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Cranial morphology of the Early Permian mesosaurid *Mesosaurus tenuidens* and the evolution of the lower temporal fenestration reassessed*Morphologie crânienne du mésosauridé Mesosaurus tenuidens du Permien inférieur et un réexamen de l'évolution de la fenestration temporale inférieure*Graciela Piñeiro^{a,*}, Jorge Ferigolo^b, Alejandro Ramos^a, Michel Laurin^c^a Departamento de Evolución de Cuencas, Facultad de Ciencias, Iguá 4225, CP 11400 Montevideo, Uruguay^b Seção de Paleontologia, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Rua Salvador França, 1427-90 690-000, Porto Alegre, RS, Brazil^c UMR 7207, CNRS/MNHN/UPMC, Centre de Recherches sur la Paleodiversité et les Paléoenvironnements, Muséum national d'Histoire naturelle, Département Histoire de la Terre, bâtiment de Géologie, case postale 48, 57, rue Cuvier, 75231 Paris cedex 05, France

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ABSTRACT

The Early Permian mesosaurids are the oldest known aquatic amniotes with an exclusively Gondwanan distribution. Although several hundred of complete skeletons have been discovered and intensively studied, the anatomy and taxonomic composition of the group, as well as its phylogenetic relationships remain controversial. Several well-preserved mesosaurid specimens found in Uruguay justify a new anatomical reconstruction of the skull of *Mesosaurus tenuidens*, differing from earlier ones especially in the presence of a lower temporal fenestra. The significance of this structure for the evolution of temporal fenestration in amniotes is evaluated according to the two most recent phylogenetic hypotheses, in which mesosaurids are basalmost sauropsids or basalmost parareptiles. A synapsid-like fenestration may be the primitive condition for Amniota, and it may be also a basal condition for parareptiles, because recent phylogenies suggest a basal position for mesosaurids and lanthanosuchoids within that group, and both possess a lower temporal fenestra. Our results also give a moderately strengthened support for diapsid affinities of turtles.

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R É S U M É

Les mésosauridés du Permien inférieur sont les plus anciens amniotes aquatiques connus, avec une distribution exclusivement Gondwanienne. Bien que plusieurs centaines de squelettes complets aient été découverts et étudiés intensivement, l'anatomie et la composition taxonomique du groupe, ainsi que ses relations phylogénétiques demeurent controversées. Plusieurs spécimens de mésosauridés bien conservés trouvés en Uruguay justifient une nouvelle reconstitution anatomique du crâne de *Mesosaurus tenuidens*, différant des plus anciennes, en particulier par la présence d'une fenêtre temporale inférieure. La signification de cette structure pour l'évolution de la fenestration temporale chez les

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amniotes est évaluée en fonction des deux hypothèses phylogénétiques les plus récentes, à savoir que les mésosauridés sont les sauropsidés les plus basaux ou les parareptiles les plus basaux. Une fenestration de type synapside peut être la condition primitive pour les amniotes et pour les parareptiles, car de récentes phylogénies suggèrent une position basale pour les mésosauridés et les *lanthanosuchoïdés* au sein de ce groupe et les deux possèdent une fenestration temporale inférieure. Nos résultats renforcent modérément le soutien pour une position des tortues au sein des diapsides.

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1. Introduction

Geologically younger than the earliest known amniotes, the aquatic Mesosauridae from the Early Permian of Gondwana have disputed phylogenetic affinities as the basalmost sauropsids (Laurin and Reisz, 1995) or as basal parareptiles (Gauthier et al., 1988; Modesto, 1999, 2000, 2006; Modesto and Anderson, 2004). More recently, a Bayesian study of amniote phylogeny placed them in various positions, including as the basalmost Eureptilia (Müller and Reisz, 2006). However, even more controversial is the configuration of their temporal region, which has shifted over time from diapsid (MacGregor, 1908), to synapsid (von Huene, 1941) and more recently, to anapsid (Modesto, 1999, 2006). Such different interpretations are surprising, considering the large number of specimens discovered in South America (mostly in Brazil) and South Africa, including mostly articulated and almost complete skeletons (Araújo, 1976). Thus, the interpretation of the skull morphology is complicated by the quality of preservation or inadequate preparation of the specimens. The latter condition prevails in specimens preserved within a calcareous matrix, which is difficult to remove without serious damage to the bones. In most cases, these skull roof bones are fractured and overlap each other and part of the palatal elements, due to compression during fossilization. Mesosaurid skull roof bones are very thin and delicate, a condition that favored distortion and fragmentation. Other specimens are preserved as natural moulds, and latex-rubber casts were commonly used to study and reconstruct the mesosaurid skeleton (e.g. von Huene, 1941; MacGregor, 1908; Modesto, 1996, 1999, 2006; Oelofsen, 1981). Although useful, the casts reproduce the distortion present in the specimens.

Uruguayan mesosaurids have been little studied until the 1990s and they were virtually absent from the literature. Preliminary studies by Piñeiro (2002, 2004, 2006) documented dozens of specimens (including cranial and postcranial elements) in the Uruguayan Early Permian (Artinskian) Mangrullo Formation. In the Uruguayan specimens, the cranial and postcranial bones can easily be removed from the sediments, and there are also very well-preserved natural moulds that show the bones in their original anatomical position, nearly without distortion. All the taphonomic categories described by Soares, 2003 from the Brazilian Iratí Formation at the Paso de São Borja (Rio Grande do Sul) locality are present in Uruguay. Nonetheless, the well-preserved moulds of isolated skulls, which can preserve a very thin layer of the original bone, are considered an additional taphonomic class (Morosi, 2011)

that, although not described by Soares, 2003, is also present among the Brazilian specimens.

The first interesting clue to the presence of a lower temporal fenestra provided by Uruguayan mesosaurid specimens was the discovery of isolated temporal bones (Piñeiro, 2002, 2004, 2006). As von Huene, 1941 noted, the triradiate morphology of the jugal and the excavated lateral area of the postorbital suggested the delimitation of a lower temporal fenestra. Later discoveries, including well-preserved natural moulds of articulated specimens showing the skull roof bones, part of the palate, as well as part of the braincase and the occipital region, allow a complete description of the mesosaurid skull morphology, particularly the temporal region. The study of those specimens is the subject of the present contribution. The implications of mesosaurid temporal fenestration for the evolution of this character within Amniota and by extension, the controversial position of turtles, are also discussed.

2. Materials and methods

The examined specimens (FC-DPV 1732, 2061, 2209, 2242, 2389, 2395, 2446, 2454, 2457, 2468 and 2534) are isolated skulls housed in the Collection of Fossil Vertebrates (FC-DPV) of the Facultad de Ciencias, Montevideo, Uruguay. They are preserved as natural moulds that reproduce details of the finest structures. The elements are articulated in anatomical position, a condition rarely observed in mesosaurid skulls. Mostly, they consist of part and counterpart of the same individual, allowing the observation of the bone morphology in more than one plane. For instance, one part can show a plane closer to the dorsal surface, while the counterpart can reveal a plane closer to the ventral surface of the skull. This configuration, which is often very useful, is not always optimal. If only one part is found for several specimens, different interpretations of the same structures can result from taphonomic differences (consisting of various fracture planes).

