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SHORT COMMUNICATION

THE ANTORBITAL FENESTRA OF METRIORHYNCHIDAE (CROCODYLIFORMES, THALATTOSUCHIA): TESTING ITS HOMOLOGY WITHIN A PHYLOGENETIC FRAMEWORK

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Metriorhynchidae is a clade of extinct marine crocodyliforms of pelagic habits that is nested within the more inclusive group Thalattosuchia that also includes a diversity of fossil taxa found in shallow marine environments (Young et al., 2009). Metriorhynchids are of particular interest given that they represent the only group of archosaurs completely adapted to marine environments (Fernández and Gasparini, 2008). Most of the members of this clade are characterized by their delicate and elongated snouts, homodont dentition, paddle-like forelimbs, and hypocercal tail, a set of characters that are thought to be marine adaptations. Among the unique traits present in metriorhynchids is an opening located anteriorly to the orbit (Fernández and Gasparini, 2000; Gandola et al., 2006; Fernández and Herrera, 2009), which has been up to now interpreted as homologous to the antorbital fenestra of other archosaurs.

The antorbital fenestra is an opening located anterior to the orbit that is usually enclosed by the maxilla and lacrimal, although other bones can contribute to its margins, and it can be surrounded by a shallow fossa (Fig. 1A; Witmer, 1995, 1997). This anatomical structure is a synapomorphy of Archosauriformes and is present in all basal lineages of this group but has been independently internalized in several clades, such as extant crocodilians (Witmer, 1997). Based on anatomical studies of extant crocodilians and birds, as well as a broad diversity of fossil archosaurs, the antorbital opening has been related to pneumatization of the archosaur skull, being the osteological correlate of the development of a conspicuous paranasal chamber connected with the fenestra (Witmer, 1997).

The metriorhynchid antorbital region has an autapomorphic fenestra opening posteromedially rather than medially and limited by the nasal, lacrimal, and (to a limited extent) maxilla. The opening is located within a deep, dorsoventrally low, and obliquely oriented fossa limited by the same bones along with the jugal posteroventrally (Gasparini et al., 2006; Fernández and Herrera, 2009; Pol and Gasparini, 2009; Fig. 1C). The recent discovery of exceptionally preserved fossils from the Late Jurassic of South America (Fernández and Gasparini, 2008) reveals that this opening has an connection with a large internal cavity enclosed within the prefrontal bone that lodged an excretory salt gland, which led some authors to cast doubts about the identity of the metriorhynchid opening and fossa (Fernández and Gasparini, 2000; Gandola et al., 2006; Fernández and Herrera, 2009). Although this proposal was echoed in some recent studies (Young and Andrade, 2009), the homology of the opening and fossa of metriorhynchids and those of other archosaurs has never been thoroughly tested within a phylogenetic framework and these structures have been assumed to be homologous in all published phylogenetic analyses of Crocodyliformes (Gasparini et al., 2006; Jouve, 2009; Pol and Gasparini, 2009; Sereno and Larsson, 2009; Young and Andrade, 2009).

The method of dynamic homology (Ramírez, 2007) has been recently proposed for testing alternative hypotheses of primary homology (de Pinna, 1991; Rieppel, 1996) for controversial structures. This method tests which of the alternative homology hypotheses (proposed upon the basis of different homology criteria) results in the most parsimonious interpretation of all of the anatomical data (Ramírez, 2007). The dynamic homology approach can be seen as an extension of the congruence test (Patterson, 1982), because it tests which of the different primary homology hypotheses is the most congruent with the rest of the characters (i.e., all of the available evidence). The aim of the present contribution is to test the homology of the fenestra located anterior to the orbit in metriorhynchids within a cladistic framework.

Institutional Abbreviations—**MLP**, Museo de La Plata, La Plata, Argentina; **MOZ**, Museo Profesor J. Olsacher, Zapala, Argentina; **NHMUK**, Natural History Museum, London, U.K.

DYNAMIC HOMOLOGY ANALYSIS

In order to test the hypotheses of primary homology of these fenestrae, three alternative schemes of homology were evaluated: the first hypothesis corresponds to the 'traditional' (null) hypothesis that considers the fenestrae of all crocodyliforms as homologous (antorbital fenestra sensu Witmer, 1997) (H0); a second hypothesis considers the fenestra of the metriorhynchids as a neomorphic feature (H1); and the third hypothesis postulates the fenestra of all thalattosuchians as a neomorphic structure (H2).

