Mandibles of mastodonsaurid temnospondyls from the Upper Permian–Lower Triassic of Uruguay

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Partially preserved temnospondyl mandibles from the Late Permian–Early Triassic Buena Vista Formation of Uruguay are referred to the basal stereospondyl taxon Mastodonsauridae. These represent the earliest known members of this group for South America. In most cases, this assignment was based on the characteristic morphology of the postglenoid (= postarticular) area of the lower jaw together with the presence of a hamate process. Comparisons with basal mastodonsaurids indicate that the Uruguayan specimens are phenetically similar to Gondwanan and Laurasian Early Triassic taxa, such as *Watsonisuchus*, *Wetlugasarus*, and *Parotosuchus*. Nevertherless, they display some characters which have not previously been described in Mesozoic temnospondyls. The Permo-Triassic Uruguayan mastodonsaurids support a Gondwanan origin for the group, an event which probably occurred sometime during the latest Permian.

Key words: Temnospondyli, Mastodonsauridae, lower jaw, Permian, Triassic, Buena Vista Formation, Uruguay.

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Introduction

Most of our knowledge of the diversity of Permian and Triassic South American temnospondyls comes from Brazilian deposits in the Paraná Basin. The probable archegosaurid *Bageherpeton longignathus* Dias and Barberena, 2001 and a mandible of uncertain taxonomic affinities (Malabarba et al. 2003) were recovered from the Middle Permian Aceguá and Posto Queimado faunas, respectively, both in the Rio do Rasto Formation (Cisneros et al. 2005). In the same formation, short and long-snouted rhinesuchoids (Barberena 1998; Barberena and Dias 1998; Dias et al. 2003) are known from the Late Permian Serra do Cadeado fauna. Archegosaurids are also represented by *Prionosuchus plummeri* (Price, 1948) from the Lower Permian Pedra de Fogo Formation (Parnaíba Basin) in northeastern Brazil. Other Brazilian temnospondyls recovered from the Lower Triassic Sanga do Cabral Formation include cranial material of rhytidosteid affinities (Dias-da-Silva et al. 2006), and some fragmentary material tentatively assigned to one of the Lydekkerinidae, Rhytidosteidae, or Temnospondyli *incertae sedis* (Barberena et al. 1981, 1985; Dias-da-Silva et al. 2005).

Outside Brazil, the only known South American temnospondyls come from the Upper Triassic of Argentina (Bonaparte 1963, 1975; Marsicano 1993, 1999, 2005) and from the Upper Permian–Lower Triassic Buena Vista Formation of northern Uruguay. Until now the Uruguayan materials consisted of a partial skull related to the *Dvinosaurus*-Tupilakosauridae clade (Marsicano et al. 2000), and a posterior half of a skull identified as a laidleriid closely related to the South African *Laidleria gracilis* (Piñeiro et al. 2007). The Uruguayan temnospondyls are associated with varanopid synapsids, procolophonoid reptiles, and probable prolacertiform archosauromorphs (Piñeiro et al. 2003, 2004; Piñeiro 2004). This continental assemblage constitutes the Colonia Orozco Fauna (Piñeiro 2004; Piñeiro et al. 2007), after the name of the locality at Cerro Largo County (Fig. 1A) that provided most of the specimens.

In the present study, we describe three isolated mandibular fragments collected by the senior author at Colonia Orozco Town from conglomerate levels of the Buena Vista Formation (Fig. 1B), a unit which was probably deposited close to the Permo-Triassic boundary (Goso et al. 2001; Piñeiro and Ubilla 2003; Piñeiro et al. 2003, 2004). These specimens are referable to the Mastodonsauridae, which were until now unknown in deposits of this age in South America. Elsewhere, mastodonsaurid temnospondyls are known from Early Triassic deposits of most Gondwanan areas including Australia (Warren 1991), India (Tripathi 1969), Madagascar (Lehman 1961), southern Africa (Damiani et al. 2001), and Antarctica (Colbert and Cosgriff 1974; Hammer 1990; Sidor et al. 2007). Therefore, their ap-
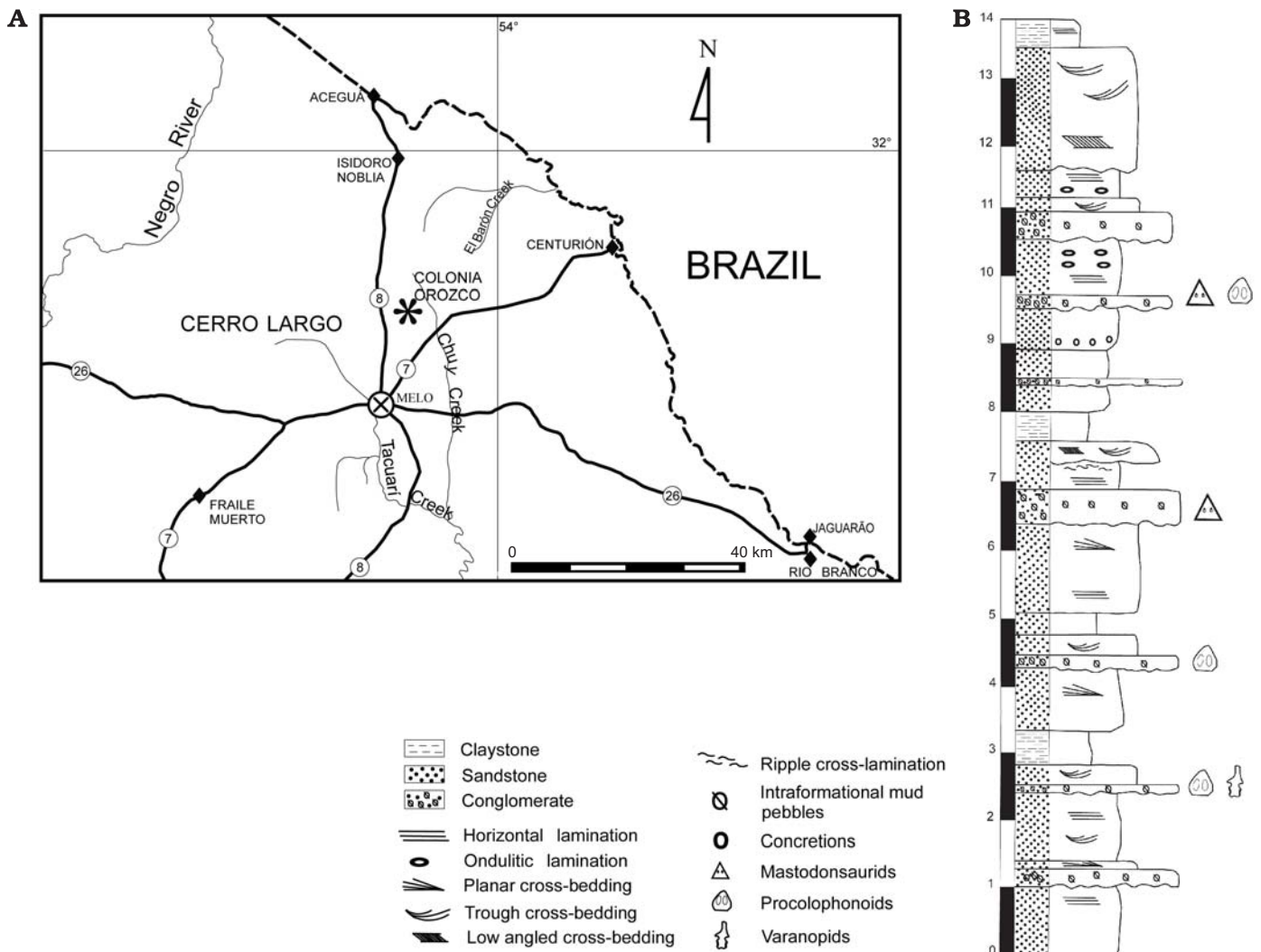
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Fig. 1. **A**. Location of the outcrops near Colonia Orozco, Cerro Largo County, northeastern Uruguay, where the fossils described herein were collected. **B**. Generalized stratigraphic section of the Permo-Triassic Buena Vista Formation of Uruguay showing the position of the mastodonsaurids with respect to the other components of the Colonia Orozco fauna. The vertical scale on the left is in meters.