The materials were collected from light and black shales of the Early Permian Mangrullo Formation, which contain a variable amount of organic matter. This unit outcrops in several localities in the north and northeast of the country, in Tacuarembó and Cerro Largo counties. They are associated with pygocephalomorph crustaceans and the trace fossil *Chondrites* (Piñeiro, 2006, 2008; Piñeiro et al., in press, 2012a). Binocular microscopes were used to study and photograph the specimens.

The evolution of temporal fenestration in amniotes was assessed through a parsimony optimization in Mesquite (Maddison and Maddison, 2011). The reference phylogeny,

compiled from the literature (see figure legend for sources), was time-calibrated using Stratigraphic Tools (Josse et al., 2006). The phylogenetic signal of the characters was assessed through comparisons between the number of steps required by the reference trees and the same statistic in a population of 10,000 random trees produced by random taxon reshuffling (Laurin, 2004) and by a Yule process (Yule, 1925).

3. Systematic palaeontology

Amniota Haeckel, 1866

Mesosauridae Baur, 1889a

Mesosaurus tenuidens Gervais, 1865

The assignment of the materials to Mesosauridae was based upon the elongate shape of the skull and its general morphology, including the long and slightly recurved teeth (von Huene, 1941; Modesto, 1999, 2006). Specific assignment to *Mesosaurus tenuidens* is supported by recent studies, which suggested that this taxon is the only mesosaurid present in Uruguay (Morosi, 2011), and by the lack of unambiguous characters that allow discrimination between this taxon and *Stereosternum tumidum* (Piñeiro et al., 2012b). According to previous authors, *Mesosaurus* appeared to differ from *Stereosternum tumidum* because the posterior projection of its frontal points laterally, whereas it is posteriorly directed in *Stereosternum* (Modesto, 1996, 1999, 2006). However, the Uruguayan materials suggest that this character is taphonomic (see below). The other cranial character that was used to differentiate the two taxa is the length of the teeth, the largest ones in a series being equivalent to the length of three tooth positions in *Stereosternum*, and more than five positions in *Mesosaurus* (Modesto, 1996, 2006). Our measurements confirm this distinction, because none of the Uruguayan specimens have teeth as short as only three tooth positions. However, measurements of the largest teeth and tooth positions in our materials suggest that this character also exhibits intraspecific variation. In most specimens, the tooth size matches the length of five tooth positions, but we found also some that are equivalent to four, and others that were between four and five. We also found that the tooth position length can vary by several millimeters, even in the same tooth series. Thus, we are more inclined to think that intraspecific variation is common in this character and we have one single taxon in Uruguay, which according to previous studies is *Mesosaurus*. However, the value of this feature to recognize *Stereosternum* should be validated by studying the Brazilian and South African specimens assigned to this taxon. At the same time, postcranial characters used to distinguish *Mesosaurus* from *Stereosternum* may be strongly influenced by taphonomy, intraspecific ontogenetic variation, and sexual dimorphism (Piñeiro, 2002, 2004, Piñeiro et al., 2012b). Some characters, such as the skull-neck proportions (Araújo, 1976), may be subject to preservation problems that prevent accurate cervical and presacral vertebral counts. The different morphology of the interclavicle (Modesto, 1996, 1999) seems to be related to ontogenetic changes, as the diamond-like shape is more frequently present in juvenile and young adults, while large, mature individuals display a more triangular

interclavicular shaft. The presence or absence of pachyostotic hemal arches (Araújo, 1976), is not a valid character, as both types can be observed on the tail of the same individual; the V-shaped, non-pachyostotic elements the posteriormost (Piñeiro, 2002). The supraneural process, a posterior projection of the neural canal observed in dorsal vertebrae assigned to *Stereosternum* (Modesto, 1996, 1999), was the only postcranial character that could not be checked because it is not present in the available materials from Uruguay. The status of those characters in *Brazilosaurus sanpauloensis* is difficult to establish because of the limited information about this taxon in the literature, and it seems not to be present in the Mangrullo Formation shales. However, the revision of some of the Brazilian specimens suggests that this taxon is a smaller mesosaurid, as suggested by the size of its teeth, which are invariably shorter than the length of two tooth positions. Moreover, all *Brazilosaurus* specimens have the centrae of anterior-most cervical vertebra (posterior to the atlas-axis complex) longer than the succeeding, producing a small increase of the length of the neck, feature that was considered to distinguish this species (Araújo, 1976; Shikama and Ozaki, 1966).

The description is based mainly upon specimens FC-DPV 2534 and FC-DPV 2061 (Fig. 1), both preserved as natural moulds of the skull roof, although a very thin and discontinuous layer of bone seems to have been present in some of the elements, recognizable for its different texture and color. Other more fragmentary materials (see Material and Methods) also preserved as natural moulds, were used as additional specimens to better document some of the characters that are not so well displayed by the more complete skulls. FC-DPV 2061 is just a single slab, and FC-DPV 2534 consists in part and counterpart of a single skull. Most of the skull roof bones are preserved in their correct anatomical position in both specimens, which correspond to adult mesosaurids, according to size comparisons with articulated skeletons from Uruguay and Brazil. One of the specimens used for comparative purposes is a *Mesosaurus* embryo (Piñeiro et al., 2012b), which displays a triradiate jugal and a temporal fenestra, suggesting that the temporal area changes little during ontogeny.

Detailed descriptions of the skull of *Mesosaurus tenuidens* were published by von Huene, 1941 and Modesto, 2006 and most of the arrangements depicted by these authors were found in our materials. Thus, we base our description on their work, and emphasize new data that allow us to discriminate between their alternative interpretations, as shown in the most spectacular way in the temporal region.

3.1. Antorbital region

In this area, a small foramen, the foramen nariale obturatum (fno), after von Huene, 1941 is found posterior to the naris (Fig. 2). This foramen is invariably present in all mesosaurids, and has been described as an indentation of the lacrimal bone, anterodorsally bounded by the nasal (Modesto, 2006), which forms a short suture with the maxilla between the septomaxilla and the fno (Piñeiro et al., in press). This