Under hypotheses H1 and H2 the antorbital fenestra of metriorhynchids is interpreted as being internalized, as occurs in extant crocodilians, and the opening is interpreted as a new structure that serves for the exit of the exocrine salt gland duct (Fernández and Herrera, 2009). Under H2 this interpretation is extended to all thalattosuchians. Basal thalattosuchians (e.g., *Teleosaurus* [Jouve, 2009], *Pelagosaurus* [NHMUK OR 32955]) lack the unique characteristics described above for the metriorhynchid antorbital region but have an unusually small fenestra located on the lateral surface of the rostrum (i.e., the fossa is absent; Fig. 1B). Studies on the internal anatomy of these forms have identified the presence of a medial bony lamina of the maxilla or lacrimal that resembles the internal pneumatic chamber of extant crocodylians and led some authors to propose that basal thalattosuchians had an internalized antorbital fenestra (Witmer, 1997; Jouve, 2009). In order to clearly reflect the differences in the homology hypotheses, under H1 and H2 the neomorphic fenestra of marine crocodyliforms is referred to as the preorbital opening (Fernández and Herrera, 2009).

The data matrix was built using Mesquite 2.72 (Maddison and Maddison, 2010), through the modification of a recently published data set (Gasparni et al., 2006), adding 'dynamic homology characters' (i.e., characters that represent the three alternative hypotheses of primary homology). These characters are an expression of the alternative hypotheses supported by

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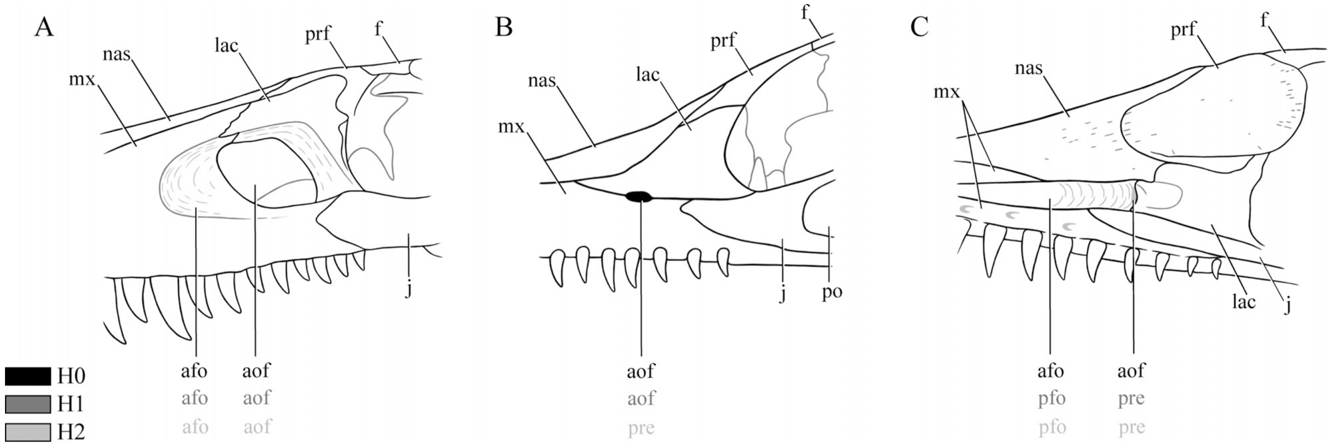

FIGURE 1. Snouts of crocodylomorphs in lateral view. **A**, *Sphenosuchus acutus* (modified from Walker, 1990); **B**, *Teleosaurus cadomensis* (modified from Jouve, 2009); and **C**, *Metriorhynchus superciliosus* (modified from Witmer, 1997). **Abbreviations**: **aof**, antorbital fenestra; **afo**, antorbital fossa; **f**, frontal; **j**, jugal; **mx**, maxilla; **lac**, lacrimal; **nas**, nasal; **pfo**, preorbital fossa; **po**, postorbital; **pre**, preorbital opening; **prf**, prefrontal. The different homology correspondences (hypotheses) are represented in grayscale. Not to scale.