parent absence in time-equivalent units of South America was regarded by previous authors as due to the lack of extensive study of the deposits (Damiani 2001). The palaeobiogeographical implications of this new South American record will also be discussed.

Institutional abbreviation.—FC-DPV, Colección de Paleontología de Vertebrados de la Facultad de Ciencias. Montevideo, Uruguay.

Descriptions

FC-DPV 1280 (Figs. 2, 3).—A partial left mandibular ramus preserved anteriorly from the suture between the middle and posterior coronoids to the posterior end of the postglenoid area (PGA, postglenoid area; *sensu* Jupp and Warren 1986). Lingually, the surface occupied by the anterior

half of the prearticular, angular and postsplenial is preserved largely as an internal mould so that sutures are not visible. The same condition occurs labially in the anteroventral part of the mandible. Dorsally, most of the articular is missing so that the glenoid (= articular) fossa is not preserved. Labially (Fig. 2A, B), only a narrow strip of the dentary is preserved dorsally up to its contact with the surangular. Posterior to this, most of the mandible is preserved as a natural internal mould and just the posterior part of the angular and surangular is present behind the level of the glenoid fossa. In this region, the mandibular sulcus is clearly visible traversing the surangular posteriorly and the angular anteriorly; poor preservation precludes the identification of the oral and accessory sulci. A sulcus-like structure posterior to the mandibular sulcus may be an artefact of preservation. A surangular foramen, otherwise typical of mastodonsaurids (Damiani et al. 2001), cannot be observed but this may be due to the state of preservation.
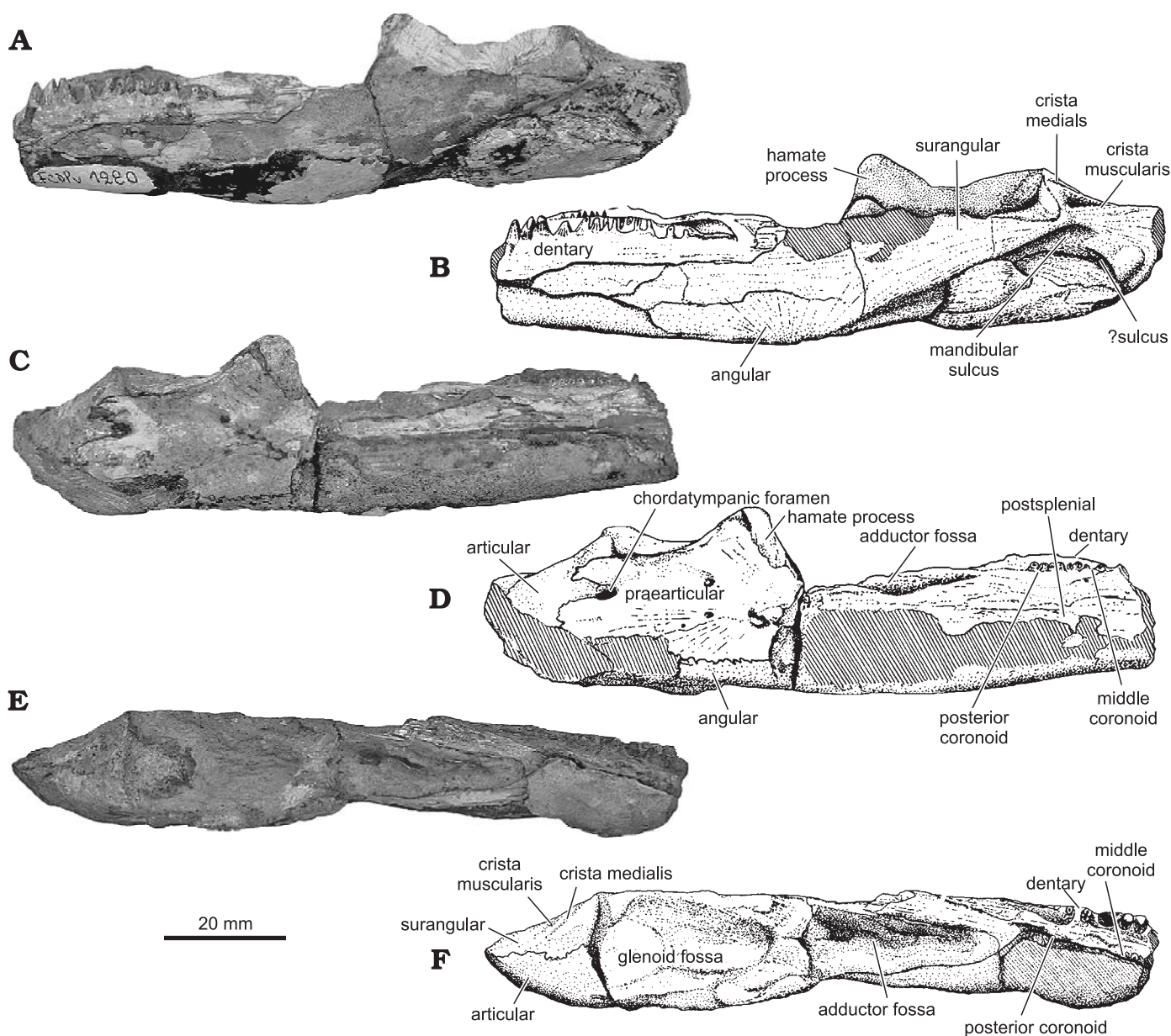
Fig. 2. Mastodonsaurid mandible FC-DPV 1280, from the Permo-Triassic Buena Vista Formation near Colonia Orozco, Cerro Largo County, Uruguay. Photographs (**A**, **C**, **E**) and interpretive drawings (**B**, **D**, **F**) in labial (**A**, **B**), lingual (**C**, **D**), and dorsal (**E**, **F**) views. Cross hatching represents damaged areas of bone.