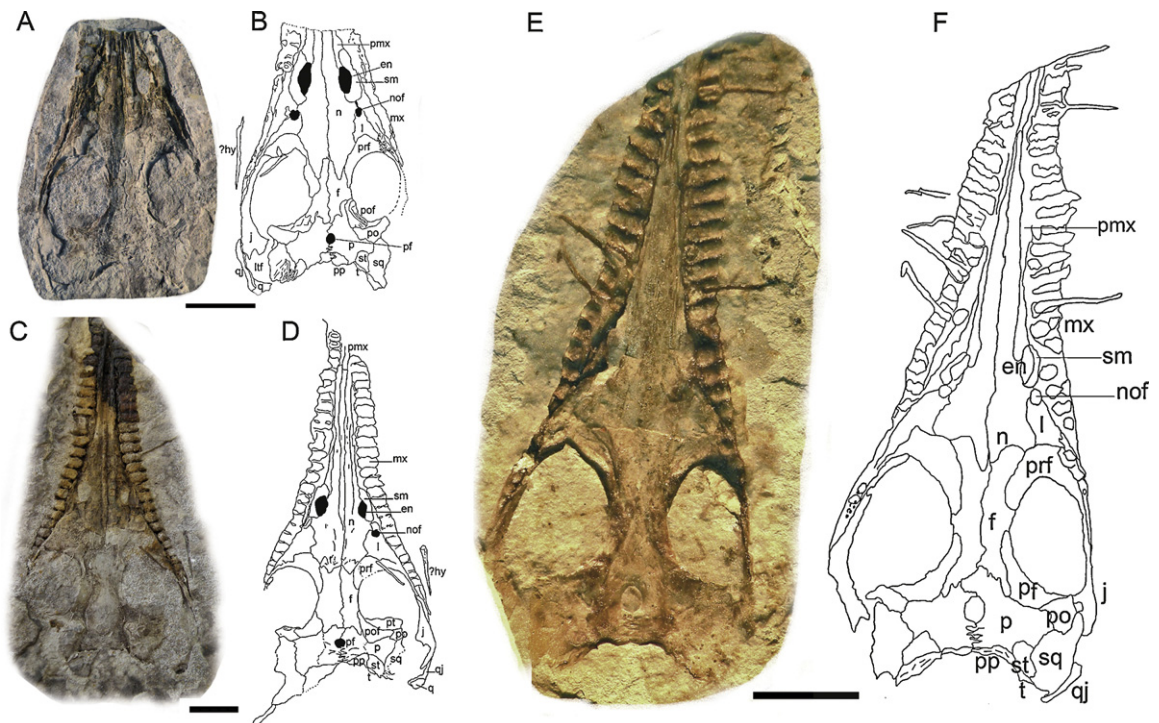


Fig. 1. *Mesosaurus tenuidens* from the Early Permian Mangrullo Formation of Uruguay. *Skull morphology.* A. FC-DPV 2534, photograph of an almost complete natural mould of the skull roof, showing most bones in their anatomical position. B. Interpretive drawing of A. C. Photograph of the counterpart of FC-DPV 2534. D. Interpretive drawing of C. E. FC-DPV 2061, photograph of an almost complete skull showing areas where a very thin sheet of the original bones was preserved (dark areas). F. Interpretive drawing of E. Scale bar: 10 mm. Anatomical abbreviations: en, external naris; f, frontal; ?hy, probable fragmentary hyoid; j, jugal; l, lacrimal; ld, lacrimal duct; ltf, lower temporal fenestra; mx, maxilla; n, nasal; fno, foramen nariale obturatum; p, parietal; pf, parietal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sm, septomaxilla; sq, squamosal; sr, sclerotic ring; st, supratemporal; t, tabular.

Fig. 1. *Mesosaurus tenuidens* de la Formation Mangrullo, Permien inférieur d'Uruguay. *Morphologie du crâne:* A. FC-DPV 2534, photographie d'un moulage naturel presque complet du toit du crâne montrant la plupart des os dans leur position anatomique. B. Dessin interprétatif de A. C. Photographie de la contre-partie de FC-DPV 2534. D. Dessin interprétatif de C. E. FC-DPV 2061, photographie d'un crâne presque complet montrant des zones où une très mince couche d'os original a été préservée (zones foncées). F. Schéma interprétatif de E. Barre d'échelle: 10 mm. Abréviations anatomiques: en, narine externe; f, frontal; hy, probablement hyoïde fragmentaire; j, jugal; l, lacrimale, ld, conduit lacrimale; ltf, fenêtre temporelle inférieure; mx, maxillaire; n, nasal; fno: foramen nariale obturatum; p: pariétal; pf: foramen pariétal; pmx: prémaxillaire; po: postorbitaire; pof: postfrontal; pp: postpariétal; prf: préfrontal; pt: ptérygoïde; q: carré; qj: quadratojugal; sm: septomaxillaire; sq: squamosal; sr: anneau sclérotique; st: supratemporal; t: tabulaire.

arrangement is reminiscent of the anteorbital fenestra of most archosaurs, which is much larger but similarly opens between the orbit and the naris and is surrounded by lacrimal, nasal and maxilla (Piñeiro et al., in press; Romer, 1956).

The prefrontal is a large bone, which forms the greatest part of the anterior orbital margin (Figs. 1–3). It is partially overlapped by the lacrimal laterally (Modesto, 2006) (Fig. 3A); and both bones extend posterolaterally towards the jugal. The lacrimal make contact with the maxilla at its more posterior section and the prefrontal meets the jugal in a short suture. This lateral extension of the prefrontal reduces the contribution of the lacrimal to the orbital margin, which is restricted to its anteroventral edge. However, in specimens that preserve the internal surface of the skull roof the lacrimal seems to not reach the anterior orbital edge (or barely), which is formed entirely by the prefrontal, or nearly so (Fig. 3). The lacrimal duct is exposed in most

specimens. Its orbital foramen opens at the posterolateral end of the lacrimal; anteriorly, it opens into the foramen nariale obturatum (Modesto, 2006) at its medial margin (Piñeiro et al., in press), as shown by some specimens that preserve the course of the lacrimal duct between both foramina (Fig. 3 F–G).

Our interpretation of the nasal differs from recently published accounts. Instead of the relatively short bone described by Modesto, 2006, it is very long, almost as long as the premaxilla, extending anteriorly to the level of the anteriormost end of the maxilla, as suggested by von Huene, 1941 and more recently by Morosi, 2011. The nasal meets the premaxilla in a long lateral and a short, fairly straight anterior suture near the middle of the snout (Figs. 1, 2 and 4). However, the internal view of these bones shows an apparently shorter nasal because it is in part hidden by the extensions of the premaxilla (Fig. 4E). As also suggested by von Huene, 1941, the premaxilla