different topologic and connectivity criteria used by us and previous authors to postulate the homology of this structure, such as the shape and size of the fenestra or fossa, the participation of different bones in the margins of the fenestra or fossa, their positional relationship with the primary choana, and the presence of paranasal diverticula and internal cavities connected with the fenestra, among others (see the character list in the Supplementary Material [available online at www.tandfonline.com/UJVP] for more details). Three data matrices with identical numbers of characters were built, one for each of the three homology schemes described above (H0, H1, H2). The taxa for which a preorbital opening is recognized (i.e., metriorhynchids under H1 and all thallatosuchians under H2) were scored with inapplicable entries for all characters related to the shape and characteristics of the antorbital fenestra. Similarly, all the characters related to the shape and characteristics of the preorbital opening were scored as inapplicable for all taxa interpreted to have an antorbital fenestra (i.e., all crocodyliforms under H0, all non-metriorhynchid crocodyliforms under H1, and all non-thalattosuchian crocodyliforms under H2).

The three data matrices (homology scenarios) were analyzed using equally weighted parsimony in TNT 1.1 (Goloboff et al., 2008). The search strategy performed was a heuristic search with 1000 random addition sequences (saving 10 trees per replicate). Once the most parsimonious trees were recovered, a final round of TBR was performed. The parsimony score (tree length) of the three data matrices was compared to determine which of the interpretations on the homology of the fenestra anterior to the orbit was the most parsimonious.

Finally, given that the phylogenetic position of thalattosuchians has been intensively debated during the last two decades (Clark, 1994; Gasparini et al., 2006; Jouve, 2009; Pol and Gasparini, 2009; Wilberg, 2010), the parsimony score of the three alternative homology schemes (data matrices H0, H1, and H2) were compared not only using the optimal topologies for this data set (that depict this clade deeply nested within neosuchians; Gasparini et al., 2006), but also using phylogenetic trees that place thallatosuchians in the two other proposed positions within Crocodyliformes: as basal mesoeucrocodylians (Sereno and Larsson, 2009; Young and Andrade, 2009) and as basal crocodyliforms (Benton and Clark, 1988). These alternative topologies were obtained through the use of monophyly constraints in TNT, finding the most parsimonious trees that depict Thalattosuchia as the most basal clade of Mesoeucrocodylia and as the most basal clade of Crocodyliformes. It is worth mentioning that the search strategy is not as exhaustive as in the application of dynamic homologies in molecular data using the program POY (Varón et al., 2010). It might be possible that these kinds of analyses could generate different optimal topology, but at present POY cannot apply them to morphological analyses.

RESULTS

The most parsimonious trees of the unconstrained parsimony analyses of the three alternative data matrices depict the thalattosuchians deeply nested within Neosuchia (Fig. 2), recovering a group of basal forms (a paraphyletic 'Teleosauridae') and the monophyletic Metriorhynchidae, as in the original analysis (Gasparini et al., 2006). The shortest tree length is obtained for the H1 data set, indicating that the most parsimonious of the homology schemes is the one that implies a neomorphic preorbital fossa and opening for metriorhynchids while considering the opening of basal thalattosuchians as homologous to the antorbital fenestra of other crocodyliforms (Fig. 2). When thalattosuchians are forced to be basal mesoeucrocodylians or basal crocodyliforms, the data matrix H1 is also the most parsimonious of the homology schemes, indicating that the preference for this interpretation is robust to the alternative phylogenetic placements proposed for Thalattosuchia.

The only difference observed in the comparisons of the homology schemes using alternative phylogenetic trees is the relative score of H2 and H0. When Thalattosuchia is depicted as part of Neosuchia (unconstrained analysis), H2 is as parsimonious as H0 (Fig. 2A, B), whereas under the basal mesoeucrocodylian and basal crocodyliform constraints, H2 is suboptimal with respect to H0 (Fig. 2C–F).

The differences in the parsimony score (tree length) for the three alternative homology schemes are exclusively based on the different scorings made for the antorbital/preorbital characters, as the rest of the data matrices H0, H1, and H2 were identical. An analysis of the variation in length of these characters under the three homology schemes (see Supplementary Material for further details) indicates that when Thalattosuchia is nested well within Neosuchia, the difference in the parsimony score implied by data set H1 and the other two matrices is five steps. In the alternative homology interpretations (H1 and H2), some