The dentary shows 14 teeth that decrease in size backwards; they are anteroposteriorly compressed and relatively closely packed. The contact between the dentary and the surangular is extensive. The surangular forms the lateral wall of the adductor fossa and contacts the posterior coronoid at the level of the anterior border of the fossa; thus, the dentary is excluded from the margin of this chamber. Due to non-preservation of the dorsal part of the articular, the glenoid fossa is absent and the limit between this fossa and the adductor fossa is not known. The posterior coronoid is complete and a small part of the middle coronoid is also present. Remarkably, the posterior coronoid bears two, near-parallel tooth rows that continue onto the preserved fragment of the middle coronoid (Fig. 3). The more medial row comprises nine teeth on the posterior coronoid and two on the middle coronoid; the teeth are approximately one-third of the size of those in the dentary tooth row. The outer coronoid tooth row extends further posteriorly than the inner row and is also developed on the middle coronoid. The teeth are approximately half the size of the inner coronoid row.

Lingually (Fig. 2C, D), a narrow strip composed of several bones is preserved dorsally in front of the hamate process of the prearticular. The ventral extent of the bones in this region is defined by the suture between the coronoid series
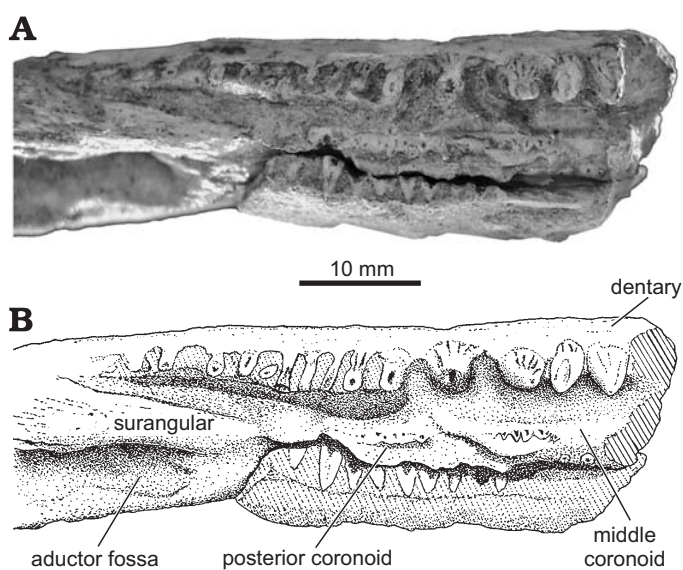
Fig. 3. Mastodonsaurid mandible FC-DPV 1280 from the Permo-Triassic Buena Vista Formation near Colonia Orozco, Cerro Largo County, Uruguay. Photograph (**A**) and interpretive drawing (**B**) of the coronoid area with two rows of teeth on the posterior and middle coronoid. Cross hatching represents damaged areas of bone.

and the postsplenial. The medial border of the adductor fossa is formed by the prearticular, which forms a large hamate process on the anterior margin of the glenoid fossa. The hamate process rises above the level of the glenoid fossa and is visible both lingually and labially; at the base of the process there is a small foramen located at the same level as the chordatympanic foramen. Posteriorly, the prearticular contacts the articular in a dorsoventrally oriented suture; at the junction of these bones there is a well developed chordatympanic foramen. Ventrally, part of the suture between the prearticular and the angular is visible. The posterior margin of the glenoid fossa is defined by a well developed post-condylar process (*sensu* Damiani et al. 2001) which separates it from the PGA.

The part of the mandible posterior to the glenoid fossa (PGA) is of Type I (*sensu* Jupp and Warren 1986), that is, relatively short with the lingual wall formed entirely by the articular, and the labial wall formed by the surangular (Fig. 2E, F). In lateral view, the dorsal border of the PGA slopes smoothly ventrally. In dorsal view, the PGA narrows markedly posteriorly and an arcadian groove seems to be absent from the posterior end of the PGA. In addition, the dorsal suture between the articular and the surangular is located longitudinally in the midline. The muscular cristae on the PGA are poorly developed. There is a low crista muscularis formed by the surangular close to the labial edge; the crista runs obliquely to the tip of the PGA. Parallel and close to this crista, a short crista medialis is present and confined to the surangular. No other cristae are visible on the PGA.

