General palaeontology, systematics and evolution (Vertebrate palaeontology)

A rhinesuchid-like temnospondyl from the Permo-Triassic of Uruguay

Nouveau temnospondyle de transition en provenance du Permo-Trias d'Uruguay

Graciela Piñeiro [a,*], Alejandro Ramos [a], Claudia Marsicano [b]

[a] *Departamento de Evolución de Cuencas, Sección Bioestratigrafía y Paleoecología, Facultad de Ciencias, Iguá, 4225, Montevideo CP 11400, Uruguay*
[b] *Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Ciudad Universitaria Pab. II, Buenos Aires C1428 EHA, Argentina*

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ABSTRACT

A new temnospondyl species, *Arachana nigra,* from the Permo-Triassic Buena Vista Forma-tion of Uruguay is described. The holotypic and only known specimen consists of an almost complete skull lacking most of the snout, the tabular horns and the posterolateral corners of the skull table. As with other specimens from the same unit, *Arachana* shows a transitional morphology. It shares several characters with rhinesuchids, such as the large size and the general shape of the skull, orbits positioned slightly posterior to the skull roof mid-length, a coarsely pitted dermal ornamentation lacking pustules, and a smoothly convex cheek contour. The palatal ramus of the pterygoid suturing with the vomer, and excluding the palatine and ectopterygoid from the margin of the interpterygoid vacuity, and the pres-ence of a small basioccipital, visible in both occipital and ventral view, also resemble the conditions found in rhinesuchids and other basal temnospondyls. Other characters present in *Arachana,* however, are commonly found in lydekkerinids, but are absent in almost all rhinesuchids: supratemporal excluded from otic notch; supraorbital and infraorbital sen-sory sulci encroaching the lacrimal, although lacking a step-like lacrimal flexure; otic notch not deeply incised; post-temporal fenestra large and rounded; occipital condyles well-separated from each other; palatine tooth row behind the palatine tusk reduced; pterygoid corpus slightly ornamented; and presence of an interorbital depression. This combination of primitive and derived characters is consistently present in most components of the Buena Vista fauna, which could thus be transitional between typical Permian and Triassic tetra-pod communities found elsewhere. The location of the PTB in the Uruguayan sequence is controversial, mainly due to the lack of clear faunal correlations with other well-known sequences, such as those of southern Africa and Russia. Moreover, the mosaic-like charac-ter combinations in most of the recorded tetrapods ally them to both Triassic and Paleozoic groups, and this has complicated even more the possibility of age assignment. Transitional faunas associated with the PTB, such as the Russian Uppermost Permian faunas, could be equivalent to the unique Colonia Orozco fauna. If true, this scenario will substantially change estimates about survivorship rates, suggesting a speciation rate increase in temnospondyls after the Permian-Triassic event. Based on taxonomic, phylogenetic, and geochronologic data, the Buena Vista fauna allows us to quantify faunal turnover across the PTB and in the aftermath of the end Permian extinction event.

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* Corresponding author.
 E-mail addresses: fossil@fcien.edu.uy (G. Piñeiro), aleramos@fcien.edu.uy (A. Ramos), claumar@gl.fcen.uba.ar (C. Marsicano).

R É S U M É

L'espèce d'un nouveau temnospondyle *Arachana nigra* du Permo-Trias de la Formation Buena Vista d'Uruguay est ici décrite. Le spécimen holotype, et le seul connu, consiste en un crâne presque complet sur lequel il manque l'essentiel du museau, les cornes tabulaires et les coins postéro-latéraux. Comme les autres spécimens de la même unité, *Arachana* montre une morphologie de transition. Il partage différents caractères avec les rhinosuchides tels une grande taille et la forme générale du crâne, des orbites en position légèrement postérieure par rapport à la mi-longueur de la calotte crânienne, une ornementation dermique grossièrement piquetée de trous sans pustules et un contour des joues légèrement convexe. Le ramus palatin du ptérygoïde suturé avec le vomer et excluant le palatin et l'ectoptérygoïde de la marge du vide interptérygoïdien et la présence d'un petit basioccipital visible à la fois en vue occipitale et en vue ventrale ressemblent aux caractéristiques observées chez les rhinosuchides ou chez d'autres temnospondyles de base. Cependant, d'autres traits présentés par *Arachana* sont comunément trouvés chez les lydekkérinides, mais sont absents chez presque tous les rhinosuchides, ainsi : supratemporal exclu de l'entaille otique, sulci sensoriels supra- et infraorbital empiétant sur le lacrimal, bien que sans flexure lacrimale en forme de marche, entaille otique peu profondément marquée, fenêtres post-temporales larges et arrondies, condyles occipitaux bien séparés l'un de l'autre, alignement dentaire palatin en arrière de la défense palatine réduite, corpus du ptérygoïde légèrement ornementé et présence d'un creusement interorbital. La combinaison de caractères primitifs et dérivés est toujours présente dans la plupart des composants de la faune de Buena Vista, qui pourraient être considérés comme de transition entre les communautés de tétrapodes typiques du Permien et du Trias, trouvées ailleurs. La localisation du PTB dans la séquence uruguayenne est controversée, surtout en raison du manque de corrélations fauniales claires avec d'autres séquences bien connues d'Afrique du Sud et de Russie. En outre, les relevés en mosaïque de la plupart des tétrapodes, aux caractères les rapprochant à la fois des groupes triasiques et paléozoïques ont compliqué encore plus la possibilité de les assigner à un âge donné. Néanmoins, l'identification de faunes de transition associées au PTB, telles que les faunes russes du Permien terminal pourrait en faire l'équivalent de la faune unique de Colonia Orozco. S'il était vrai, ce scénario changerait substantiellement les estimations des taux de survivants, particulièrement en croissance pour les temnospondyles après l'évènement permo-triasique. Cependant, sur la base des données taxonomiques, phylogénétiques et géochronologiques, la faune de Buena Vista pourrait représenter les changements qui se sont produits au PTB suivant la plus importante extinction jamais connue.

1. Introduction

Several tetrapods have been recently described from the Uruguayan Buena Vista Formation. They are collectively referred to as the "Colonia Orozco fauna" (Piñeiro and Ubilla, 2003). This fauna includes reptiles and temnospondyls, the latter being the most abundant specimens in the fossiliferous intraformational conglomerates that characterize the sequence. These temnospondyls, together with the age and correlations of the Colonia Orozco fauna, have been recently reappraised by Piñeiro et al. (2007a). The imprecise Permo-Triassic age is proposed for this fauna mainly because the constituent taxa have so many transitional features (see Marsicano et al., 2000; Piñeiro et al., 2004, 2007a, 2007b, 2007c). Some features ally them to typical Triassic groups, although they also retain primitive characters absent in Triassic taxa. Therefore, as with other groups represented in the Colonia Orozco fauna, temnospondyls are not useful in discriminating between a Late Permian (Lopingian) and an Early Triassic age for this community, which thus has been considered as Permo-Triassic (Piñeiro, 2006). Dias da Silva et al. (2006) and Modesto and Damiani (2007) criticized this hypothesis because of the proposed lateral correlation of the Buena Vista Formation with the Early Triassic Sanga do Cabral Formation of Brazil,

based upon the fact that they are part of the Paraná Basin (see Dias da Silva et al., 2006; Modesto and Damiani, 2007). These authors also discussed the affinities of the fauna known from the Buena Vista Formation, and suggested that the taxa described from this unit belong to Triassic groups (Modesto and Botha, 2010). Despite the above-mentioned lateral stratigraphic equivalence of the Uruguayan and Brazilian units, recent studies involving detailed geological and sedimentological analyses performed in Uruguay, in collaboration with Brazilian colleagues, suggest that the faunas from the two units might not be contemporary (Da-Rosa et al., 2009, 2010).

Here, we describe a new temnospondyl skull from the Buena Vista Formation of Uruguay, which also has a transitional morphology. We further discuss the relationships of the new taxon and provide a revised scheme for the biostratigraphic correlations between Uruguayan and Brazilian basins. Finally, we discuss the location of the PTB in Uruguay.

2. Material and methods

The holotype (FC-DPV 1369) was included in a mostly sandy concretion, surrounded by a thin but hardened black

iron film and prepared mechanically. Despite the three-dimensional preservation, the posterolateral areas of the skull are considerably weathered, so that only a mold of some of the bones can be seen. This is particularly evident in both squamosals, which were weathered almost symmetrically (Fig. 1). During fossilization, the anterior region of the skull was severely distorted by compression in a left-right direction, resulting in the loss of the anteriormost part of the snout. Therefore, the reconstructions of the snout and tabular horns are conjectural and were produced by projecting the maxillary margin anteriorly and the preserved margins of the tabular bone posteriorly.

The coarse ornament in the skull precludes a clear identification of the sutures. Therefore, the detailed drawings and reconstructions of the skull were performed using a Zeiss stereomicroscope with camera lucida.