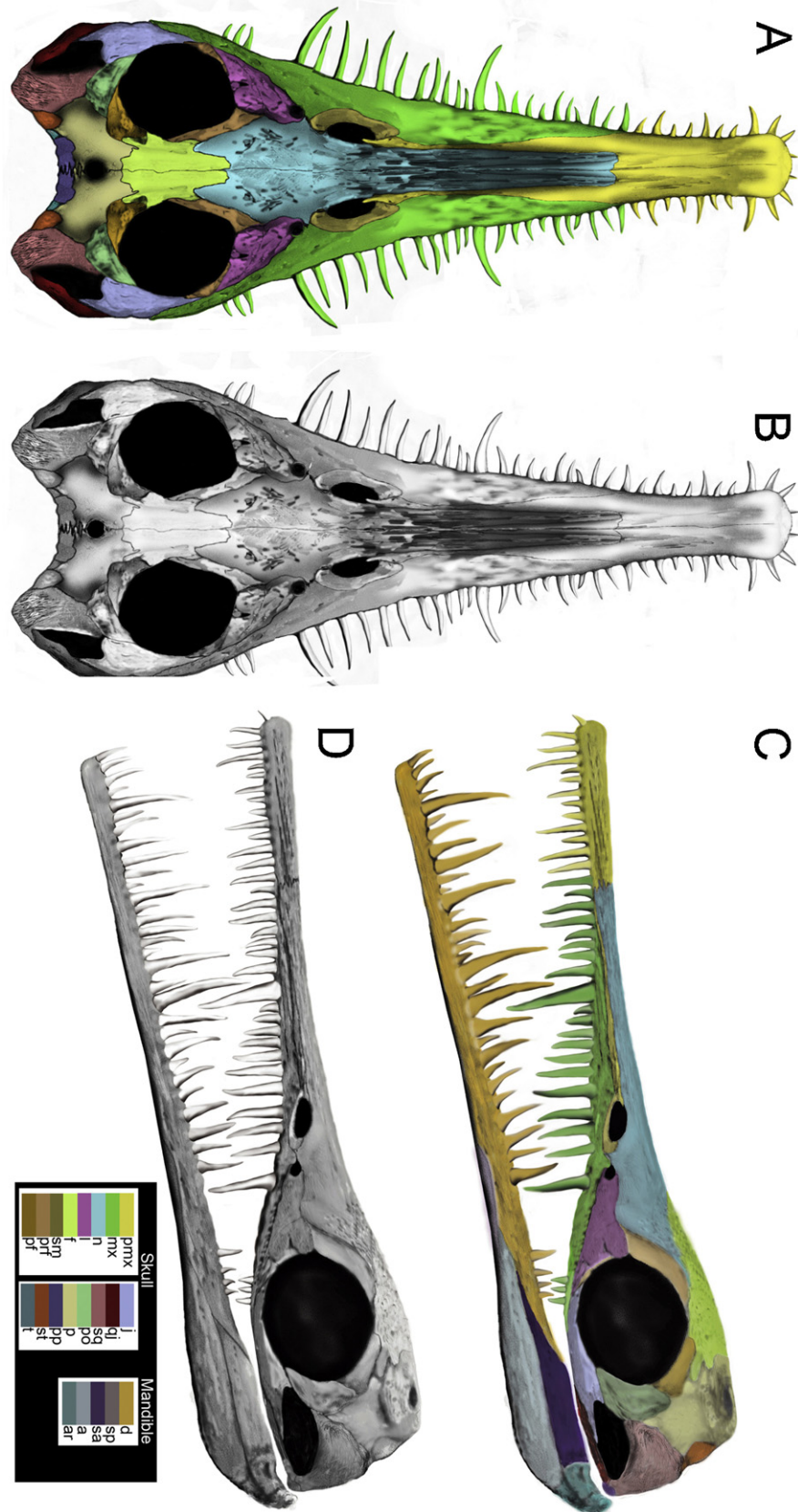


Fig. 2.

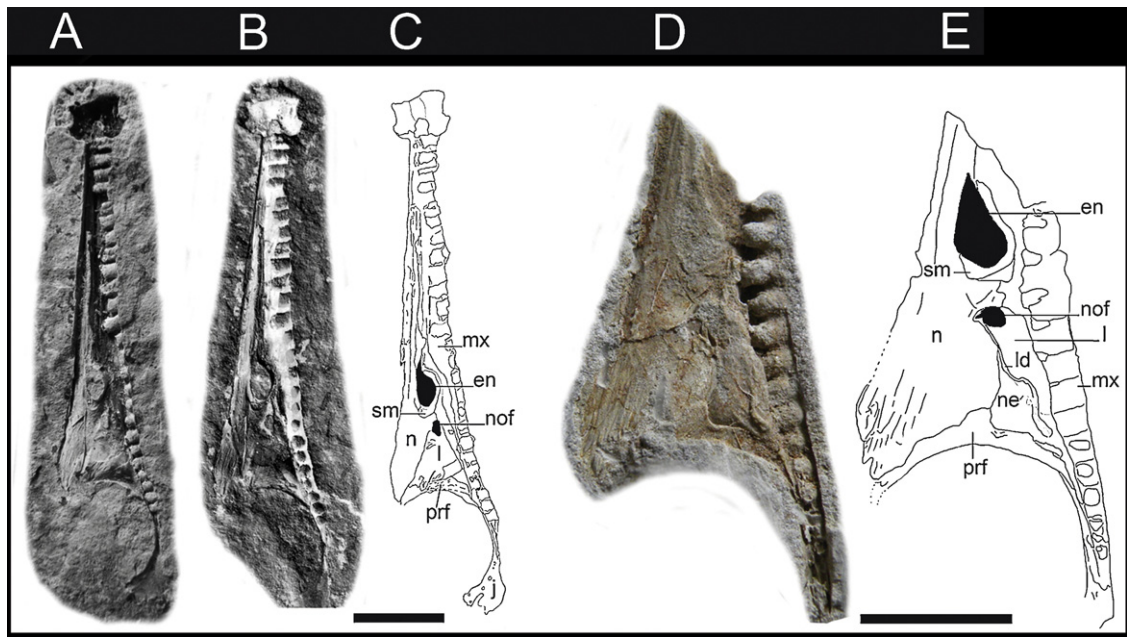


Fig. 3. *Mesosaurus tenuidens* from the Lower Permian Mangrullo Formation of Uruguay. *Lacrimal/prefrontal configuration.* A and B. Part and counterpart of specimen FC-DPV 2389 respectively, a partial anterior skull, showing apparently different configurations of the lacrimal-prefrontal contact and of their contribution to the anterior orbital margin (because of the different planes). C. Composite interpretive drawing of A and B. D. FC-DPV 2446, a partial anterior fragment of the skull roof displaying an internal view of the lacrimal and prefrontal. E. Interpretive drawing of D. Scale bars: 10 mm. Anatomical abbreviations as for Fig. 1.

Fig. 3. *Mesosaurus tenuidens* de la Formation Margrullo, Permien inférieur d'Uruguay. *Configuration lacrimale/préfrontale.* A et B. Partie et contre-partie du spécimen FC-DPV 2389 respectivement, un crâne antérieur partiel montrant apparemment différentes configurations du contact entre lacrimale et préfrontal et de leur contribution à la marge orbitale antérieure (à cause des différents plans de fracture). C. Dessin interprétatif composite de A et B. D. FC-DPV 2446, fragment antérieur partiel de la calotte crânienne montrant une vue interne du lacrimale et du préfrontal. Dessin interprétatif de D. Barres d'échelle : 10 mm. Abréviations anatomiques comme pour la Fig. 1.

sends posterior processes lateral to the nasal, which defines nearly the entire dorsomedial margin of the naris (Fig. 4 C–G). This configuration differs from that favored by Modesto, 2006, in which the anterior end of the nasal is placed at the level of the anterior narial margin, where the bone bears extensive longitudinal ornamentation (Fig. 4C,D).

3.2. Interorbital region

The mesosaurid frontal has been described as transversely broadened posteriorly and bearing processes directed either posteriorly (as in *Stereosternum*) or latero-posteriorly (as in *Mesosaurus*), a condition unique among early amniotes (Modesto, 1996, 1999, 2006). The analyzed Uruguayan specimens suggest that the presence of long posterior processes of the frontal in mesosaurids may be a taphonomic artifact instead of an anatomical attribute

(contra Modesto, 1996, 1999, 2006 and Piñeiro, 2004), although as with all mesosaurid material, this interpretation has to be treated with caution. Several natural moulds of the dorsal skull roof, preserved as part and counterpart, suggest that the frontal has an almost conventional transverse suture with the parietal and the postfrontal, displaying only short projections medial to the latter (Figs. 1 and 5). Those projections are not visible on the internal surface of the skull roof, and the postfrontal appears to occupy the position of the lateral tongue-like processes figured by Modesto (1996, 1999, 2006) (Fig. 5 B).