FC-DPV 1600 (Fig. 4).—A fragment of the posterior end of a right mandible including most of the glenoid fossa and the

PGA. Labially (Fig. 4A, B), the surangular forms most of the surface preserved, although ventrally part of the surangular-angular suture is visible. The surface of the surangular is ornamented especially anteriorly. On this surface, two well developed sensori sulci are distinguishable, the mandibular sulcus and the accessory sulcus. Posterior to the mandibular sulcus the surangular is only weakly ornamented. The surangular of FC-DPV 1600 bears a small surangular foramen close to the edge of the glenoid fossa, as is typical of mastodonsaurids (Damiani et al. 2001). In dorsal view, the glenoid fossa is partially preserved and only one of the articular facets for the quadrate is preserved. The posterior margin of the glenoid fossa is defined by a well developed post-condylar process.

Lingually (Fig. 4C, D), the prearticular and the articular form most of the preserved surface, although ventrally a suture indicates that part of the angular is present. A relatively large chordatympanic foramen is present on the prearticular-articular suture. Posterior to this foramen and separated from it by a vertical boss, there is a longitudinal shallow groove on the articular, running forwards and upwards on the lingual surface of the PGA. In lateral view, the dorsal border of the PGA slopes smoothly ventrally. The PGA is Type I (*sensu* Jupp and Warren 1986) and relatively short.

Dorsally (Fig. 4E, F), the PGA narrows backwards and the articular-surangular suture runs longitudinally close to its lingual margin. This suture is straddled by the crista medialis which is itself separated from the crista muscularis by a smooth groove; the crista muscularis is formed entirely by the surangular.

FC-DPV 1305 (Fig. 5).—A fragment of the posterior part of a right mandibular ramus including the glenoid fossa and the PGA. On the labial surface, the bones are highly weathered, precluding a good description of the angular and surangular. Nevertheless, a small portion of the angular preserved ventrally reveals that the ornamentation on this bone was weakly developed. In labial view (Fig. 5A, B) it is apparent that the mandible was relatively low, at least in its most posterior part, and that the ventral angular curvature, if present, would be moderately developed. The PGA is elongated with its dorsal surface sloping downwards.

Lingually (Fig. 5C, D), the prearticular-articular suture extends just behind the level of the posterior border of the glenoid fossa where it meets a large, chordatympanic foramen. The chordatympanic foramen is connected by a shallow groove with a more posterior and smaller foramen on the articular. As far as can be determined, this feature appears to be unique to FC-DPV 1305 among mastodonsaurids. The suture of the angular with the prearticular is located very low on the mandible. The prearticular bears two small foramina close to the edge of the glenoid fossa, and an additional small foramen near its suture with the articular.

In dorsal view (Fig. 5E, F), the preserved portion of the glenoid fossa is obliquely oriented, and its anterolingual part, although incompletely preserved, is thickened, which sug-
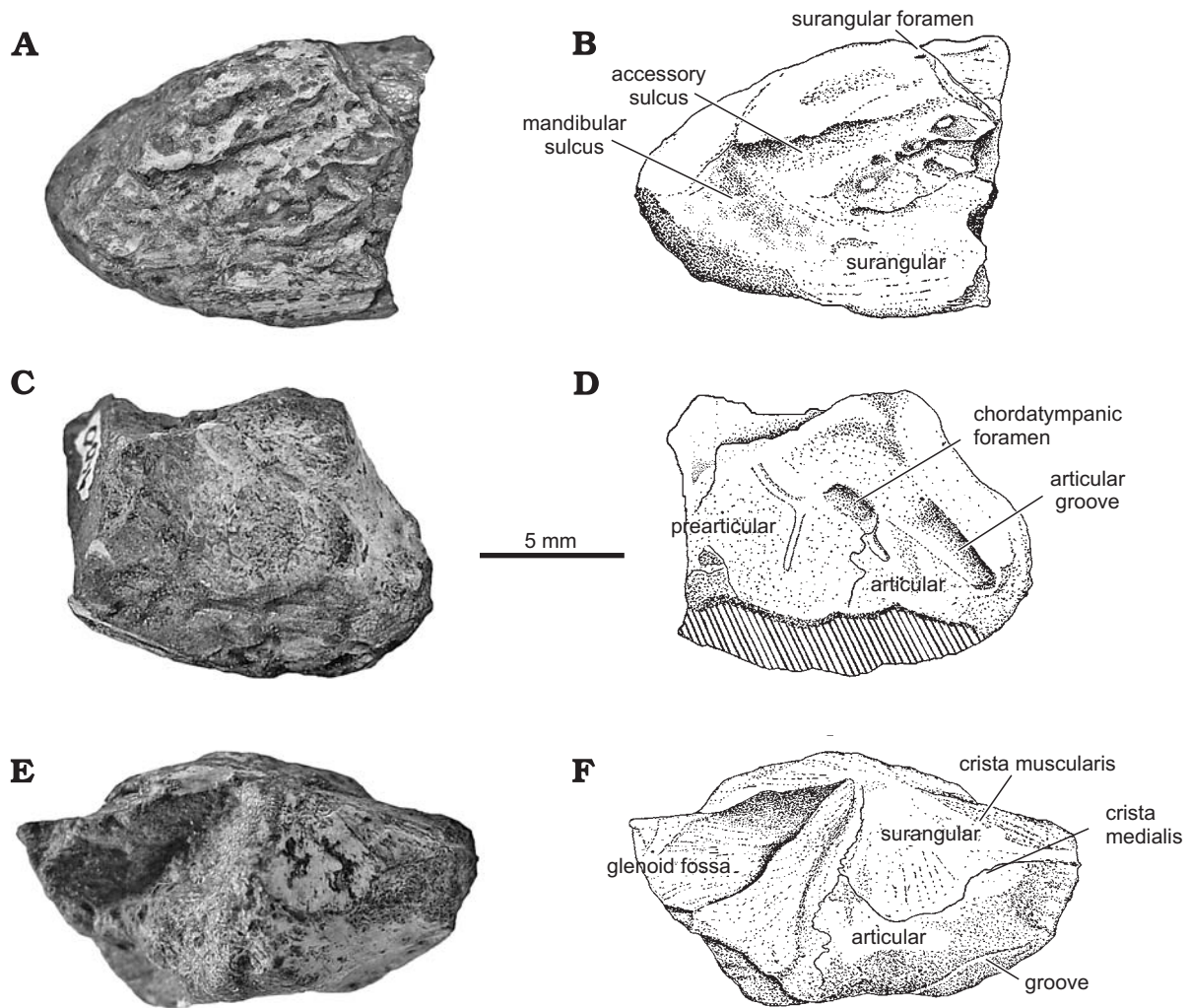
Fig. 4. Mastodonsaurid mandible FC-DPV 1600 from the Permo-Triassic Buena Vista Formation near Colonia Orozco, Cerro Largo County, Uruguay. Photographs (**A**, **C**, **E**) and interpretive drawings (**B**, **D**, **F**) in labial (**A**, **B**), lingual (**C**, **D**), and dorsal (**E**, **F**) views. . Cross hatching represents damaged areas of bone.