3. Systematic palaeontology

Order Temnospondyli von Zittel, 1887–1890.
Stereospondyli *incertae sedis*.
Genus *Arachana* nov.
Etymology: the generic word honours the Arachanes, aborigines that lived in the area where the specimen was collected in the Cerro Largo County (northeastern Uruguay).

Type and the only known species: *Arachana nigra* sp. nov.
Diagnosis: As for the species.
Arachana nigra sp. nov.
(Figs. 1–6).
Etymology: From Latin, *niger*, black, alluding to the color of the skull.
Arachana nigra n. gen et n. sp.
Holotype: FC-DPV 1369, an almost complete skull deposited in the Collection of Vertebrate Palaeontology of the Facultad de Ciencias of Montevideo, Uruguay (FC-DPV).

Locality and Horizon: Colonia Orozco village, Cerro Largo County (Uruguay), around 6 km northeast of Melo City. It was found in the stratigraphically lowest intraconglomerate levels of the Permian-Triassic Buena Vista Formation, Colonia Orozco Member, Norte Basin (*sensu* De Santa Ana et al., 2006, northeastern Uruguay).

3.1. Diagnosis

Medium-sized to large temnospondyl distinguished by the following combination of characters: skull elongate with maximum width across the jugal-quadratojugal contact; interorbital longitudinal trough extending as far posteriorly as skull roof posterior margin; frontal excluded from orbital margin; orbits located slightly posterior to the skull mid-length, and set neither far apart nor close to the skull margins; ornamentation markedly pitted, lacking pustules; sensory sulci discontinuous, with infraorbital sulci lacking a step-like or Z-shaped lacrimal flexure, deeply impressed between orbits and nostrils, where they approach each other over the lacrimal; skull table posterior border sufficiently concave to allow for occipital condyles full exposure in dorsal view; skull ventral surface straight in occipital view, as occipital and quadrate condyles are aligned; lacrimals entering external nostril, thus preventing maxilla-nasal contact; supratemporal excluded from margin of moderately incised otic notches; pterygoid palatal ramus of the pterygoid contacting vomer anteriorly, excluding palatine and ectopterygoid from the interpterygoid vacuity; pterygoid posterolateral flange poorly developed or absent; parasphenoid plate bearing separate, crescentic cristae musculari; narrow cultriform process; interpterygoid vacuity widest in its anterior one-third; small basioccipital ossification, visible in palatal and occipital views, not contributing to the exoccipital condyles; shagreen on palatal bones series; smooth ornamentation on pterygoids, parasphenoid and vomers;
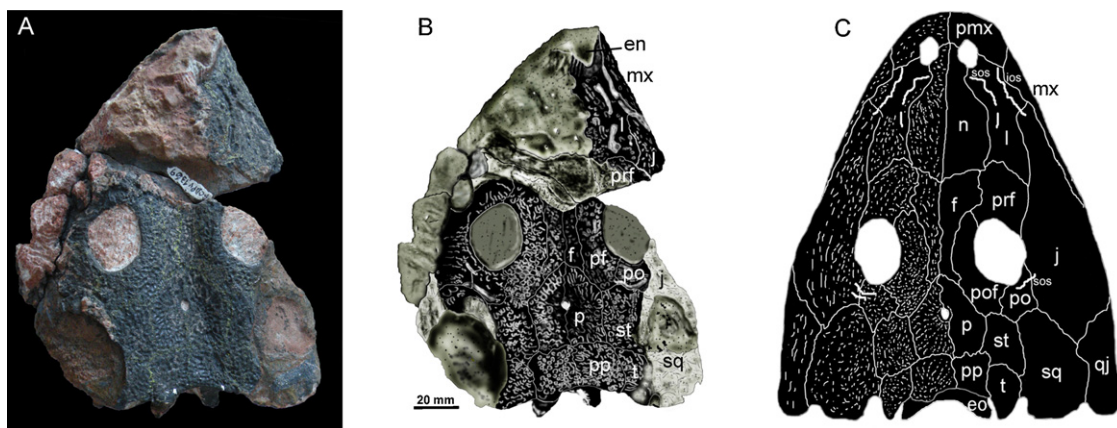

Fig. 1. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Dorsal view of the preserved skull. B. Interpretative drawing of A. C. Reconstruction of the dorsal skull. Anatomical abbreviations: en: external naris; eo: exoccipital; f: frontal; ios: infraorbital sulcus; j: jugal; l: lacrimal; n: nasal; mx: maxilla; p: parietal; pmx: premaxilla; po: postorbital; pof: postfrontal; pos: postorbital sensory sulcus; pp: postparietal; prf: prefrontal; qj: quadratojugal; sq: squamosal; st: supratemporal; t: tabular.
Fig. 1. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation permo-triasique de Buena Vista (Norte Basin, Uruguay nord-oriental). A. Vue dorsale du crâne conservé. B. Dessin interprétatif de A. C. Reconstitution du crâne en vue dorsale. Abréviations anatomiques : en : narine externe ; eo : exoccipital ; f : frontal ; ios : sulcus infraorbital ; j : jugal ; l : lacrimal ; mx : maxillaire ; p : pariétal ; pmx : prémaxillaire ; po : postorbital ; pof : post-frontal ; pos : sulcus sensoriel postorbital ; pp : postpariéral ; prf : préfrontal ; qj : quadratojugal ; sq : squamosal ; st : supratemporal ; t : tabulaire.
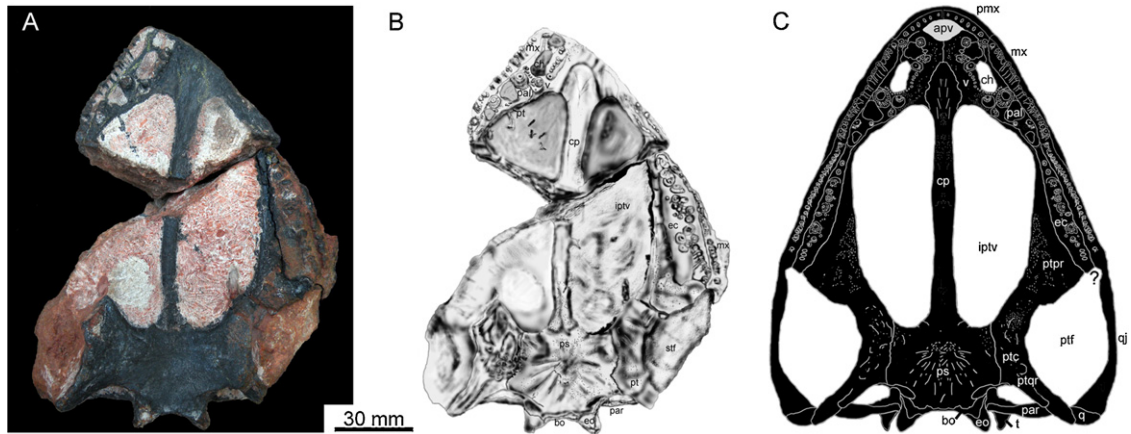
Fig. 2. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Ventral view of the preserved skull. B. Interpretative drawing of A. C. Reconstruction of the ventral skull. Anatomical abbreviations: apv: anterior palatal vacuity; bo: basioccipital; ec: ectopterygoid; eo: exoccipital; ch: choana; cp: cultriform process; iptv: interpterygoid vacuity; mx: maxilla; pal: palatine; par: paroccipital process; pmx: premaxilla; ps: parasphenoid; ptc: pterygoid corpus; ptqr: pterygoid quadrate ramus; ptpr: pterygoid palatine ramus; q: quadrate; qj: quadratojugal; stf: subtemporal fenestra; t: tabular. The interrogative sign indicates the place where an alar process of the jugal could have been present.
Fig. 2. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation permo-triasique de Buena Vista (Norte basin, Uruguay nord-oriental). A. Vue ventrale du crâne conservé. B. Dessin interprétatif de A. C. Reconstitution du crâne en vue ventrale. Abréviations anatomiques : apv : vide palatin antérieur ; bo : basioccipital ; ec : ectoptérygoïde ; eo : exoccipital ; ch : choane ; cp : processus cultriforme ; iptv : vide interptérygoïde ; mx : maxillaire ; pal : palais ; par : processus paroccipital ; pmx : prémaxillaire ; ps : parasphénoïde ; ptc : corpus ptérygoïde ; ptqr : ramus ptérygoïde quadratique ; ptpr : ramus ptérygoïde palatin ; q : quadratique ; qj : quadratojugal ; stf : fenêtre sub-temporale ; t : tabulaire. Le point d'interrogation indique la place où un processus alaire du jugal aurait pu être présent.

palatine tooth row very reduced or absent posterior to palatine tusks; ectopterygoid teeth similar in size to or larger than maxillary teeth; pterygoid ascending ramus contacting squamosal dorsally (palatoquadrate fissure absent); pterygoid quadrate ramus with low longitudinal ledge; post-temporal fenestra teardrop-shaped.