3.3. Postorbital and temporal regions

Paired postparietals are almost always present in the studied materials (Figs. 1, 2 and 5). They most likely were confined entirely to the occipital region, even though their

Fig. 2. *Mesosaurus tenuidens* from the Lower Permian Mangrullo Formation of Uruguay. *Anatomical reconstruction.* A. Reconstruction of the dorsal view of the skull based mostly on FC-DPV 2534 (part and counterpart) and FC-DPV 2061. FC-DPV 2109, 2377 and 2395 were used for the reconstruction of the snout. B. Black and white version. C. Lateral reconstruction. D. Black and white version. Colour code and anatomical abbreviations as for Fig. 1.

Fig. 2. *Mesosaurus tenuidens* de la Formation Margrullo, Permien inférieur d'Uruguay. *Reconstitution anatomique.* A. Reconstitution de la vue dorsale du crâne, fondée pour la plus grande partie sur FC-DPV 2534 (partie et contre-partie) et FC-DPV 2061. FC-DPV 2109, 2377 et 2395 ont été utilisés pour la reconstitution du museau B. Version noir et blanc. C. Reconstitution latérale. D. Version noir et blanc. Le code de couleur et les abréviations anatomiques sont les mêmes que pour la Fig. 1.

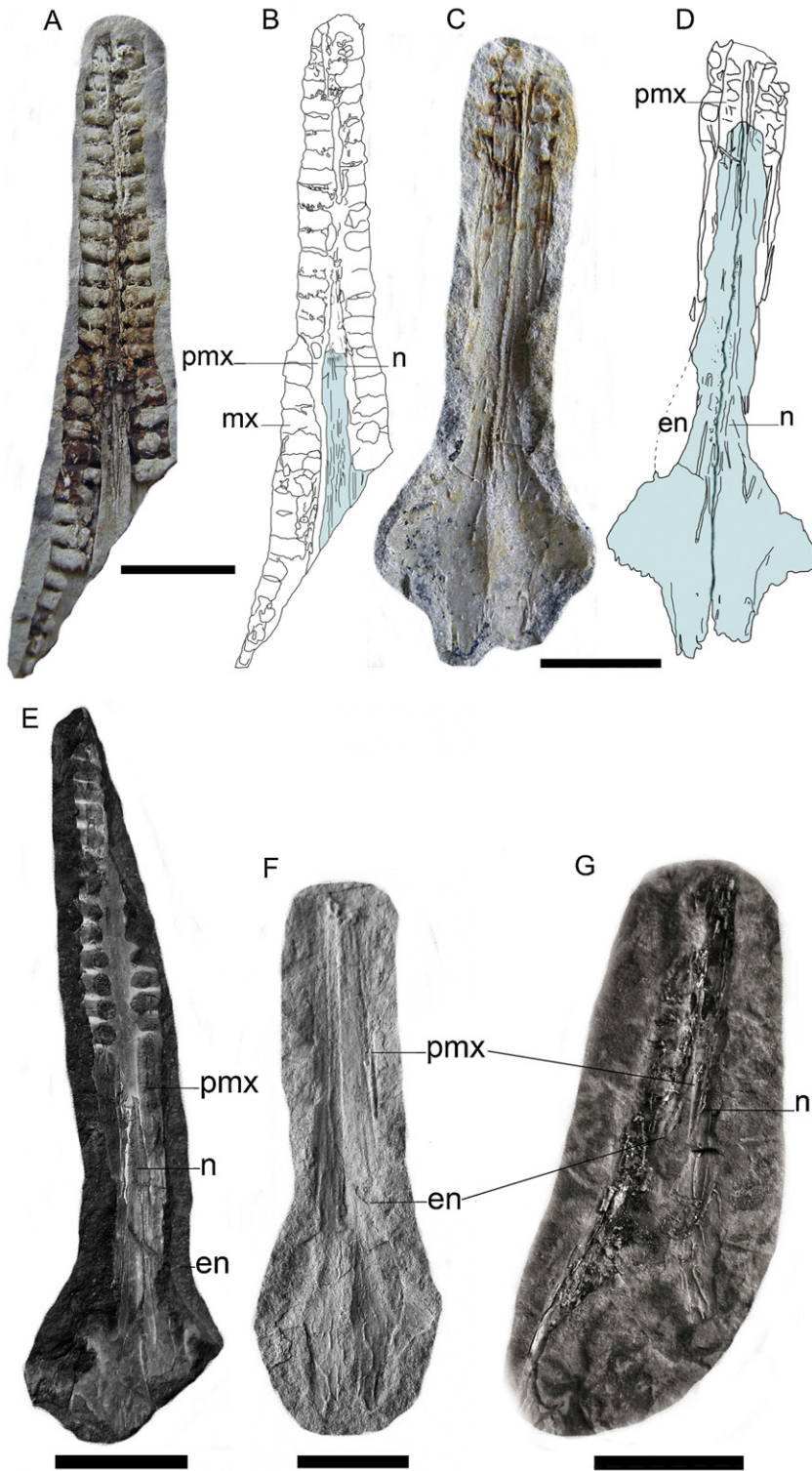


Fig. 4.