gests that a hamate process was present. The posterior margin of the glenoid fossa is delimited by a well developed post-condylar process. The PGA is Type I and, in dorsal view, it narrows backwards. The dorsal surface of the PGA is nearly flat and is laterally and medially bordered by strong muscular cristae. The crista muscularis projects dorsolaterally and forms a distinct angular protuberance close to the border with the glenoid fossa. The crista medialis is located on the articular-surangular suture near the lingual side of the PGA. A prominent knob occurs lingually, in the position of the crista lingualis. A crista articularis is not visible on the PGA due to damage.

Comparisons

The three specimens described in the present analysis have a type I PGA, which, together with a well developed hamate process that is visible both lingually and labially, have been widely used to characterize mastodonsaurid mandibles (Jupp and Warren 1986; Damiani 2001; Damiani et al. 2001). Nevertheless, the distribution and morphology of the muscular cristae on the dorsal surface of the PGA of FC-DPV 1280 (Fig. 2E, F) is different from that described for most mastodonsaurids (Novikov and Shishkin 1992; Maryańska and Shishkin 1996; Damiani 1999, 2001). Specifically, the crista medialis is formed only by the surangular, close to the crista muscularis, and does not straddle the articular-surangular suture, unlike the condition in other mastodonsaurids with known mandibular morphology (Damiani 1999, 2001), including also FC-DPV 1600. However, the configuration of the muscular cristae in FC-DPV 1280, as well as the elongation and posterior narrowness of the PGA, is very similar to that present in *Komatosuchus chalyshevi* (Novikov and Shishkin 1992). Maryanska and Shishkin (1996) and Damiani (2001) regarded that taxon to be of uncertain affinity within the Mastodonsauridae because the PGA did not fit into any of the structural types established by these authors. A posteri-
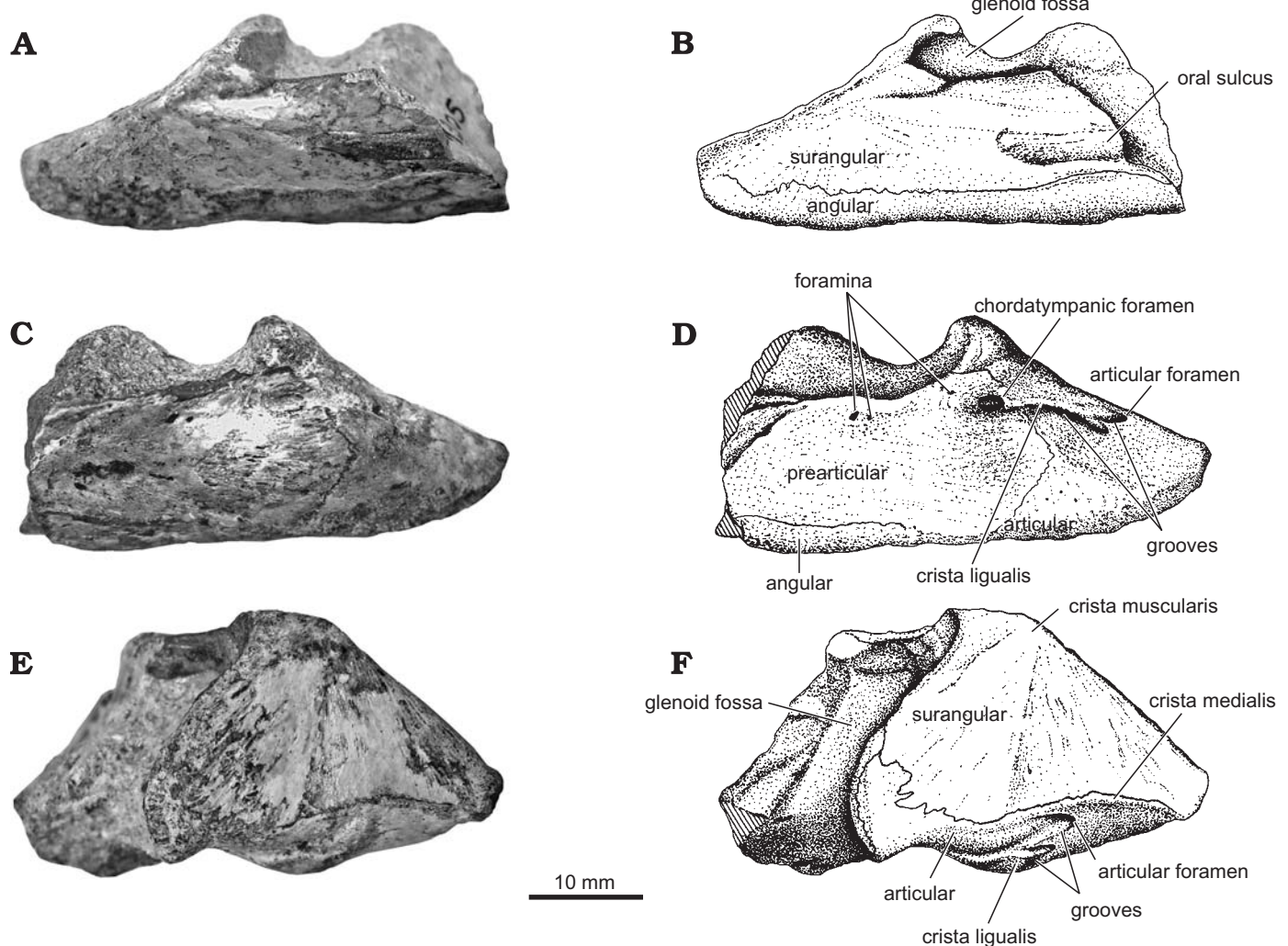
Fig. 5. Mastodonsaurid mandible FC-DPV 1305 from the Permo-Triassic Buena Vista Formation near Colonia Orozco, Cerro Largo County, Uruguay. Photographs (**A**, **C**, **E**) and interpretive drawings (**B**, **D**, **F**) in labial (**A**, **B**), lingual (**C**, **D**), and dorsal (**E**, **F**) views. Cross hatching represents damaged areas of bone.