3.2. Description

3.2.1. General morphology

The skull (as preserved, 162 mm in length, excluding the snout) consists of two fragments that comprise a significant part of the skull table and palate, along with the occipital region. A transverse section of the skull at the level of the anterior border of the orbits shows that the dermal bones are moderately thick (around 3 mm high). This value becomes significant, when compared with the less than 1 mm deep bones of the lydekkerinid *Lydekkerina huxleyi* (Jeannot et al., 2006). The skull table preserves the orbits and the postorbital area with the exception of both posterolateral corners, which were severely damaged by erosion. Moreover, most of the preorbital area is visible on the right side of the skull, where the almost complete right naris is present. The left external nostril may be
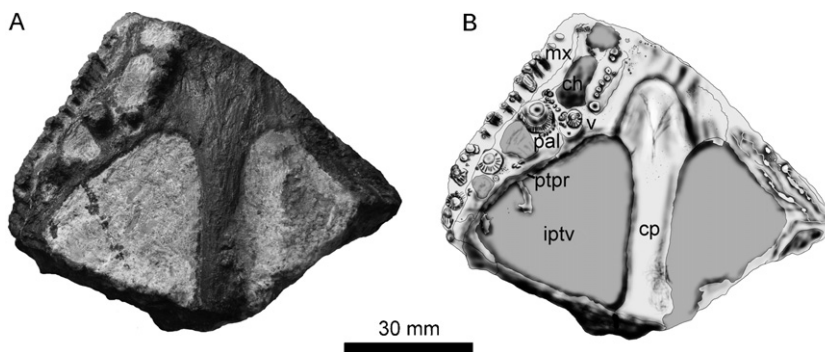

Fig. 3. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Photograph of the anterior ventral view of the skull showing pterygoid-vomer contact. B. Interpretative drawing of A. Anatomical abbreviations: ch: choana; cp: cultriform process; iptv: interpterygoid vacuity; mx: maxilla; pal: palatine; ptpr: pterygoid palatine ramus; v: vomer.
Fig. 3. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation permo-triasique de Buena Vista (Norte Basin, Uruguay nord-occidental). A. Photographie du crâne en vue antérieure ventrale, montrant le contact ptérygoïde-vomer. B. Dessin interprétatif de A. Abréviations anatomiques : ch : choane ; cp : processus cultriforme ; iptv : vide interptérygoïde ; mx : maxillaire ; pal : palais ; ptpr : ramus ptérygoïde palatin ; v : vomer.
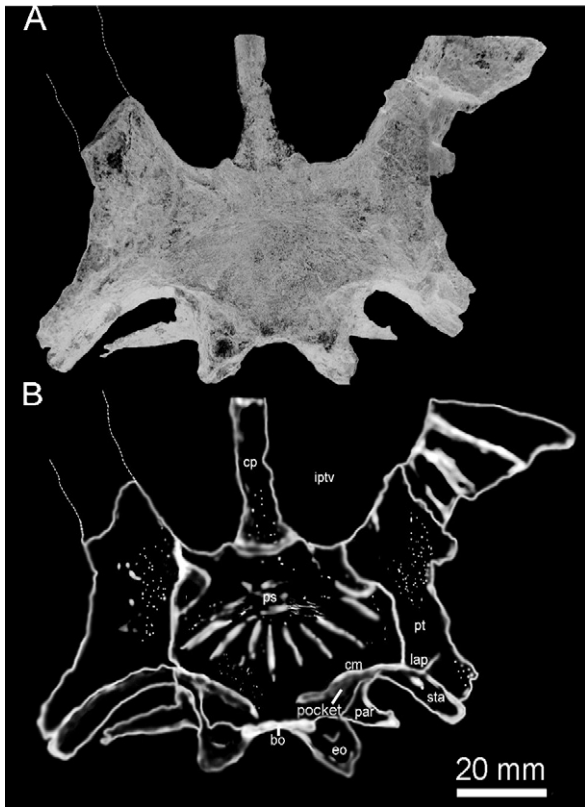
Fig. 4. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Photograph of the posteroventral view of the skull showing the ossified basioccipital positioned between the exoccipitals. B. Interpretative drawing of A. Anatomical abbreviations: bo: basioccipital; cm: crista muscularis; cp: cultriform process; eo: exoccipital; iptv: interpterygoid vacuity; lap: lappets; par: paroccipital process; pt: pterygoid; ps: parasphenoid; sta: stapes.

Fig. 4. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation de Buena Vista (Norte Basin, Uruguay nord-occidental). A. Photographie du crâne en vue postéroventrale, montrant le basioccipital ossifié positionné entre les deux exoccipitaux. B. Dessin interprétatif de A. Abréviations anatomiques : b : basioccipital ; cm : *crista muscularis* ; p : processus cultriforme ; eo : exoccipital ; iptv : vide interptérygoïde ; lap : « lappets » ; par : processus paroccipital ; pt : ptérygoïde ; ps : parasphénoïde ; sta : étriers.

Fig. 5. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Ventral view of the posterior region of the skull showing "lappets" on the pterygoid instead of over the parasphenoid corpus (see text for additional information of these structures). B. Interpretative drawing of A. Anatomical abbreviations: ar: ascending ramus of the pterygoid; bo: basioccipital; cp: cultriform process; eo: exoccipital; fm: foramen magnum; lap: lappets; par: paroccipital process; pt: pterygoid; ps: parasphenoid; sta: stapes; staf: stapedial foramen; t: tabular.

Fig. 5. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation permo-triasique de Buena Vista (Norte Basin, Uruguay nord-oriental). A. Vue ventrale de la région postérieure du crâne montrant des « lappets » sur le ptérygoïde et non sur le corpus parasphénoïde (voir le texte pour des informations supplémentaires sur ces structures). B. Dessin interprétatif de A. Abréviations anatomiques : ar : ramus ascendant du ptérygoïde ; bo : basioccipital ; cp : processus cultriforme ; eo : exoccipital ; fm : foramen magnum ; par : processus paroccipital ; pt : ptérygoïde ; ps : parasphénoïde ; sta : étriers ; staf : foramen stapédial ; t : tabulaire.

concealed by sediment left in place. The tip of the snout is compressed to such an extent that the premaxillae are not preserved.

In ventral view, most of the palate is preserved, and only a small fragment on the left side (involving part of the palatine ramus of pterygoid, the left ectopterygoid and part of the palatine) is missing (Fig. 2), as are the posterolateral corners, which are strongly weathered.

The skull is approximately triangular in outline with slightly convex posterolateral corners, and it widens posteriorly at the level of the anterior margin of the orbits. The posterior margin of the table is smoothly concave, allowing the occipital condyles and part of the occiput to be visible in dorsal view. In lateral view, the skull table slopes gently anteriorly, and the occiput seems to have been distinctly higher than the snout, even considering the lateral compression undergone by the latter. In occipital view, the
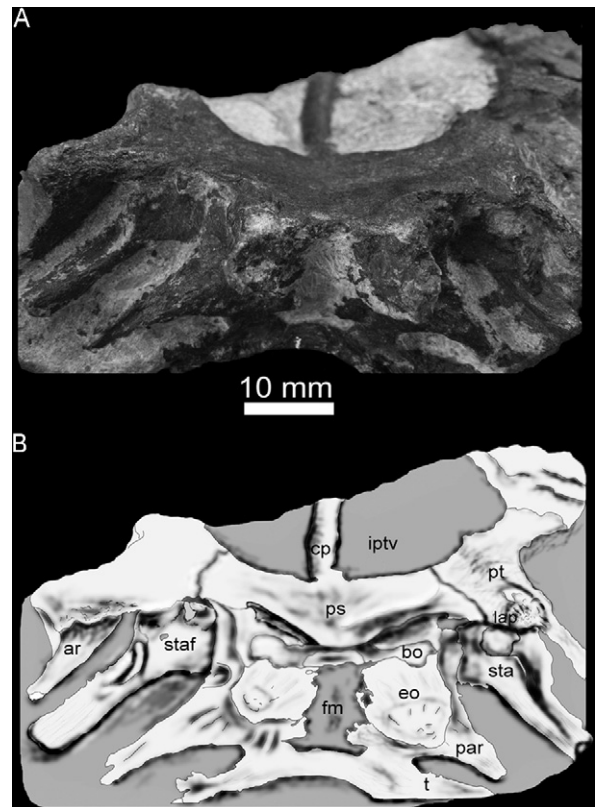
margins of both cheeks are smoothly convex and converge on the midline of the skull. Here, a pronounced concavity forms an extensive longitudinal trough, particularly evident at the level of the orbits. As a result, orbits are slightly raised above the table (Fig. 1A, B). The ventral margin of the skull is straight in occipital view, because the occipital condyles are at the same level as the quadrate condyles.