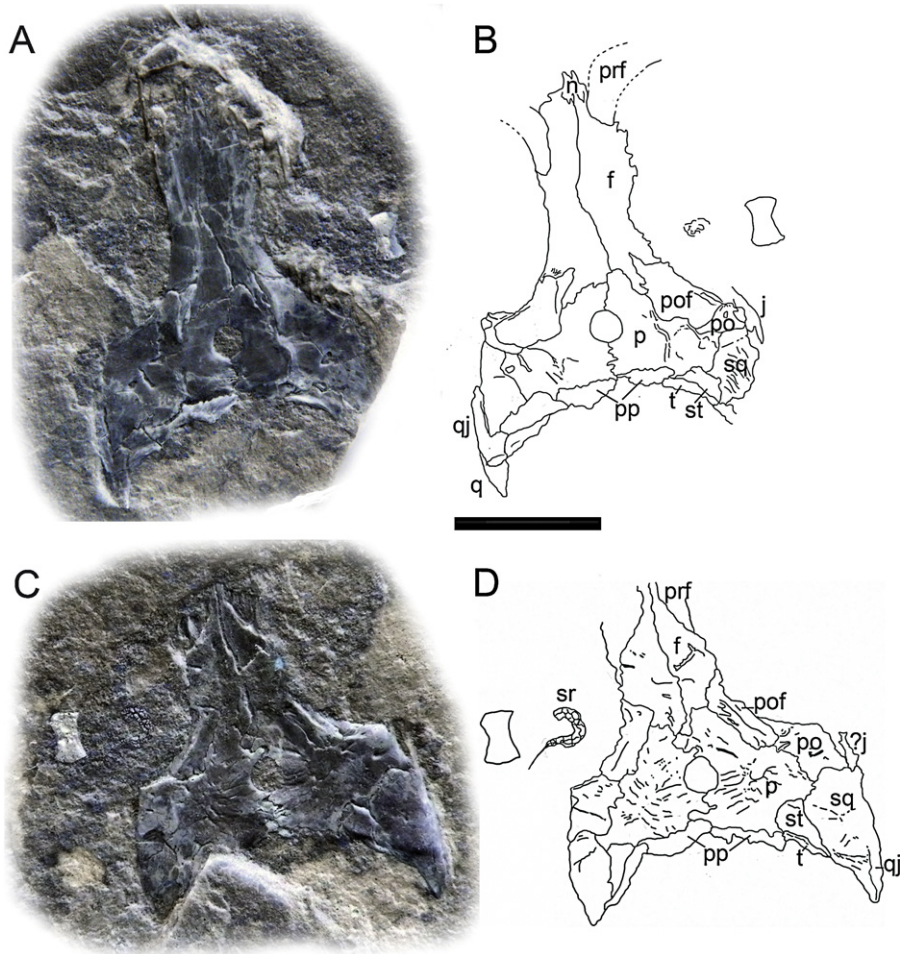


Fig. 5. *Mesosaurus tenuidens* from the Lower Permian Mangrullo Formation of Uruguay. Paired postparietals. A. FC-DPV 2457, photograph of the part of a well preserved posterior fragment of the skull showing the skull table, along with some of the elements from the occiput, such as the paired postparietals and the tabulars. B. Interpretive drawing of A. C. Photograph of the counterpart of the specimen. D. Interpretive drawing of C. Scale bar: 10 mm. Anatomical abbreviations in Fig. 1.

Fig. 5. *Mesosaurus tenuidens* de la formation de Margrullo, Permien inférieur d'Uruguay. Paires de post-pariétaux. A. FC-DPV 2457, photographie de la partie d'un fragment de crâne bien préservé montrant le plateau du crâne, ainsi que certains éléments de l'occiput, tels que la paire de pariétaux et les tabulaires. B. Dessin interprétatif de A. C. Photographie de la contre-partie du spécimen. D. Dessin interprétatif de C. Barre d'échelle : 10 mm. Abréviations anatomiques comme pour la Fig. 1.

Fig. 4. *Mesosaurus tenuidens* from the Lower Permian Mangrullo Formation of Uruguay. Nasal/premaxilla configuration. A. FC, DPV 2395, a fragment of the anterior region of the snout, showing the anterior extension of the nasal and its contact with the premaxilla. B. Interpretive drawing of A. C. FC-DPV 1732, a complete, nearly isolated long nasal bone, preserving the related lateral posterior process of the premaxilla. D. Interpretive drawing of C. E. FC-DPV 2468, a fragment of the narial region and incomplete snout preserving the outline of the nasal and premaxilla in internal view. F and G. FC-DPV 2454 and FC-DPV 2209 respectively, a complete nasal and a fragment of the anterior skull roof with the nasal completely preserved. Both specimens display the same configuration as in A-E. Scale bars: 10 mm. Anatomical abbreviations as for Fig. 1.

Fig. 4. *Mesosaurus tenuidens* de la Formation Margrullo, Permien inférieur d'Uruguay. Configuration nasale/prémaxillaire. A. FC-DPV 2395, fragment de la région antérieure du museau montrant l'extension antérieure du nasal et son contact avec le prémaxillaire. B. Dessin interprétatif de A. C. FC-DPV 1732, os nasal long, complet, presque isolé, préservant le processus postérieur latéral du prémaxillaire qui lui est lié. D. Dessin interprétatif de C. E. FC-DPV 2468, fragment de la région nasale et museau incomplet préservant les contours du nasal et du prémaxillaire en vue interne. F et G. FC-DPV 2454 et FC-DPV 2209 respectivement un nasal complet et un fragment de la partie antérieure de la calotte crânienne totalement conservé. Les deux spécimens montrent la même configuration qu'en A-E. Barres d'échelle : 10 mm. Abréviations anatomiques comme pour la Fig. 1.

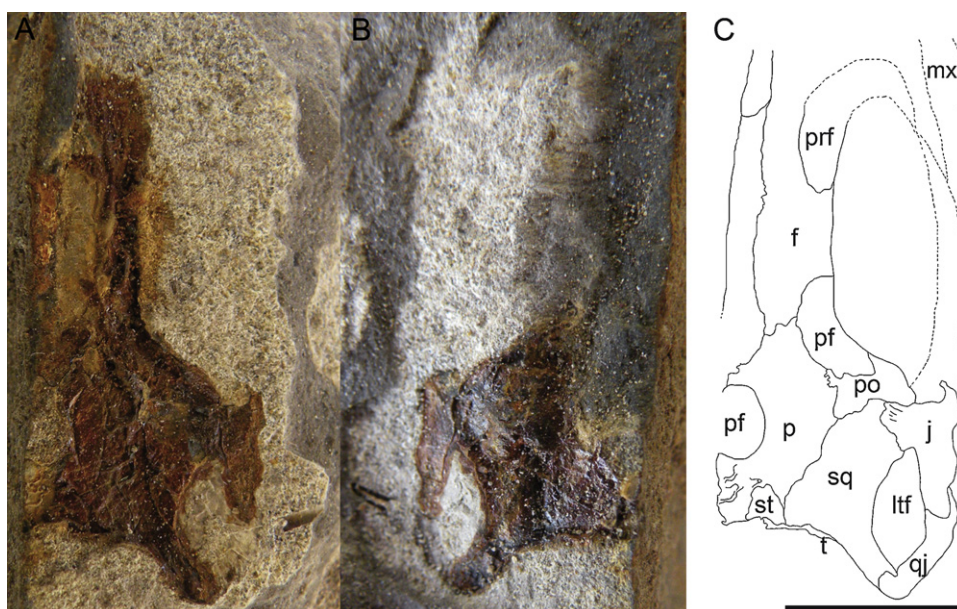


Fig. 6. *Mesosaurus tenuidens* from the Lower Permian Mangrullo Formation of Uruguay. *Temporal fenestration*. A. FC-DPV 2242, photograph of a fragmentary skull of a very small individual preserved as part and counterpart showing the configuration of the temporal area and the presence of a relatively large lower temporal fenestra, delimited by postorbital, squamosal, jugal and quadratojugal. The apparent lack of the postorbital contribution is due to the disarticulation and posterior disruption of the jugal from its original anatomical position. B. Counterpart of A. C. Composited interpretive drawing of A and B. Scale bar: 10 mm. Anatomical abbreviations in Fig. 1.

Fig. 6. *Mesosaurus tenuidens* de la Formation Margrullo, Permien inférieur d'Uruguay. *Fenestration temporale*. A. FC-DPV 2242, photographie d'un crâne fragmentaire d'un très petit individu, préservé en tant que partie et contre-partie montrant la configuration de la zone temporale et la présence d'une fenestra inférieure relativement grande, délimitée par l'ensemble postorbitaire, squamosal, jugal et quadratojugal. L'apparent manque de contribution du postorbitaire est dû à la désarticulation et à la rupture postérieure du jugal à partir de sa position anatomique originelle. B. Contre-partie de A. C. Dessin interprétatif composite de A et B. Barre d'échelle : 10 mm. Abréviations anatomiques comme pour la Fig. 1.

flattened preservation occasionally gives the impression that a dorsal exposure was present. Thus, it is possible that the smooth ventromedial concavity met the ridged dorsal surface of the supraoccipital, thus forming the junction between braincase and skull roof, as suggested by von Huene, 1941.