orly narrowing PGA also occurs in basal mastodonsaurids such as *Wetlugasaurus* and *Watsonisuchus* (Damiani 1999, 2001; Damiani et al. 2001), but in a less marked fashion than that observed in FC-DPV 1280.

The presence of two parallel rows of teeth on both the posterior and middle coronoids in FC-DPV 1280 has not previously been reported in mastodonsaurids, which normally possess only a single row of teeth on the posterior coronoid. Intruigingly, a double row of coronoid teeth is also present in some Permian rhinesuchids from Brazil (GP and CAM, personal observation); as far as can be determined, all other rhinesuchids have denticles—that is, small, rounded domes which lack both pulp cavities and labyrinthine infolding— rather than teeth on all three coronoids (RD, personal observation). This suggests that the condition present in the Brazilian rhinesuchids and in FC-DPV 1280 might be acquired independently. Nevertheless, this character should be evaluated in a phylogenetic context in order to resolve this question.

A short type I PGA, the morphology of the muscular cristae on the PGA, and the presence of a dorsally placed surangular foramen suggests that FC-DPV 1600 is a mastodonsaurid. In addition, the short PGA excludes more derived representatives of this group. Nevertheless, the shallow groove on the articular observed in FC-DPV 1600, which runs forward from the posterior end of the mandible to reach a large chordatympanic foramen, was described for some rhinesuchids such as *Rhineceps* and *Rhinesuchoides* (Watson 1962).

The structure of the PGA and the presence of muscular cristae on the dorsal surface of FC-DPV 1305 ally this specimen with mastodonsaurids. Moreover, the probable presence of a hamate process supports this conclusion. It is important to note the unusual development of the crista muscularis and the crista lingualis as well as the presence of a small foramen on the articular, posterior to the chordatympanic foramen. Whereas an articular foramen has already been noted in one large specimen of *Watsonisuchus rewanensis* as an unusual
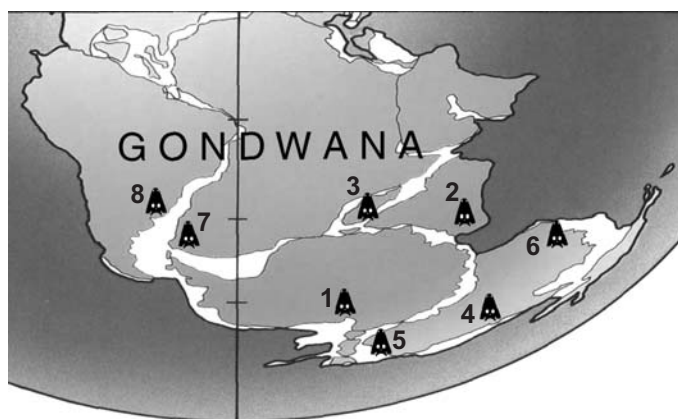
Fig. 6. Records of the earliest Triassic mastodonsaurids in Gondwana: (1) lower Fremouw Formation of Antarctica (Colbert and Cosgriff 1974); (2) Panchet Formation of India (Tripathi 1969); (3) Lower Sakamena Formation of Madagascar (Lehman 1961; Steyer 2003); (4) Arcadia, (5) Knocklofty, and (6) Blina Shale formations of Australia (Warren 1980; Cosgriff and DeFauw 1987; Warren and Hutchinson 1988; Damiani 2000); (7) *Lystrosaurus* Assemblage Zone of South Africa (Damiani et al. 2001); (8) Buena Vista Formation of South America (Piñeiro and Ubilla 2003; this paper).

condition for Mesozoic temnospondyls (Damiani 2001), a bulge-shaped crista lingualis is not known in other mastodonsaurid temnospondyls.

Discussion

Jupp and Warren (1986) showed that the study of isolated mandibles, mainly those preserving the PGA, could help to identify some Permian and almost all Triassic temnospondyl families. Using a combination of characters, Jupp and Warren (1986) identified two basic PGA types: the plesiomorphic type I PGA is present in Permian and some Early Triassic taxa, whereas the more derived type II PGA is restricted to Mesozoic groups. More recent studies have shown that it is possible to distinguish among mastodonsaurid genera using PGA morphology (Novikov and Shishkin 1992; Maryańska and Shishkin 1996; Damiani 1999, 2001; Damiani et al. 2001).