The orbits are relatively small, subcircular, and located at a roughly equivalent distance from the midline and from the lateral margins of the skull. Based upon our reconstruction, including the estimated length of the snout, orbits appear to have been situated immediately posterior to the skull table mid-length (Fig. 1C). A small pineal foramen is located in a subcircular depressed area, immediately
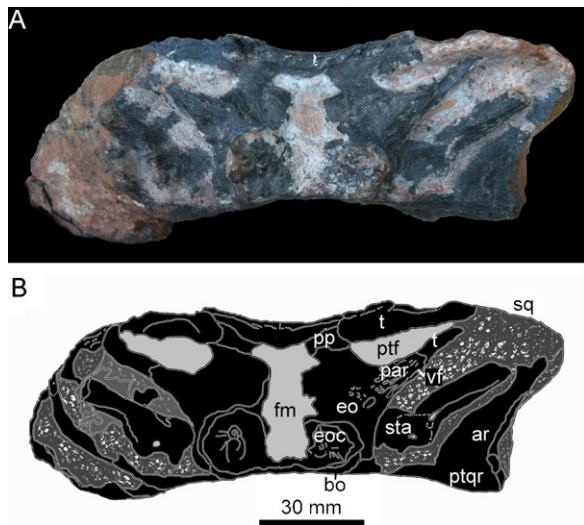
Fig. 6. The temnospondyl *Arachana nigra* (holotype specimen, FC-DPV 1369) from the Permo-Triassic Buena Vista Formation (Norte Basin, Northeast Uruguay). A. Oblique palatal and occipital view of the preserved skull. B. Interpretative drawing of A. Anatomical abbreviations: ar: ascending ramus of the pterygoid; bo: basioccipital; eo: exoccipital; eoc: exoccipital condyl; fm: foramen magnum; par: paroccipital process; pp: postparietal; ptf: post-temporal fenestra; ptqr: pterygoid quadrate ramus; sq: squamosal; sta: stapes; t: tabular; vf: vagal foramen.

Fig. 6. Temnospondyle *Arachana nigra* (spécimen holotype, FC-DPV 1369) de la Formation permo-triasique de Buena Vista (Norte Basin, Uruguay nord-oriental). A. Vue occipitale du crâne conservé. B. Dessin interprétatif de A. Abréviations anatomiques : ar : ramus ascendant du ptérygoïde ; bo : basioccipital ; eo : exoccipital ; eoc : condyle exoccipital ; fm : foramen magnum ; par : processus paroccipital ; pp : postpariétal ; ptf : fenêtre post-temporale ; ptqr : ramus ptérygoïde quadratique ; sq : squamosal ; sta : étriers ; t : tabulaire ; vf : foramen vagal.

anterior to the middle point of the suture between the parietals, well behind the posterior margin of the orbits.

3.2.2. Skull table (Fig. 1)

The bones of the skull roof are covered by a coarse, mainly pitted ornamentation without pustules or conules at the junction of the ridges, unlike rhitydosteids in which pustules are visible at these junctions (Cosgriff and Zawiskie, 1979) and *Uruyiella liminea*, from the same unit (Piñeiro et al., 2007b); evident zones of intensive growth are also absent on the preserved areas. The ornamentation closely resembles that in rhinesuchids, particularly in the uniformity of the network of ridges enclosing mostly rounded depressions (CM pers. obs.). The lateral line sensory sulci are discontinuous and part of the supraorbital and infraorbital canals are clearly visible on the preserved skull. They are deeply impressed and curve smoothly to approach each other over the lacrimal. The infraorbital canal lacks an infraorbital flexure such as is observed in many Palaeozoic and Mesozoic temnospondyls (Yates and Warren, 2000), and extends posterolaterally producing a short portion over the jugal. Part of the interorbital section of the supraorbital sulcus is probably present at the right side, represented by a series of depressions over the prefrontal. Behind the orbits, the infraorbital sulcus is represented by short canals visible over the postorbitals and the left jugal (see Fig. 1). Despite its peculiar features, the

described distribution of the sensory canals in *Arachana* appears to be similar to that present in rhinesuchids, and is different to that exhibited by *Lydekkerina huxleyi* and most lydekkerinids, where the infraorbital canal forms a step to Z-shaped flexure over the lacrimal (Jeannot et al., 2006; Hewison, 2007). Nonetheless, it resembles the condition with the Australian lydekkerinid *Chomatobatrachus halei* (after Hewison, 2007, Text-figure 44; page 54).

Part of a narrow strip of the maxilla is present along the right anterolateral border of the skull, suturing with the lacrimal very close to the infraorbital sensory sulcus. Medially, it fails to contact the nasal as the lacrimal reaches the naris, in the preorbital area. This primitive condition is observed in forms such as *Dvinosaurus*, but it is also seen in the lydekkerinids *Chomatobatrachus halei* (Cosgriff, 1974; Schoch and Milner, 2000) and *Broomulus dutoiti* (Hewison, 2007; Jeannot et al., 2006; Shishkin et al., 1996) and is also present in older taxa such as the Carboniferous *Iberospondylus* (Laurin and Soler-Gijón, 2006). However, recent work by Warren et al. (2006) did not consider this character distinctive, and it was featured neither in the description nor in the Interpretative drawings of *Chomatobatrachus*. Jeannot et al. (2006) suggest a putative "intraspecific" variation of this character in *Lydekkerina huxleyi*, resulting in individuals that may exhibit different conditions, either the lacrimal entering the naris or a nasal-maxillary contact. The nares of *Arachana* are large, round, and placed close to midline of the snout.

The prefrontals are partially preserved on both sides of the skull, sufficiently to allow for a partial reconstruction. From the left preserved fragment, it is possible to place it on the anteromedial margin of the orbit. From the right side, its anterior margin can be followed approximately until the level of the middle length of the lacrimal.

Elongate frontals occupied the midline of the skull roof between the orbits. They are excluded from the orbital margin by a prefrontal-postfrontal contact. Posterolaterally, their suture with the post-frontals is almost parallel to the midline. Their contact with the nasals is not visible, but it is situated in front of the orbits. Anteriorly, they seem to project laterally where they reach their maximum width. This inference was based on the position of the preserved medial border of the prefrontal (Fig. 1).

The post-frontals are narrow, laterally curved bones that form the medial and posterior border of the orbit. They expand posteriorly to suture with the postorbital posterior to the orbits.

The parietals are distinctly trapezoidal bones, with their anterior margin being narrower than the posterior. The pineal foramen is located slightly forward of the midpoint of their length. As in most stereospondyls, the parietals suture anterolaterally with the post-frontals and laterally with the supratemporals; posteriorly they form a nearly straight contact with the postparietals.

The postorbitals are almost complete and border the orbit posterolaterally. They are relatively short and roughly trapezoidal, having their anterior border narrower than the posterior. A small portion of the postorbital sensory sulcus is present on the left postorbital, represented by a short canal, which apparently also enters the jugal.

The jugals are partially preserved on both sides; the left jugal shows its contribution to the lateral margin of the orbit and the shape and extension of its posterior portion, which appear to end anterior to the level of the parietal-postparietal contact. On the right side, the jugal extends well anterior to the orbit as is usual in rhinesuchids, lydekkerinids and other basal stereospondyls (Yates and Warren, 2000), but not in most rhytidosteids, in which the jugal does not extend far beyond the anterior level of the orbit or extends only slightly beyond this level.

Both supratemporals are incompletely preserved because of surface weathering. They appear to be roughly diamond-shaped bones, but it is not possible to determine if they contribute to the otic notch margin, as they do in rhinesuchids. We have reconstructed the skull as lacking that contribution because of the structure of this area in *Arachana* (e.g. shallowly incised otic notches).

Approximately quadrangular postparietals occupied the posteromedial, fairly concave border of the table. This concavity was apparently continuous with the medial border of the tabular horns, which are broken on both sides; their position can be determined by the shape and orientation of the paraoccipital processes. On both sides of the skull table, incomplete tabulars are present and part of the anterior margin of the right otic notch is preserved. This margin is located at the same level as the posterior border of the postparietals, and thus, the notch was not deeply incised along the margin of the table, as in the lydekkerinid *Lydekkerina huxleyi* (Hewison, 2007; Jeannot et al., 2006; Shishkin et al., 1996).

3.2.3. Palate (Figs. 2–4)

The morphology of either the premaxillary region and the anterior palatal vacuity is unknown. The interpterygoid vacuities are large and elongated and slightly pointed anteriorly. They are transversely widest at the level of the palatine-ectopterygoid suture (Fig. 2) and are separated from each other by the slender cultriform process of the parasphenoid. The subtemporal fossae are partially preserved on both sides and they appear to have been teardrop-shaped. Only the right choana is preserved. This is anteroposteriorly elongate and located just in front of the anterior border of the vacuities.