There is a historical debate about the nature of the mesosaurid temporal area; however, Uruguayan skull materials suggest that at least in *Mesosaurus*, a lower temporal opening was present, in the shape and configuration described by von Huene, 1941. The fenestra is relatively large and it is clearly delimited by the triradiate jugal and contributions of the postorbital, the squamosal and the quadratojugal (Figs. 1, 2 and 6), a configuration reminiscent of some early synapsids, namely caseids (e.g., Romer and Price, 1940; Sigogneau-Russell and Russell, 1974) and varanodontines (except *Elliotsmithia*; e.g., Campione and Reisz, 2010), given that the quadratojugal is excluded from the lower temporal fenestra in other synapsids. This configuration is shared also with a few reptiles such as *Petrolacosaurus* (Reisz, 1981) and, more interestingly, *Australothyris* (Modesto et al., 2009), *Millerosaurus nuffieldi* (Gow, 1972), and *Lanthanosuchus watsoni* (deBraga and Reisz, 1996).

The fenestra is an elongate window, with its maximum height at mid-length. The postorbital and jugal define its anterior edge. The postorbital is roughly triangular, with an acute lateral end that fits into a notch in the dorsal process of the jugal (Fig. 1 A,B). The squamosal forms the dorsal and posteroventral margin of the fenestra; its edge is smoothly concave along almost all its extension, and curves ventrally and slightly anteriorly to meet the quadratojugal at the posterolateral corner. The quadratojugal probably contributed to a short portion of the ventral edge of the fenestra, between the squamosal and jugal (Fig. 6).

The mesosaurid tabular has been interpreted in most previous studies as a predominantly occipital bone, or was considered to be absent (Modesto, 2006). On the contrary, other workers argued for the plesiomorphic condition of a large tabular in mesosaurids (Laurin and Reisz, 1995). Nevertheless, Uruguayan materials suggest that the tabulars are present on the dorsal skull table as thin slivers of bone, positioned lateral to the postparietals and flooring the supratemporals (Figs. 1, 2, 5, 6). The contribution of these bones to the occipital area is speculative at this stage, as we have no specimens that preserve this region completely.

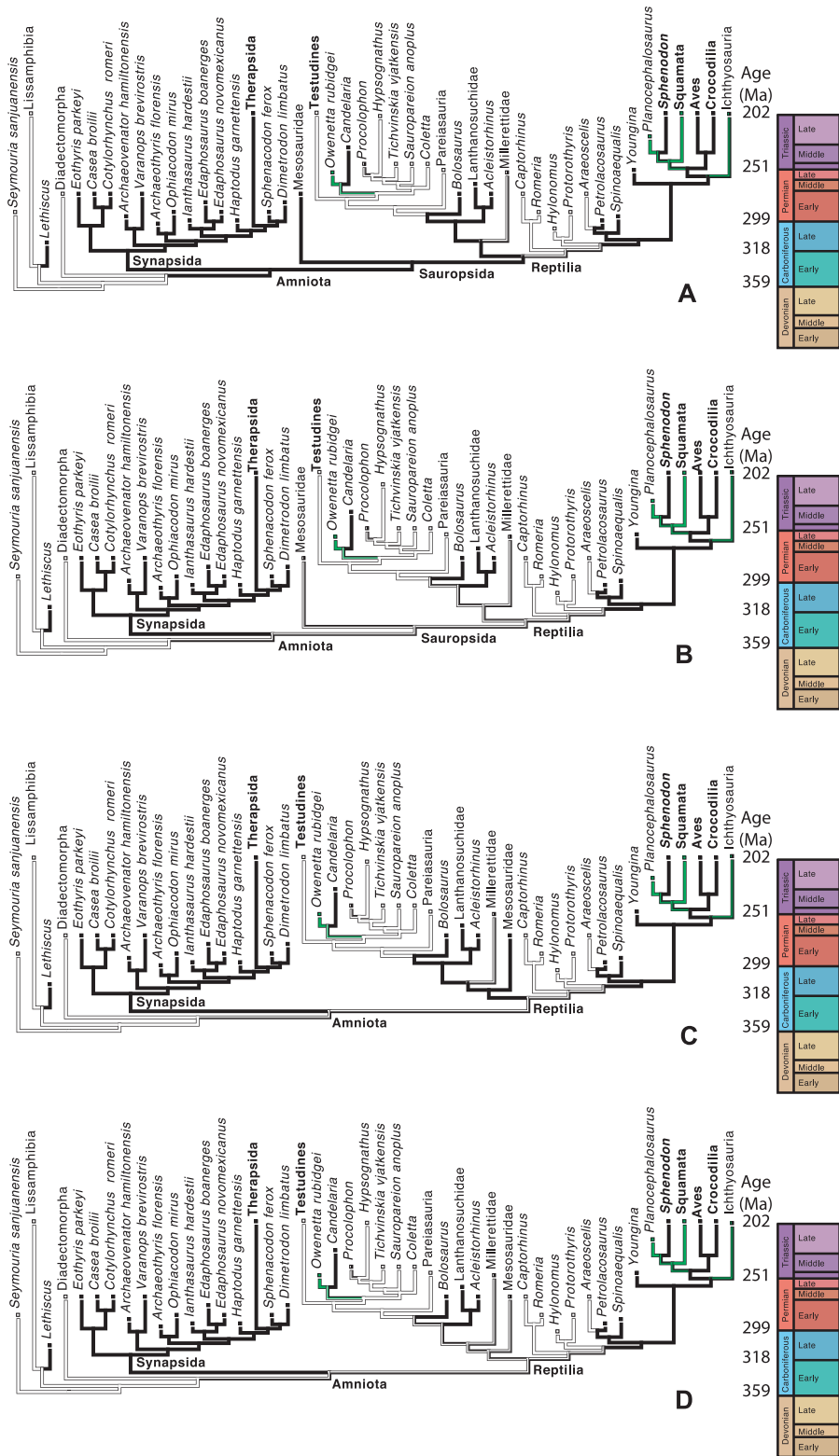


Fig. 7.

4. Discussion and conclusions

The restoration of some areas in dorsal and lateral views of the *Mesosaurus tenuidens* skull presented herein suggests that the anatomy of this basal amniote is far from completely known. The interpretation of mesosaurid cranial anatomy is complicated by taphonomic factors, and the same problem was experienced during the study of the associated pygocephalomorph crustaceans, (Piñeiro et al., in press, 2012a). Nevertheless, the availability of specimens preserved with little or no postmortem disruption, where bones remained in their anatomical disposition, allowed us to present a new reconstruction of *Mesosaurus tenuidens*, which confirms early interpretations by von Huene, 1941. The presence of fenestration in *Brazilosaurus* is difficult to assert, since we have no specimens assignable to this taxon among the well-preserved skulls yielded by the Mangrullo Formation.