The specimens described herein display several diagnostic characters that strongly support their inclusion in the Mastodonsauridae, including the distinctive morphology of the PGA and the presence of a well developed hamate process. In their general morphology, the mandibles are comparable to the most basal members of the Mastodonsauridae, such as the Early Triassic genera *Watsonisuchus*, *Wetlugasarus*, and *Parotosuchus*. The absence of associated skull material precludes further generic or specific comparisons, but the unique combination of characters exhibited by each specimen suggests that they could represent new taxa. Some of those characters have not previously been described in Mesozoic temnospondyls, such as the presence in FC-DPV

1280 of two rows of teeth on the posterior coronoid which are continuous at least onto the middle coronoid. Dentigerous coronoids are frequently found in primitive temnospondyls and this condition is retained in rhinesuchids (Watson 1962; Schoch and Milner 2000; Yates and Warren 2000) and rhytidosteids (Warren and Black 1985; Marsicano and Warren 1998; Schoch and Milner 2000; Yates and Warren 2000) as a shagreen field that extends over the entire coronoid series. In all other stereospondyl families the coronoid teeth, when present, are usually restricted to a single row on the posterior coronoid (Schoch and Milner 2000; Yates and Warren 2000). Thus, the double-row condition, as observed in FC DPV 1280, may represent the retention of a plesiomorphic condition—convergent with that present in some South American rhinesuchids—such as in early tetrapods and tetrapodomorph fishes. Apart from this peculiarity, the Uruguayan materials seem to follow the general pattern of Gondwanan and Laurasian Early Triassic mastodonsaurids, with some differences that may be autapomorphic conditions for each taxon.

The specimens described herein are the oldest record of mastodonsaurids from South America and possibly from Gondwana. The only previous record of mastodonsaurids from this continent is *Promastodonsaurus bellmanni*, a fragmentary skull and associated right mandible from the Carnian Ischigualasto Formation of Argentina (Bonaparte 1963). The presence of mastodonsaurids in a unit which is considered as Permo-Triassic in age (Goso et al. 2001; Piñeiro and Ubilla 2003; Piñeiro et al. 2003, 2007) suggests that they could be representatives of a mastodonsaurid lineage that lived in South America perhaps earlier than the beginning of the Triassic. Corroboration of this assumption must await the discovery of more complete specimens, in order to evaluate them in a phylogenetic context. However, a Late Permian divergence of lydekkerinids, mastodonsaurids and trematosauroids from rhinesuchids was already suggested by previous workers (Warren et al. 2000; Yates and Warren 2000; Damiani 2001) based on phylogenetic analysis and stratigraphic calibration of the resultant cladograms. These suggest that mastodonsaurids and trematosauroids, as well as lydekkerinids, have ghost lineages that span most of the Late Permian (Yates and Warren 2000; Damiani 2001).

Finally, the mastodonsaurids from the Permo-Triassic Colonia Orozco assemblage lend further support for a Gondwanan origin of the group sometime during the Late Permian. Subsequently, after a rapid radiation event, the group achieved a cosmopolitan distribution as early as the earliest Triassic (Fig. 6), as was suggested by Damiani et al. (2001).

Acknowledgements

References

Barberena, M.C. 1998. *Australerpeton cosgriffi*, n. g., n. sp., a Late Permian rhinesuchoid amphibian from Brazil. *Anais da Academia Brasileira de Ciências* 70: 125–137.

Barberena, M.C. and Dias, E.V. 1998. On the presence of a short-snouted rhinesuchoid amphibian in the Rio do Rasto Formation (Late Permian of Paraná Basin, Brazil). *Anais da Academia Brasileira de Ciências* 70: 465–468.

Barberena, M.C., Lavina, E., and Becker, M. 1981. Sobre a presença de tetrápodos na Formaçno Sanga do Cabral (Grupo Rosario do Sul), Triássico do Rio Grande do Sul, Brasil. *Anais do II Congresso Latino-Americano de Paleontologia* 1: 295–306.

Barberena, M.C., Araújo, D.C., and Lavina, E.L. 1985. Late Permian and Triassic tetrapods of southern Brazil. *National Geographic Research* 1: 5–20.

Bonaparte, J.F. 1963. *Promastodonsaurus bellmanni* n.g. et n. sp. capitosáurido del Triásico Medio de Argentina (Stereospondyli–Capitosauroidea). *Ameghiniana* 3: 67–78.

Bonaparte, J.F. 1975. Sobre la presencia del laberintodonte *Pelorocephalus* en la formación Ischigualasto y su significado estratigráfico (Brachyopoidea Chigutisauridae). *Actas del 11 Congreso Argentino de Paleontología y Bioestratigrafía* 1: 537–544.

Cisneros, J.C., Abdala, F., and Malabarba, M.C. 2005. Pareiasaurids from the Rio do Rasto Formation, southern Brazil: biostratigraphic implications for Permian faunas of the Paraná Basin. *Revista Brasileira de Paleontologia* 8: 13–24.

Colbert, E.H. and Cosgriff, J.W. 1974. Labyrinthodont amphibians from Antarctica. *American Museum Novitates* 2552: 1–30.

Cosgriff, J.W. and Defauw, S.L. 1987. A capitosaurid labyrinthodont from the Lower Scythian of Tasmania. *Alcheringa* 11: 21–41.

Damiani, R.J. 1999. Giant temnospondyl amphibians from the Early to Middle Triassic Narrabeen Group of the Sydney Basin, New South Wales, Australia. *Alcheringa* 23: 87–109.

Damiani, R.J. 2000. Early Triassic mastodonsaurids (Temnospondyli, Stereospondyli) from Western Australia, with remarks on mastodonsauroid palaeobiogeography. *Alcheringa* 24: 299–305.

Damiani, R.J. 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* 133: 379–482.

Damiani, R.J., Neveling, J., and Hancox, J. 2001. First record of a mastodonsaurid (Temnospondyli, Stereospondyli) from the Early Triassic *Lystrosaurus* Assemblage Zone (Karoo Basin) of South Africa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221: 133–144.

Dias-da-Silva, S., Marsicano, C., and Schultz, C.L. 2005. Early Triassic temnospondyl skull fragments from Southern South America (Paraná Basin, Brazil). *Revista Brasileira de Paleontologia* 8: 43–50.

Dias-da-Silva, S., Marsicano, C., and Schultz, C.L. 2006. A new rhytidosteid (Temnospondyli, Stereospondyli) from Southern South America (Lower Triassic of Brazil). *Palaeontology* 49: 381–390.

Dias, E.V. and Barberena, M.C. 2001. A temnospondyl amphibian from the Rio do Rasto Formation, Upper Permian of Southern Brazil. *Anais da Academia Brasileira de Ciências* 73: 135–143.