The maxilla is a narrow strip of bone only partially preserved on the right and left sides of the palate and posterolaterally on the left margin of the skull. It forms the lateral margin of the choana. There is no contribution to this margin from an anterior extension of the palatine (Figs. 2 and 3). This condition is similar to that present in rhinesuchids, lydekkerinids and other basal temnospondyls (Shishkin et al., 1996; Watson, 1962; Yates and Warren, 2000) and it differs from that of most mastodonsaurids (Damiani, 2001), rhytidosteids (Schoch and Milner, 2000; Yates and Warren, 2000) and *Chomatobatrachus halei* (Warren et al., 2006), in which the contribution of the maxilla to the choana is reduced or minimal.

Along its length the maxilla forms straight sutures with the palatine and ectopterygoid, and it probably contributed to the formation of the anterolateral border of the subtemporal fenestra.

Both vomers are partially preserved along the anterior border of the interpterygoid vacuities. Although their surface was slightly damaged during preparation, it shows a smooth ornamentation including some patches of shagreen. Just in front of the choana, a replacement pit for the vomerine tusk can be seen on the right vomer. The medial margin of the choana bears a row of small teeth, which is continuous with a row along the posterior margin (Fig. 3). The vomers cover the anterior tip of the cultriform process with which they form an inverted V-shaped suture. The posterior extensions of the vomers do not overlap the lateral margins of the cultriform process unlike the condition in *Lydekkerina huxleyi* (*processus parasphenoidales*, *sensu* Jeannot et al., 2006). The vomers overlap the process along a short distance immediately anterior to the anterior border of the interpterygoid vacuities. The narrow and almost parallel-margined cultriform process is slightly convex and elliptical in cross section, without any signs of a ventral keel. Unlike in most rhinesuchids and lydekkerinids, except *Deltacephalus whitei* (Hewison, 1996, 2007), the cultriform process expands laterally its anterior portion and extends well anterior to the anterior margin of the interpterygoid vacuity.

Anterolaterally, on the right side of the skull, the palatine is complete and bears a large palatine tusk with its replacement pit, followed posteriorly by one or two teeth. The palatine-ectopterygoid contact is visible on the right side, immediately behind the most posterior palatine replacement pit for the palatine tusk. The posteromedial corner of the palatine is simple and does not extend posteriorly to the most anterior ectopterygoid tooth. This condition is similar to that present in all rhinesuchids. However, there is an elongated palatine posteromedial process in lydekkerinids, which extends posterior to the most anterior ectopterygoid tooth (Hewison, 2007; Jeannot et al., 2006; Warren et al., 2006).

The long and narrow ectopterygoid stretches between the palatine ramus of the pterygoid and the maxilla. It bears a tooth row of at least 11 teeth, which are similar in size to or a little larger than the maxillary teeth. Ectopterygoid tusks are absent. We are not sure whether the ectopterygoid entered the subtemporal fenestra or whether an alar process of the jugal was present. Although a space is visible where the palatal exposure of the jugal normally occurs in other taxa, the broken pterygoid corpus precludes any firm conclusion. However, a posterolateral flange seems to have been absent from the posterior surface of the palatine ramus of pterygoid, bordering the subtemporal fossa.

The parasphenoid corpus is approximately hexagonal; its ventral surface is smoothly concave and weakly ornamented (Figs. 2 and 4). Laterally, it contacts with the pterygoids along a flat, posterolaterally directed interdigitated suture, as in all stereospondyls (Yates and Warren, 2000). Posteriorly, the parasphenoid corpus contacts a small relict of an ossified basioccipital, which is visible in both ventral and occipital views of the skull. The exoccipitals occur just anterolateral to this contact (see Figs. 5 and 6). The presence of a small basioccipital between the exoccipitals characterizes rhinesuchids among stereospondyls (e.g. Schoch and Milner, 2000; Watson, 1962). However, Watson (1919) suggested that

the basioccipital was exposed between the exoccipital condyles in the lydekkerinid *Lydekkerina huxleyi* (see also Hewison, 2007, Text-fig. 21a) although, sutures were not observed in the corresponding area by Warren et al. (2006). Perhaps a thin ossified strip of this bone remains preserved in some lydekkerinid specimens (Shishkin, pers. comm. 2010), but detailed descriptions of them are not available to compare with the condition present in *Arachana*. The exoccipital condyles seem to have been located almost at level with or a little anterior to the quadrate condyles.

Posterolaterally, the parasphenoid corpus bears low crescent-shaped cristae musculari. Each crest surrounds ventromedially orientated muscular "pockets" which remain fairly separated (Figs. 2 and 4), as in all Palaeozoic temnospondyls and Triassic taxa such as lydekkerinids and mastodonsaurids (Damiani, 2001).

Both pterygoids are partially preserved and the left one is nearly complete. The pterygoid corpus is slightly dorsoventrally concave and bears a faint ornamentation. Under magnification, sporadically distributed small patches of denticles can be observed (Figs. 2–4), suggesting the presence of extensive shagreen. The palatine ramus extends anteriorly to make contact with the vomer at the level of the palatine tusk, where it narrows before disappearing beneath the vomer (Fig. 3). This condition excludes the palatines and ectopterygoids from the border of the interpterygoid vacuities, as in the rhinesuchid *Rhineceps nyasaensis* and other basal temnospondyls (see Laurin and Soler-Gijón, 2006; Watson, 1962; Yates and Warren, 2000). Both quadrate rami are broken mesiodistally but they were nearly vertically orientated.

3.2.4. Palatal dentition

A shagreen of denticles, almost invariably damaged during preparation, is represented by scattered patches on the base and anterior one-third of the cultriform process, on the corpus and palatine ramus of the pterygoids, and on the vomers. Moreover, small, isolated denticles can be observed on the palatines and ectopterygoids, suggesting that shagreen was also developed on these bones. Widespread shagreen of denticles on the palatal series is present in rhinesuchids and rhytidosteids, but it is observed just in the parasphenoid and pterygoids of *Lydekkerina huxleyi* (e.g. Jeannot et al., 2006; Warren and Black, 1985; CM pers. obs.).

A continuous tooth row is visible on the vomers (medially and posterior to the choana) and this continues on the palatines, and ectopterygoids. The row includes tusks and teeth of variable sizes that are of equivalent size to or slightly larger than those preserved on the maxilla. All marginal teeth curve lingually, and are anteroposteriorly compressed; they are, thus, oval in transverse cross-section. In contrast, the palatine tusks and their replacement pits are comparatively larger than the marginal teeth, and their bases are circular. Well-developed carina can be observed on the external surface of all the teeth.

The palatine tusk is followed by just one or probably two teeth, a feature that differentiates *Arachana* from both rhinesuchids and lydekkerinids except *L. huxleyi*, where a well-developed tooth row is present (Watson, 1962). The condition in *Arachana* is more similar to some

lydekkerinids, which possess a small number of teeth behind the palatine tusk (Shishkin et al., 1996; Jeannot et al., 2006). Due to the great asymmetry and variation recorded in temnospondyl taxa, comparisons between different types of dentitions cannot be assessed with great confidence (Watson, 1962).

A large replacement pit of the vomerine tusk is preserved anterior to the anterior margin of the choana. The presence of vomerine tusks has been described for lydekkerinids, as well as in most other temnospondyls, including rhinesuchids (CM pers. obs.).

3.2.5. Occiput (Figs. 5 and 6)

The central part of the occiput is dominated by exoccipitals. They contact the postparietals dorsally, and extend dorsolaterally onto the paroccipital process where they meet the ventral extension of the tabular. The paroccipital process is robust and rod-like, having an irregular surface near its contact with the parotic process of the tabular, where a round and relatively large vagal foramen is located. The paroccipital processes are dorsolaterally orientated and form the ventral margin of the posttemporal fenestra. The latter is relatively large and teardrop-shaped as in most stereospondyls excluding rhinesuchids, in which the fenestra is very thin and laterally expanded due to the almost horizontal orientation of the paroccipital process (Watson, 1962; CM pers. obs.). Medially, the exoccipitals enclose the foramen magnum, and ventrally, they are sutured with a small ossified basioccipital, which forms a narrow strip of bone between the exoccipital condyles (Figs. 5 and 6). The latter are formed entirely by the exoccipitals and the condylar facets are nearly flat and face somewhat medially. The occipital condyles are visible in dorsal view, and positioned at level of the quadrate condyles.

