythrosuchus* + Archosauria support a phylogenetic position of Pterosauria within Archosauriformes. All well sampled, numerical phylogenies including a variety of archosauriforms (e. g., Juul 1994; Bennett 1996; Benton 1999; Brusatte et al. 2010; Nesbitt in press) have found pterosaurs as archosauriforms (Bennett 1996) or within Archosauriformes as the sister-taxon to Dinosauromorpha within Archosauria (Juul 1994; Benton 1999; Brusatte et al. 2010; Nesbitt in press). However, the highly modified anatomy of early pterosaurs has still been reported to preserve character states not found in Archosauriformes and Archosauria (Benton 1985; Bennett 1996). A rapid increase in the discovery of a variety of new archosauriforms including basal dinosauromorphs (e. g., *Dromomeron romeri*, Irmis et al. 2007; Nesbitt et al. 2009a), better preserved material of previously named taxa (e. g., *Herrerasaurus*; Sereno & Novas 1994), better understanding of character distributions among archosauriforms (Brusatte et al. 2010; Nesbitt in press), and more precise character definitions and descriptions (Nesbitt in press), has led to new observations that contradict previous citations of character states that seem to exclude pterosaurs from Archosauria. For example, the presence of palatal teeth in the basal pterosaur *Eudimorphodon ranzii* has been suggested to be a character state that excludes pterosaurs from Archosauria. However, palatal teeth are now known in both major groups of archosaurs, the pseudosuchians (e. g., *Turfanosuchus*) and dinosauromorphs (e. g., *Eoraptor*) (Rauhut 2003; Nesbitt 2009).

Another character state also cited (Bennett 1996) as inconsistent with an archosaur ancestry is the absence of serrated teeth. A recently described basal pterosaur, *Austriadactylus cristatus* (SMNS 56342) clearly has coarsely serrated teeth as does *Preondactylus* (Dalla Vecchia 2003) – widely regarded as the most basal of pterosaurs (Dalla Vecchia 2009a, b; Lü et al. 2009; Andres et al. 2010). Furthermore, the third premaxillary tooth of *Dimorphodon* (BMNH R 41212; Fig. 4a) appears to have fine serrations. The coarse serrations in *Austriadactylus cristatus* (described as small cusps by Stecher 2008) may suggest that the large cusps of the teeth of taxa such as *Eudimorphodon ranzii* or *Carniadactylus rosenfeldi* (MFSN 1797) may be homologous with serrations as has been suggested by Bennett (1996). Indeed, the small cusps of the teeth of *Raeticodactylus* and the 'monocuspid' tooth of BSP 1994 I 51 as described by Wellnhofer (2003) are similar to the very large serrations seen in basal ornithischians (Sereno 1991b), basal sauropodomorphs (Galton 1985), some troodontid theropods (Makovicky & Norell 2004) and thus show the possible continuum between the cusps of *Eudimorphodon* teeth and the serrations of basal archosaurs.

Another example also cited is that pterosaurs lack any antorbital fossa. A clear antorbital fossa is present on the dorsal process of the maxilla and lacrimal of the recently named pterosaur *Raeticodactylus filisurensis* (BNM 14524; Stecher 2008) and one appears to be present on the dorsal and ventral process of the maxilla in *Dimorphodon* (BMNH R 41212; Fig. 4b). The distribution of this character is clearly complex given that it also appears in basal pterodactyloids (e. g., *Pterodactylus*).

Finally, the absence of a fourth trochanter has also been cited as a character state not present in pterosaurs (Bennett 1996). Although a large ridge for articulation with caudifemoralis musculature (which attaches to the fourth trochanter, see Hutchinson 2001) does not appear to be present in any pterosaur, a distinct muscle scar is present on the medial side of the femur of *Dimorphodon* (BMNH R 41212; Fig. 4c). Additionally, the muscle scar is located one third of the way down the shaft from the proximal surface – the same position where the fourth trochanter is present in *Vancleavea*, proterochampsids, *Euparkeria*, and Archosauria (Nesbitt et al. 2009b). Moreover, a distinct ridge for the attachment of the caudifemoralis musculature is absent among some pseudosuchians (e. g., the poposauroid *Effigia*, Nesbitt 2007) and some basal dinosauromorphs (*Dromomeron romeri*, Irmis et al. 2007; Nesbitt et al. 2009a). These two examples of archosaurs may lack a distinct ridge of attachment, but both have distinct muscle scars in the position of the fourth trochanter of archosaurs, similar to that of *Dimorphodon*.

Granted, these character states discussed above are found in a variety of basal pterosaurs, but not all of the character states discussed are found in the same taxon, with the possible exception of *Dimorphodon*. *Dimorphodon*, which has the most completely known and best preserved material of any early basal pterosaur, possesses at least one serrated tooth, an antorbital fossa, a scar for the attachment of the caudifemoralis, and a clear external mandibular fenestra (the presence or absence of palatal teeth is unknown). All of these character states are found within an exclusive clade of archosauriforms and not found, in combination, in any other clade of diapsids (Nesbitt in press).

With the discovery of new characters and the increasing rigor in character definition and cladistic analysis, a revision of pterosaur origins is now due. Whereas the character states we present here are shared between Pterosauria and *Erythrosuchus* + Archosauria, they do not solve the relationships of Pterosauria alone, though they do add congruence to other characters supporting an archosaurian position for pterosaurs. The results presented here exemplify the importance of outgroup selection for polarizing pterosaur apomorphies among pterosaurs and this, in turn, has important implications for the early evolutionary history and fossil record of the group. For example, *Dimorphodon*, an Early Jurassic taxon, may be found to be more basal than previously found when an archosauriform (e. g., *Euparkeria*) or archosaurian outgroup (e. g., Dinosauromorpha) is used. The evidence and interpretations presented here show that at least some pterosaurs had an antorbital fossa, an external mandibular fenestra, serrated teeth, and a feature homologous with a fourth trochanter on the femur of archosauriforms, and these characters are present in pterosaurs even if the optimization of their presence is complex or ambiguous at present.

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