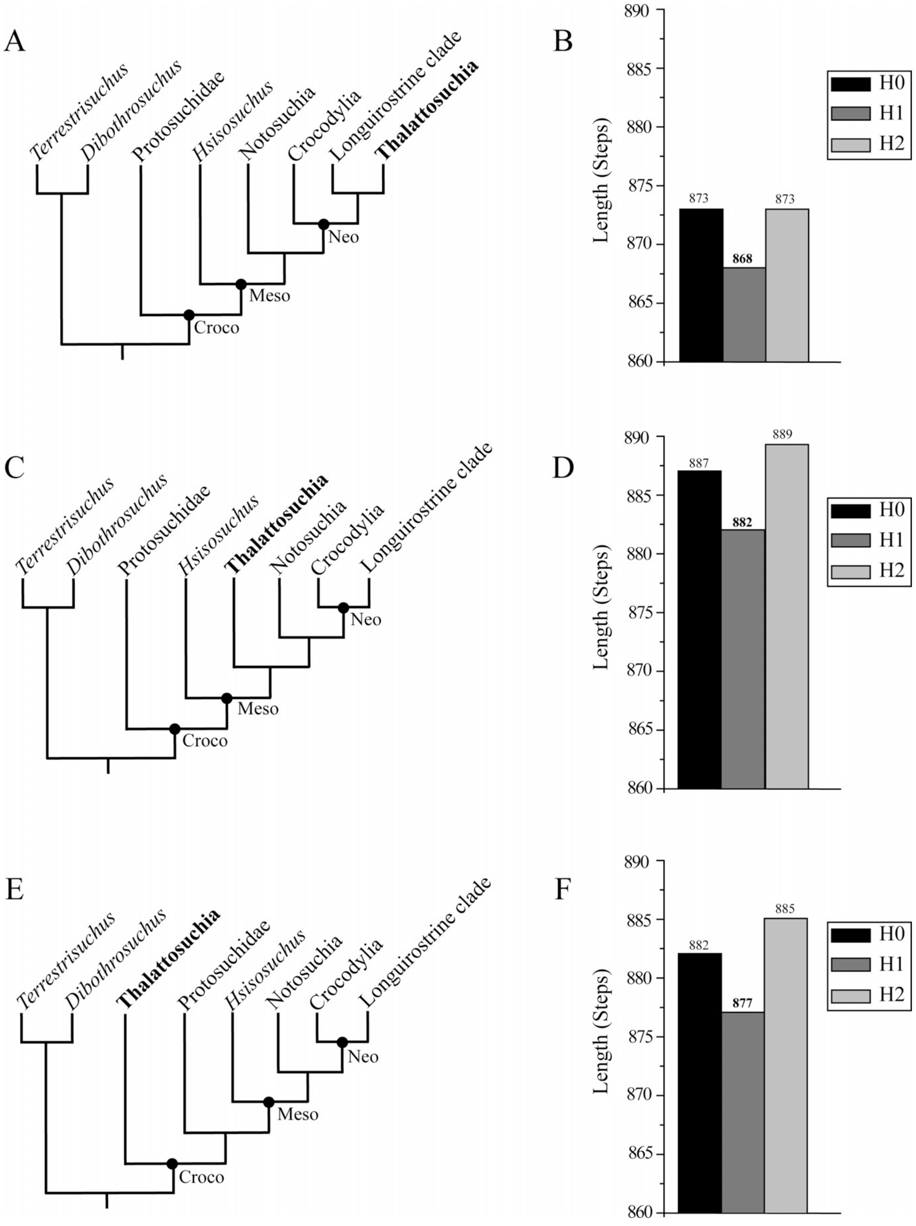

FIGURE 2. Different topologies analyzed in this contribution and the length for each one in all homology scenarios. **A**, **B**, Thalattosuchia as neosuchians (unconstrained); **C**, **D**, as basal mesoeucrocodylians; and **E**, **F**, as basal crocodyliforms. **Abbreviations**: **Croco**, Crocodyliformes; **Meso**, Mesoeucrocodylia; **Neo**, Neosuchia.

characters imply additional steps (e.g., characters 67 and 258), but the characters related to the antorbital fenestra that were mapped as metriorhynchid synapomorphies in H0 (e.g., characters 257, 261, 262, and 263, among others) are, under this scenario, primitive characters for the group having 0 steps in the resulting trees. This kind of response is to be expected when a neomorphic interpretation is considered, because it makes some features present in a restricted group incomparable with other taxa (e.g., bone participation in a fenestra) (Ramirez, 2007). When the basal thalattosuchians (i.e., 'telosaurids') lacking most of these characters are considered as having a preorbital fenestra (H2), these characters are optimized as synapomorphies of Metriorhynchidae (adding steps to the resulting tree/s), as in the case of H0.