A tall, posteriorly convex ascending ramus of the pterygoid arises from the occipital border of the quadrate ramus and broadly contacts the squamosal. On the lower margin of the quadrate ramus of the pterygoid is an apparently shallow and elongated ledge. It is partially preserved because of the damage of the specimen in this area. This ledge is similar to that described for *Lydekkerina huxleyi* and *Eolydekkerina magna* as the crista obliqua pterygoidei (Jeannot et al., 2006; Shishkin et al., 1996), and apparently differs from the tall and sharp-edged crista obliqua present in rhinesuchids (see Watson, 1962).

Small triangular posterior projections are present lateral to the parasphenoid-pterygoid suture, which can also be seen in a ventral view of the skull (Figs. 4 and 5). These projections were previously described in *Lydekkerina* and *Eolydekkerina* as "lappets" belonging to the parasphenoid and providing attachment for the stapes (Watson, 1919). Shishkin et al. (1996) suggested that they are formed by the contribution of both the parasphenoid and the pterygoid. In *Arachana*, the triangular projections seem to belong to the pterygoid, as they are present immediately lateral to the pterygoid-parasphenoid suture; the posterior border where these bones meet each other forms a slightly excavated edge. The transverse notch characteristic of lydekkerinids (*sensu* Shishkin et al., 1996) separating the lappet from the subotic procces of the exoccipital, is not observed in *Arachana*. The identity of

both previously described structures has been recently questioned by Jeannot et al. (2006) who argued that the "lappets" represent the most extreme lateral projection of the muscular cristae and the notch is produced as an effect of the exoccipital recess behind the pockets. In *Arachana*, the posterior projections of the pterygoid do not appear to be related to the crista muscularis and even with the presence of an exoccipital recess behind the pockets, a parasphenoid notch seems to be absent.

Both left and right stapes are preserved in anatomical position (Figs. 4–6). They are relatively robust, slightly anteroposteriorly compressed, and rest in an apparently firm connection against the parasphenoid and exoccipital lateral margin. A similar condition is also present in many Palaeozoic temnospondyls and the South African lydekkerinids (e.g. Jeannot et al., 2006; Yates and Warren, 2000). The massive footplate bears a small stapedial foramen facing posteromedially, close to the base of the shaft. The stapedial shaft is also robust and of nearly equivalent size to the paroccipital process; it curves slightly dorsolaterally to end distally just underneath the otic notch. The shaft bears an oblique ridge (*sensu* Bystrow and Efremov, 1940) along its ventral surface, which has not been described in lydekkerinids or in rhinesuchids.

4. Phylogenetic relationships

In order to provide a preliminary approach about the position of *Arachana* within Stereospondyli, we performed a phylogenetic analysis of 15 taxa that represent all known stereospondyl families, and some not well defining taxa as *Uruyiella liminea* (Piñeiro et al., 2007b) and *Sangaia lavinai* (Dias da Silva and Marsicano, 2011) (see Appendix A). A single most parsimonious tree (Tree length: 141 steps; CI: 0.511; RI: 0.589; RC: 0. 301) was found in which *Arachana* displays a basal position close to rhinesuchids, being the sister taxon of the remaining stereospondyls (Fig. 7). The position of the rhytidosteid *Pneumatostega* nested within the clade including brachyopoids and plagiosaurs was unexpected, as well as the basal placement of the putative rhytidosteids *Sangaia* and *Arcadia* with respect to *Uruyiella*. These results are subject to caution due to the incompleteness of these taxa. The weakness of these results is demonstrated by the low Bremer support for these nodes (see Fig. 7).

5. Discussion

Arachana is undoubtedly a member of the stereospondyl clade, because of the presence of an extensive suture between the pterygoids and the parasphenoid corpus (see Yates and Warren, 2000). The combination of characters featured in *Arachana* suggests a transitional morphology between rhinesuchid and lydekkerinid temnospondyls, although this does not imply that the new taxon is phylogenetically intermediate between these two families, as suggested by the phylogenetic analysis (see Fig. 7). However, the analysis indicates close relationships of *Arachana* with rhinesuchids, as demonstrated by the presence of several characters shared with this group. Thus, rhinesuchid characters include the size and the general shape

of the skull, particularly the slightly posterior position of the orbits and the cheek contour, which is smoothly convex when seen from behind; the uniform, coarsely pitted ornamentation on the bones of the skull table, without pustules or conules at the junctions of the ridges (also shared with lydekkerinids); the absence of a step-like flexure in the infraorbital sensory sulcus; the presence of denticles on the vomers and palatines; posteromedial corner of palatine simple and not extending posterior to the most anterior ectopterygoid tooth, and the presence of a small basioccipital between the exoccipitals, visible in both ventral and occipital views. The palatal ramus of the pterygoid suturing with the vomer, thereby excluding both the palatine and ectopterygoid from the interpterygoid vacuity margin is a very primitive character among temnospondyls, but it was retained by *Arachana* and rhinesuchids among sterospondyls.

Lydekkerinid characters of *Arachana* not observed in most rhinesuchids include: supratemporal excluded from otic notch (bordering the notch in all rhinesuchids); grooves of the infraorbital sensory sulci crossing the lacrimal; otic notch not deeply incised; posttemporal fenestra large and tear-shaped (narrow, more slit-like opening in rhinesuchids); occipital condyles well-separated from each other; absence of a well-developed palatine tooth row behind the palatine tusk; ornamentation (although not conspicuous) over the corpus of the pterygoid, and the presence of an interorbital hollowing. Among the previously mentioned characters, the first and the latter need to be commented. The supratemporal failing to enter the otic notch is an inferred feature, as the specimen is severely damaged in that area. However, we argue for this condition to be present, since the otic notch appears to have been shallow. The longitudinal interorbital hollow is known to be present in all lydekkerinids except *Broomulus*, and absent in all rhinesuchids except *Rhineceps* (Hewison, pers. comm.). Nevertheless, the trough in *Arachana* is different from the condition in lydekkerinids in that it extends anteriorly well in front of the orbits as well as posteriorly (despite becoming shallower) to reach the posterior margin of the skull. Such a longitudinal trough has only previously been described in stem-stereospondyls, such as archegosaurids and melosaurids (e.g. Gubin, 1991). It was mentioned for the rhytidosteid *Arcadia myriadens* (Warren and Black, 1985), but in this taxon, it appears to have been shallower than in *Arachana*.

Arachana is not a rhytidosteid because of the presence of a well-developed lacrimal, the absence of a palatoquadrate fissure, the presence of cristae musculari and pockets in the parasphenoid; and the lack of pustules on the dermal ornamentation pattern. Similarly, the presence of a frontal that is excluded from the orbital margin (Damiani, 2001; Yates and Warren, 2000) suggests, along other characters, that *Arachana* is not a mastodonsauroid, although this condition is retained in *Wetlugasaurus*.

The new taxon displays an interesting mosaic of derived and primitive features, which have been considered to be diagnostic of lydekkerinids and rhinesuchids respectively (e.g. Jeannot et al., 2006; Watson, 1919, Yates and Warren, 2000). A mosaic of features has been noted for almost
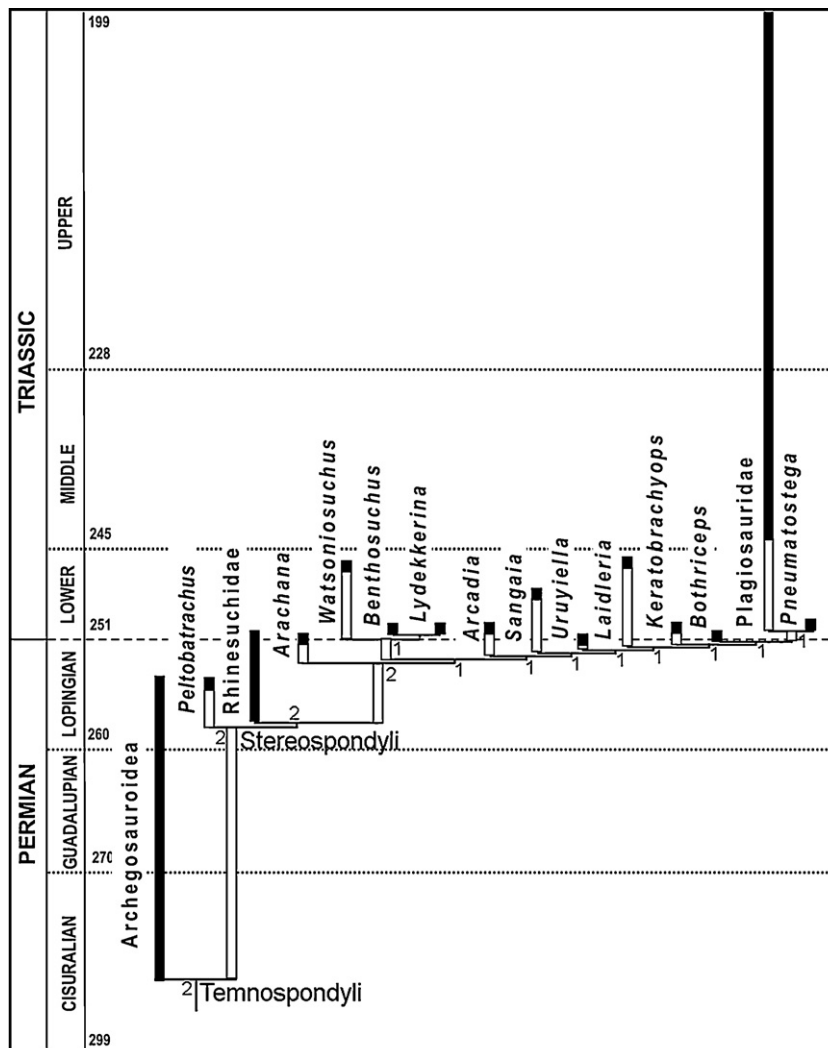
Fig. 7. Time-calibration of the single MPT obtained in the performed phylogenetic analysis (see the text for more references). The outgroup was excluded. Arabic numbers indicate the Bremer support for each node.
Fig. 7. Calibration en temps d'un MPT simple, qui vient de l'analyse phylogénétique de cette étude (voir texte pour plus de détails).