Without doubt, the main contribution of the present work is the reconstruction of the temporal area in *Mesosaurus*, which suggests the presence of a lower temporal fenestra, because of the historical importance of this character in the taxonomy and nomenclature of amniotes. Although its function is controversial (Case, 1924; Cisneros et al., 2004, and references cited therein), the presence/absence of temporal fenestration has been long been considered a taxonomically very important character, long used in the Amniota classification (Baur, 1889b; Günther, 1867; Osborn, 1903). Indeed, the taxa Synapsida, Diapsida, Euryapsida, Parapsida and Anapsida were all named according to the type of temporal fenestration. However, the description of several parareptiles with temporal fenestration (Cisneros et al., 2004; deBraga and Reisz, 1996; Gow, 1972; Hamley and Thulborn, 1993; Reisz et al., 2007, among others) has impacted the relevance of this character by showing that it exhibits more homoplasy than previously thought. Furthermore, the bones bordering the lower temporal fenestra are not the same in all taxa; this is not reflected in the character coding of most analyses (e.g. deBraga and Rieppel, 1997; Laurin and Reisz, 1995; Müller and Reisz, 2006). Thus, the phylogenetic implications of the presence of a synapsid-like fenestra in *Mesosaurus tenuidens* needs to be investigated by adding the new anatomical information described above; this will be included in a forthcoming paper.

Here, we analyze only the impact that the presence of a synapsid-like fenestra in mesosaurids has on the inferred ancestral condition for Amniota, by considering the two most probable hypotheses of mesosaurid relationships. If mesosaurids are the basalmost sauropsids as suggested by Laurin and Reisz (1995) and by Müller and Reisz (2006: Fig. 3b–d), and if all mesosaurids have a lower temporal fenestra, the fenestra is most parsimoniously interpreted as primitively present in Amniota and Sauropsida (Fig. 7A). Thus, the absence of a lower temporal fenestra or the presence of a ventral emargination in some parareptiles and in turtles may be a secondary condition (Piñeiro, 2004). However, the earliest known turtles (e.g. *Triassochelis* or *Proganochelis*) suggest that the primitive condition for turtles is the absence of temporal fenestration and ventral emargination appears to be absent or weakly developed. Under the phylogeny of Laurin and Reisz (1995), if mesosaurids are scored as polymorphic for this character, the primitive condition for Amniota, Sauropsida, and various basal reptilian sub-clades becomes ambiguous (Fig. 7B). However, if mesosaurids were the basalmost parareptiles (Gauthier et al., 1988; Modesto, 1999, 2000, 2006) the primitive condition for Amniota, Reptilia, and Eureptilia is ambiguous, whether mesosaurids are scored as having the fenestra or as polymorphic, although the exact scoring of mesosaurids impacts on the most parsimonious condition in Parareptilia (Fig. 7C–D). For all four cases illustrated in Fig. 7, the phylogenetic signal in the character is highly significant ($p \leq 0.0025$), whether the random trees are generated by random reshuffling or by a Yule process. Thus, our parsimony optimizations should yield reliable data on ancestral states (Laurin, 2004). The slight differences in results depending on scoring of Mesosauridae and in the position of this taxon among amniotes clearly show that more investigations about these topics are warranted. Nevertheless, the common and long-held view that amniotes were primitively anapsid seems to rest on shaky grounds.

Our new findings reduce somewhat the apparent conflict between morphological and molecular data concerning the position of turtles. Many (Laurin and Reisz, 1995; Lyson et al., 2010; Modesto, 1999;) but not all (deBraga and Rieppel, 1997; Hill, 2005; Li et al., 2008) morphological and some total evidence (Lee, 2001) analyses place turtles within parareptiles, a placement that was usually interpreted as implying that the absence of

Fig. 7. Parsimony optimization of the lower temporal fenestra (white, absent; black, present; green, ventral emargination) on a reference phylogeny of amniotes. This ternary character is considered unordered for optimization and phylogenetic signal purposes as there is evidence of changes from the fenestrate condition to the emargination (as in squamates and ichthyosaurs) and of appearance of an emargination directly from the anapsid condition, as in *Owenetta rubidgei* (Reisz and Laurin, 1991 and this figure). Topology from Laurin and Reisz, 1995 for basal amniotes, Reisz et al., 2007 for parareptiles, and Laurin, 2004 for other taxa, for A and B; from Modesto, 1999 for the position of mesosaurids, for C and D. Temporal fenestration is present in Ankyramorpha (deBraga and Reisz, 1996). To save space, the geological timescale is restricted to the Devonian–Triassic interval. Extant taxa are in bold type. For all taxa, we attempted to score the primitive condition. For Ichthyosauria, polymorphism follows Liu et al., 2011.

Fig. 7. Optimisation par parcimonie de l'évolution de la fenêtre temporelle inférieure (blanc, absente ; noire, présente ; verte, émargination ventrale) sur une phylogénie de référence des amniotes. Ce caractère ternaire est considéré comme non ordonné pour l'optimisation et le signal phylogénétique car les données suggèrent des transitions entre fenêtre et émargination (comme dans les squamates et les ichtyosaures) ainsi que l'apparition d'une émargination directement à partir de la condition d'anapside, comme chez *Owenetta rubidgei* (Reisz and Laurin, 1991 et Fig. 7). Topologie d'après Laurin and Reisz, 1995 pour les Amniotes basaux, d'après Reisz et al., 2007 pour les parareptiles et d'après Laurin, 2004 pour les autres taxons, pour A et B ; d'après Modesto, 1999 pour la position des Mésosauridés, pour C et D. La fenestration temporelle est présente chez les Ankyramorpha (deBraga and Reisz, 1996). Pour économiser de l'espace, l'échelle des temps géologiques est cantonnée à l'intervalle Dévonien–Trias. Les taxons actuels sont indiqués en gras. Pour tous les taxons, les auteurs ont tenté de coder la condition primitive. Pour les Ichthyosauriens, le polymorphisme suit Liu et al., 2011.

a lower temporal fenestra in turtles was primitive. On the contrary, most (e.g. Iwabe et al., 2005; Hugall et al., 2007) but not all (Frost et al., 2006) molecular phylogenies place turtles within diapsids, which implies that the absence of temporal fenestrae in turtles is secondary rather than primitive. The position of turtles remains a difficult problem, as shown by some recent analyses (e.g. Becker et al., 2011). Our results raise the possibility that the lower temporal fenestra was indeed present in some ancestors of turtles, but this does not explain the absence of an upper temporal fenestra, if turtles are placed among diapsids. The upper temporal fenestra seems to have appeared only once and to have been lost only very slowly, according to the fossil record (Carroll, 1988). In that respect, it differs strongly from the lower temporal fenestra, whose evolutionary rate is apparently very high (Fig. 7), with multiple appearances and losses. Also, the temporal fenestration in recent morphological data matrices plays a more minor role than in early 20th century works; the position of turtles among parareptiles is supported by several osteological characters, most of which are not linked with temporal fenestration (Laurin and Reisz, 1995; Lyson et al., 2010). Thus, our findings strengthen only moderately support for the position of turtles within Diapsida, but much work will be needed to resolve this outstanding problem.

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