Homology Implications

As mentioned above, irrespective of the position of Thalattosuchia in the phylogeny of Crocodyliformes, the traditional interpretation, which postulates that the fenestra located anterior to the orbit of metriorhynchids is homologous with the antorbital fenestra (sensu Witmer, 1997) of other archosaurs, is rejected based on the parsimony criterion. Given that this homology is rejected and that other functions have been proposed for this structure based on the exceptional preservation of soft tissues in some metriorhynchid specimens (Fernández and Gasparini, 2000; Gandola et al., 2006), we advocate using the name preorbital opening (Fernández and Herrera, 2009) for this structure in metriorhynchids. By contrast, the small fenestra of basal thalattosuchians ('teleosaurids') is most parsimoniously interpreted as homologous to the antorbital fenestra of other archosaurs. This interpretation of the openings of the rostrum in thalattosuchians is consistent with the inferred lifestyle of metriorhynchids and 'teleosaurids.' The association of the preorbital opening of metriorhynchids with an exocrine gland (probably a salt gland) has been interpreted as an adaptation to the completely pelagic lifestyle traditionally proposed for metriorhynchids (Fernández and Herrera, 2009). This adaptive explanation is therefore compatible with the neomorphic origin of the preorbital opening of metriorhynchids. The absence of distinctive features that characterize the preorbital opening and fossa of metriorhynchids in basal thalattosuchians is consistent with the less well developed marine adaptations of these forms (based on the presence of fully developed limbs and dermal armor resembling that of amphibious or terrestrial crocodyliforms). However, we underscore that the homology of the antorbital opening of basal thalattosuchians should be carefully considered in future anatomical studies, paying special attention to the internal structure of the rostrum on well-preserved specimens of the numerous species that have been referred to Teleosauridae.

As the fenestra of metriorhynchids is most parsimoniously interpreted as not homologous with those in other crocodyliforms, the antorbital fenestra must have been laterally closed, internalizing the associated pneumatic structures within the rostrum of metriorhynchids. In internal casts of the snout of *Cricosaurus araucanensis*, an accessory paranasal diverticulum that is not connected to the preorbital opening was identified as the antorbital sinus (Fernández and Herrera, 2009), a pneumatic structure present in the snouts of extant birds and crocodilians (Witmer, 1995). A similar internalization process has been previously hypothesized to occur multiple times in the evolutionary history of crocodyliform archosaurs, including the lineage leading to extant crocodylians (Witmer, 1997). Our phylogenetic analysis identifies this process as occurring independently in five lineages: in two basal crocodyliforms (*Edentosuchus* and *Fruitachampsa*), in derived notosuchians, in neosuchians more derived than atoposaurids (*Theriosuchus* + *Alligatorium*), and in metriorhynchids, because basal thalattosuchians are recovered as having an external antorbital fenestra (see Supplementary Material).

CONCLUSION

The application of the dynamic homology approach provides an objective and sound criterion for choosing between competing homology hypotheses. The merit of alternative interpretations of fossil structures has been the focus of intense debates in paleontology and the dynamic homology approach has therefore a great potential for analyzing these problems within a phylogenetic framework (see also Xu et al., 2009). The application of this methodology allowed us to reject, based on the available anatomical data, the homology of the fenestra anterior to the orbit of metriorhynchids with the antorbital fenestra of other archosaurs. This structure is instead most parsimoniously interpreted as a neomorph (i.e., preorbital opening sensu Fernández and Herrera, 2009). The fenestra in basal thalattosuchians is instead interpreted as homologous to the antorbital fenestra of other archosaurs, suggesting that the early evolution of Thalattosuchia must have included remarkable anatomical (and physiological) changes in the excretory and pneumatic structures located in the rostrum. These results emphasize the need for further anatomical and phylogenetic studies on thalattosuchians, particularly the diverse 'teleosaurids' and basal metriorhynchids not included in this study (e.g., *Teleidosaurus*), because they are critical for evaluating the relationships of these to other Crocodyliformes and are also essential for studying the acquisition of the key innovations of metriorhynchids, which allowed them to be the only archosaur group to thrive in marine environments.

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