all the taxa described from the intraformational conglomerates of the Buena Vista Formation (the "Colonia Orozco fauna") (see Piñeiro et al., 2004, 2007a, 2007b, 2007c). Until now, we have not found convincing arguments to place the fossiliferous levels in the Permian (even the Latest Permian), or the Triassic, contra Dias da Silva et al. (2006), Modesto and Damiani (2007), and Modesto and Botha (2010). However, the reasoning that has been used to argue for an Early Triassic age for the Colonia Orozco fauna is the supposed correlation of the Buena Vista sequence to the Sanga do Cabral Formation in Brazil, which yielded the Triassic taxon *Procolophon trigoniceps* (after Cisneros, 2008). But the tetrapod assemblages in both units are very different (Da-Rosa et al., 2009, 2010). While only Lower Triassic (Induan) taxa have been described from the Sanga do Cabral Formation, two Permian taxa have been identified in Uruguay: the basal synapsid family Varanopidae (Piñeiro and Ubilla, 2003)

and a dvinosauroid inferred to be close to *Dvinosaurus* (Piñeiro et al., 2007a). Both assignations have been disputed by Modesto and collaborators in recent papers (Dias da Silva et al., 2006; Modesto and Botha, 2010; Modesto and Damiani, 2007). Their concerns about the affinities of the described varanopid vertebrae are based upon the following reasons: varanopids cannot be identified by considering exclusively vertebral characters and "varanopids have been misidentified as diapsids in the past" (Modesto and Botha, 2010). The varanopid material, initially misidentified as a "basal archosaur" was not represented solely by an assemblage of vertebrae but also by a partial skull. As an example, *Mesenosaurus romeri* was formerly assigned to diapsids but later reinterpreted as a varanopid (see Reisz et al., 2010 and references therein). Piñeiro (2006) and collaborators (this paper) still support their former interpretation as they analyzed carefully the combination of the characters present in the

described vertebrae and found that they matched better with basal synapsids than with basal diapsids. Modesto and Botha (2010) provided a careful review of the characters used recently by Piñeiro et al. (2007a) for the recognition of FC-DPV 285, a partial temnospondyl skull, as a *Dvinosaurus*-related taxon. In Modesto and Botha's review, a different arrangement of the skull bones was proposed, but this was based on the misinterpretation of a fracture in the medial border of the orbit as the suture between prefrontal and postfrontal bones. Thus, we emphasize our initial interpretation about the presence of a large postfrontal in FC-DPV 285, supporting dvinosaurid rather than tupilakosaurid affinities for this specimen.

The remaining specimens described from the Buena Vista Formation were treated as belonging to putative exclusively Triassic taxa such as Mastodonsauridae (*sensu* Damiani, 2001), Procolophonidae (*sensu* Cisneros and Ruta, 2010), and Plagiosauroidea. However, recent phylogenetic analyses suggest long ghost lineages that extend well into the Permian for at least the first two groups (Cisneros et al., 2004; Damiani, 2001; Modesto et al., 2001; Yates and Warren, 2000). Indeed, the fact that the specimens described from the Buena Vista Formation were found to be phylogenetically related to Triassic taxa does not necessarily imply that they are contemporaneous, although it lends support to this idea.

The identification of the PTB in the Uruguayan succession could be crucial for studies of tetrapod survivorship after the end Permian extinction event, as well as for calibration of the first appearance of traditional Triassic groups (Modesto and Botha, 2010). Indeed, stratigraphic and sedimentological studies recently performed in collaboration with Brazilian colleagues suggest that the PTB boundary may be present in the Buena Vista succession or close to the transitional contact with the underlying Yaguarí Formation. This last idea is improbable because of the Middle Permian (Late Guadalupian) age recently assigned to the later. Moreover, the possibility that the Buena Vista fauna might be older than that present in the Brazilian, Early Triassic Sanga do Cabral Formation was also discussed (Da-Rosa et al., 2009, 2010). Comparisons with South African sequences, where the PTB was previously established are difficult because most of the data are based almost exclusively on therapsids (Botha and Smith, 2006; Smith and Botha, 2005; Smith and Ward, 2001; Ward et al., 2005), a group that intriguingly is not represented in the Buena Vista fossiliferous conglomerates, although they might be present whether Buena Vista is Permian or Triassic. In contrast, the placement of the PTB in the Russian succession is supported by a broader range of taxa, including therapsids plus other vertebrate groups (actinopterygian and reptiles), as well as arthropods (ostracodes) (Newell et al., 2010; Shishkin et al., 2006). In Uruguay, none of these groups were found associated to the tetrapods of the Colonia Orozco fauna, although indeterminate actinopterygians, bivalves and conchostraceans dominate the underlying deposits of the Yaguarí Formation (Goso et al., 2001; Piñeiro, 2006) (Fig. 8). We are currently studying these materials in order to cast new light on correlation. A similar, actinopterygian-dominated fauna characterizes also

Early Triassic sequences, as those of the Arcadia Formation in Australia (Northwood, 1999, 2005). Indeed, when the Uruguayan Permo-Triassic assemblage is compared with the Australian faunas, some interesting similarities are evident. For instance, narrow, subcircular vertebral centrae found in the Buena Vista Formation are very similar to diplospondylous vertebrae recently found in the Upper Parmineer Group of Tasmania, from levels that are very close to the PT boundary, and thus, probably Permo-Triassic in age (Warren, pers. comm. 2011; Warren et al., in press). Diplospondylous vertebrae are known to belong to *Tupilakosaurus*, but those from the Tasmania have been found in association with several skulls of the basal brachyopid *Bothriceps australis* and thus, they were related to this taxon (Warren et al., in press). The presence of brachyopids and of *Tupilakosaurus* has not yet been confirmed in the Buena Vista conglomerates, and Uruguayan vertebrae are considerably smaller than those figured in Warren et al. (in press), and thus, they remind the condition described by diplospondylous vertebrae from the Upper Permian of southern France (Wernerburg et al., 2007). According to the transitional features of the components of the Buena Vista fauna and its different taxonomic identity with respect to well-defined Triassic communities elsewhere (including the Fauna of Catuçaba in the Brazilian Sanga do Cabral Formation), the assignment of a Permo-Triassic age for that unit is at the moment the most parsimonious hypothesis. This age is indeed partially supported by recent radiometric studies performed in bentonitic layers from the top of the Yaguarí Formation, which suggest a Late Guadalupian age for this unit (De Santa Ana et al., 2006). Besides, the Yaguarí and the Buena Vista formations show a conformable transition from multi-coloured marginal marine and lacustrine mudstones and sandstones to fluvial reddish sandstones with intercalated intra-formational conglomerates containing the tetrapod assemblage. This led some workers to place the Buena Vista Formation entirely in the Lopingian (Late Permian) (De Santa Ana et al., 2006), thus excluding the possibility that the PTB is present in Uruguay. If this stratigraphic scheme is correct, survivorship rates of the involved taxa would be increased, particularly that of temnospondyls, which comprise the most abundant group in the Buena Vista fossiliferous conglomerates. Unfortunately, the calibration of the age of the Buena Vista Formation could not be based on comparisons with overlying communities as occurs in Africa and Russia successions, since no other units that could represent the Triassic are preserved in Uruguay. Palaeomagnetic studies that are being currently performed in the Yaguarí and Buena Vista sequence will provide useful data for comparison with those suggested for the South African and Russian Permo-Triassic successions, where the PTB is at the end of a reversal period in the latter region and well inside of a normal one in the former (see Newell et al., 2010; Ward et al., 2000).