Dias, E.V., Barberena, M.C., and Schultz, C.L. 2003. The first Paleozoic temnospondyl postcranial skeleton from South America. *Revista Brasileira de Paleontologia* 6: 29–42.

Goso, C., Piñeiro, G., de Santa Ana, H., Rojas, A., Verde, M., and Alves, C. 2001. Caracterización estratigráfica de los depósitos continentales cuspidales neopérmicos (Formaciones Yaguarí y Buena Vista) en el borde oriental de la Cuenca Norte Uruguaya. *XI Congreso Latinoamericano de Geología, III Congreso Uruguayo de Geología*: 1–18. CD-ROM.

Hammer, W.R. 1990. Triassic terrestrial vertebrate faunas of Antarctica. *In*: T.N. Taylor and E.L. Taylor (eds.), *Antarctic Paleobiology: its Role in the Reconstruction of Gondwana*, 42–50. New York, Springer Verlag.

Jupp, R. and Warren, A.A. 1986. The mandibles of the Triassic labyrinthodont amphibians. *Alcheringa* 10: 99–124.

Lehman, J.-P. 1961. Les Stégocéphales du Trias de Madagascar. *Annales de Paléontologie (Vertébrés)* 47: 109–154.

Malabarba, M.C., Abdala, F., Weiss, F.E., and Perez, P.A. 2003. New data on the Late Permian vertebrate fauna of Posto Queimado, Rio do Rasto Formation, southern Brazil. *Revista Brasileira de Paleontologia* 6: 49–54.

Marsicano, C.A. 1993. Evolutionary relationships in the Triassic Gondwanan family Chigutisauridae (Amphibia, Temnospondyli). *Journal of Vertebrate Paleontology* 13: 48A.

Marsicano, C.A. 1999. Chigutisaurid amphibians from the Upper Triassic of Argentina and their phylogenetic relationships. *Palaeontology* 43: 1–21.

Marsicano, C.A. 2005. A new temnospondyl record from the Upper Triassic of Argentina. *Ameghiniana* 42: 501–504.

Marsicano, C.A. and Warren, A.A. 1998. The first Paleozoic rhytidosteid record: *Trucheosaurus major* Watson 1956 from the Late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli). *Bulletin of the British Museum (Natural History), Geology* 54: 147–154.

Marsicano, C.A., Perea, D., and Ubilla, M. 2000. A new temnospondyl amphibian from the Lower Triassic of South America. *Alcheringa* 24: 119–123.

Maryańska, T. and Shishkin, M.A. 1996. New cyclotosaurid (Amphibia: Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Ziemi* 43: 53–83.

Novikov, I.V. and Shishkin, M.A. 1992. New Middle Triassic labyrinthodonts from the Pechora Urals. *Paleontological Journal* 26: 92–102.

Piñeiro, G. 2004. *Faunas del Pérmico y Permo-Triásico de Uruguay: Bioestratigrafía, Paleobiogeografía y Sistemática*. 215 pp. Unpublished Ph.D. thesis, Universidad de la República, Montevideo.

Piñeiro, G. and Ubilla, M. 2003. Unidades Pérmico-Triásicas en la Cuenca Norte: paleontología y ambientes. *In*: G. Veroslavsky, M. Ubilla, and S. Martínez (eds.), *Cuencas Sedimentarias de Uruguay: Geología, Paleontología y Recursos Minerales, Mesozoico*, 33–49. Dirac–Facultad de Ciencias, Uruguay.

Piñeiro, G., Verde, M., Ubilla, M., and Ferigolo, J. 2003. First basal synapsids ("pelycosaurs") from South America, Late Permian–?Early Triassic of Uruguay. *Journal of Paleontology* 77: 38–392.

Piñeiro, G., Rojas, A., and Ubilla, M. 2004. A new procolophonoid (Reptilia: Parareptilia) from the Upper Permian of Uruguay. *Journal of Vertebrate Paleontology* 24: 814–821.

Piñeiro, G., Marsicano, C., and Lorenzo, N. 2007. A new temnospondyl from the Upper Permian–Lower Triassic of Uruguay. *Palaeontology* 40: 627–640.

Price, L.I. 1948. Um anfibio labirintodonte da Formaçno Pedra de Fogo, Estado de Maranhno. *Boletim da Divisno de Geologia e Mineralogia, Departamento Nacional de Produção Mineral* 124: 1–32.

Schoch, R.R. and Milner, A.R. 2000. Stereospondyli. *Handbuch der Paläoherpetologie, Teil 3B*. 203 pp. Verlag Dr. Friedrich Pfeil, Munich.

Sidor, C.A., Steyer, J.S., and Damiani, R. 2007. *Parotosuchus* (Temnospondyli: Mastodonsauridae) from the Triassic of Antarctica. *Journal of Vertebrate Paleontology* 27: 232–235.

Steyer, J.S. 2003. A revision of the Early Triassic "capitosaurs" (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. *Journal of Vertebrate Paleontology* 23: 544–555.

Tripathi, C. 1969. Fossil labyrinthodonts from the Panchet Series of the Indian Gondwana. *Paleontologia Indica* (N.S.) 38: 1–45.

Warren, A.A. 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* 4: 25–36.

Warren, A.A. 1991. Australian fossil amphibians. *In*: P. Vickers-Rich, J.M Monaghan, M.F. Baird, and T.H. Rich (eds.), *Vertebrate Palaeontology of Australasia*, 569–590. Pioneer Design Studio, Melbourne.

Warren, A.A. and Black, T. 1985. A new rhytidosteid (Amphibia: Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology* 5: 303–327.

Warren, A.A., Damiani, R.J., and Yates, A.M. 2000. Palaeobiogeography of Australian fossil amphibians. *Historical Biology* 15: 171–179.

Warren, A.A. and Hutchinson, M.N. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* 31: 857–876.

Watson, D.M.S. 1962. The evolution of the labyrinthodonts. *Philosophical Transactions of the Royal Society of London, Series B* 245: 219–265.

Yates, A.M. and Warren, A.A. 2000. The phylogeny of 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* 128: 77–121.