Botha and Smith (2006) recognized three stages of faunal assemblages at the Permo-Triassic transition: a fauna composed of exclusive Permian taxa affected by the extinction, a transitional community surviving the extinction, and a well-established mostly Triassic recovery fauna derived from the transitional one, in which Latest
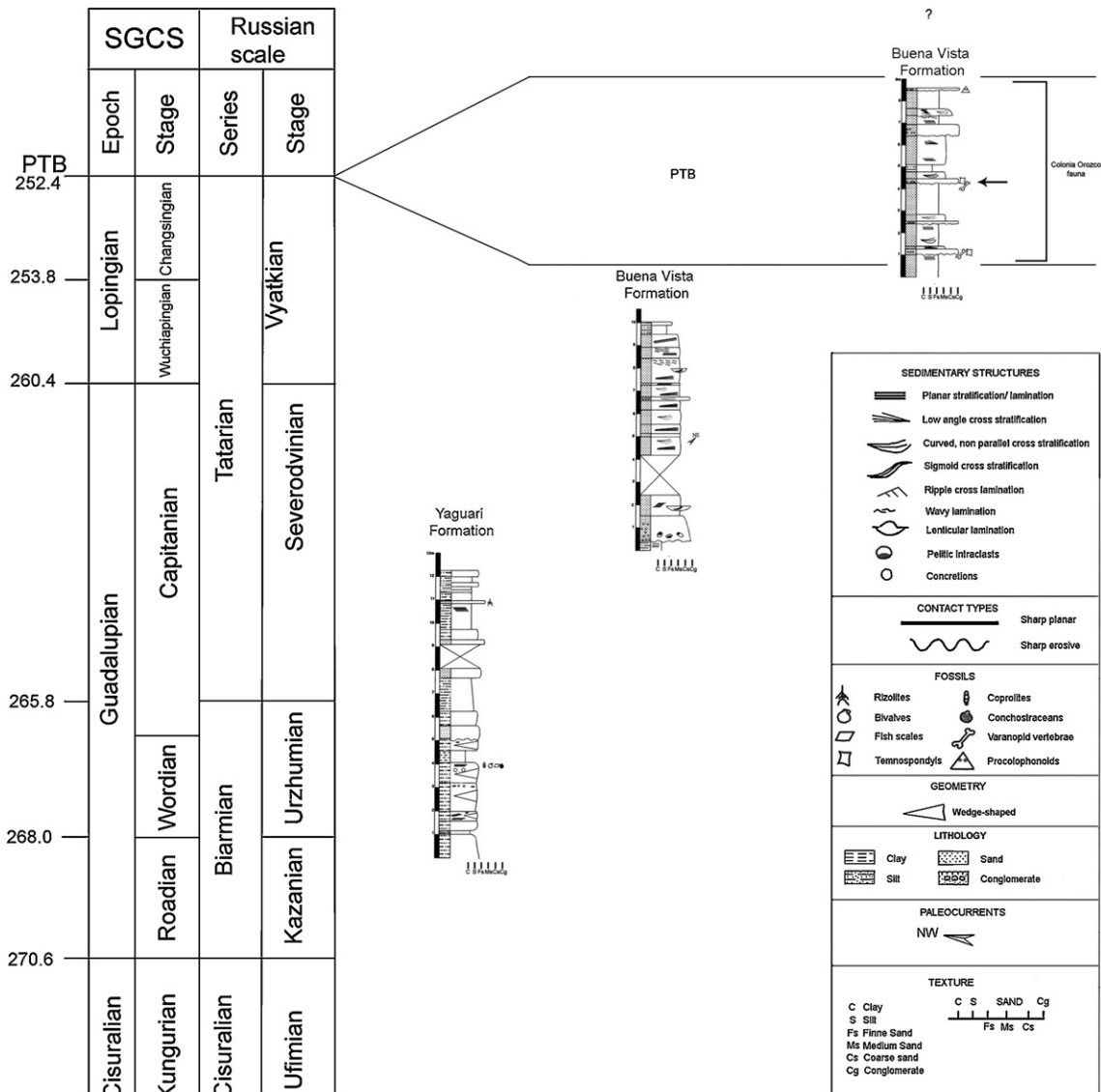
Fig. 8. Composite stratigraphic column of the successive Yaguari and Buena Vista Formation (Norte Basin, Northeastern Uruguay) and their known fossil record. Sections belong to the same locality (Colonia Orozco) where they outcrop conformably, but they were separated to better show the time calibration. Chronostratigraphy calibrated on the basis of recent radiometric data from bentonite layers of the Yaguarí Formation, and data from the tetrapod assemblage found in the Buena Vista Formation (the Colonia Orozco fauna). The Permo-Triassic boundary is suggested to be represented by the red sandstones with intercalated red mudstones and intraformational conglomerates of the Buena Vista Formation where the transitional Colonia Orozco fauna is found. The arrow points to the conglomerate level where *Arachana* was found. (Chronostratigraphic scale modified from Ogg et al., 2008).

Fig. 8. Colonne stratigraphique composite de la succession Formation Yaguari et Formation Buena Vista (Norte Basin, Uruguay nord-oriental) et leurs fossiles répertoriés connus. La chronostratigraphie a été calibrée sur la base de données radiométriques récentes, obtenues à partir de lits de bentonite de la Formation de Yaguari et de données relatives à l' assemblage de tétrapodes trouvés dans la Formation de Buena Vista (faune Colonia Orozco). La limite Permien–Trias est supposée être représentée par les grès rouges à intercalations de *mudstones* rouges et les conglomérats intraformationnels de la Formation de Buena Vista, où la faune transitionnelle Colonia Orozco est observée. La flèche pointe le niveau conglomératique où *Arachana* a été trouvée (échelle chronostratigraphique modifiée d'après Ogg et al., 2008).

Permian and Earliest Triassic forms should have coexisted. On the other hand, the Permo-Triassic transition in the Russian continental sequence includes the Vyatkian-Vokhmian gorizonts, and the PTB could be placed in both units (Newell et al., 2010). Nonetheless, the Nedubrovian horizon has been recently recognized (although disputed, see Newell et al., 2010) as an additional unit, considered to be transitional by some workers, between the former two mainly on the basis of plants and the presence of the temnospondyl *Tupilakosaurus* (Krassilov and Karasev, 2009). This implies that the PTB cannot be illustrated as a simple time line, but may be represented by a relatively longer period of biotic changes. This transition may not be accurately represented in the fossil record of all known Permo-Triassic sequences elsewhere, but only as transient faunas forming part of that transition. The "Colonia Orozco

fauna" recovered from the fossiliferous intraconglomerates of the Buena Vista Formation could represent just one of such transitional scenarios (see Fig. 8), where Latest Permian and Earliest Triassic representatives either coexisted together or were nearly contemporaneous.

6. Conclusions

The new described temnospondyl *Arachana nigra* from the Buena Vista Formation of Uruguay displays a transitional morphology that precludes an assignment to any of the previously known temnospondyl groups. It shares several characters with lydekkerinids such as *Lydekkerina huxleyi* and *Eolydekkerina magna*, as well as with *Chomatobatrachus halei* in some respects, but it differs from all of them and other lydekkerinids by its large size (*Arachana* is about 2.25 times larger than *Eolydekkerina*, the largest known lydekkerinid, and five times larger than *Lydekkerina huxleyi*). Along with its large size, the most intriguingly primitive features of *Arachana*, viz. the palatine ramus of pterygoid extending anteriorly to contact the vomer and the presence of an ossified basioccipital, relate this taxon to rhinesuchids. Nevertheless, other characters separate *Arachana* from rhinesuchids and also from lydekkerinids, such as the dorsal medial interorbital trough that extends anteriorly and posteriorly to the posterior border of the skull. The phylogenetic analysis precludes placing *Arachana* in these taxa, or it would make them paraphyletic.

The continental tetrapod assemblage from the Buena Vista Formation (the Colonia Orozco Fauna) has given support to a Permian or Permo-Triassic age for this unit, historically correlated to the Lower Triassic Sanga do Cabral Formation of Brazil. The new specimen described herein, like previously described material from the Buena Vista Formation, displays the same transitional morphology between what is expected of Permian and of Triassic taxa. Comparisons with the South African Permo-Triassic communities are difficult to establish due to the total and unexpected absence of therapsids in the Colonia Orozco fauna. On the Russian Platform, the Permo-Triassic succession is studied in the light of a more diverse range of groups, including vertebrates and other metazoans, and also magnetostratigraphy. Some of these groups are represented in Uruguay in stratigraphically lower units (e.g. the Yaguarí Formation) and they are not found in association with tetrapods. Palaeomagnetic studies are currently being undertaken along the sequence that could include the Permian-Triassic transition in Uruguay, and our proposed study of the actinopterygians and other metazoans of the Yaguarí Formation will supply important new data to advance on this investigation.

Acknowledgements

Appendix A. Supplementary data

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