

TEMNOSPONDYL DIVERSITY OF THE PERMIAN-TRIASSIC COLONIA OROZCO LOCAL FAUNA (BUENA VISTA FORMATION) OF URUGUAY

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ABSTRACT – Temnospondyls are the most abundant constituent of the Colonia Orozco Local Fauna of the Uruguayan Buena Vista Formation (Paraná Basin), contrasting with that observed at most latest Permian and earliest Triassic assemblages elsewhere. The components of the Colonia Orozco fauna, appear to represent early stages of the turnover evidenced in the communities of continental tetrapods at the Permo-Triassic boundary. They include plesiomorphic representatives of groups present in Early Triassic assemblages as well as relicts of Late Permian taxa. In particular, the presence of a close relative of the Russian dvinosauroid, *Dvinosaurus*, implies a dispersal event of this taxon to Gondwana probably during the Late Permian. Comparisons of the Colonia Orozco fauna to other Permo-Triassic communities indicate that it could be older than the Brazilian Lower Triassic Catuçaba Local Fauna of the Sanga do Cabral Formation (Paraná Basin) and probably equivalent to the latest Permian Russian Vyazniki Community. Moreover, the Colonia Orozco fauna could be close to the assemblages represented in the lowermost portion of the South African Lower Triassic *Lystrosaurus* Assemblage Zone and probably to the Arcadia Formation of Australia.

Key words: Temnospondyli, Colonia Orozco Local Fauna, Buena Vista Formation, latest Permian, earliest Triassic.

RESUMO – Os Temnospondyli constituem o grupo mais abundante na Fauna Local de Colonia Orozco da Formação Buena Vista no Uruguay (bacia do Paraná), contrastando com o observado na maior parte das associações conhecidas em depósitos do final do Permiano e início do Triássico. A fauna de Colonia Orozco parece representar estágios primitivos da substituição faunística que se constata nas comunidades de tetrápodos continentais no limite Permo-Triássico. Os temnospondilos da Formação Buena Vista incluem representantes plesiomórficos de grupos presentes no início do Triássico, como também relictos de componentes típicos do Permiano superior. Entre eles se destaca a presença de um dvinosaurídeo proximamente relacionado com o gênero *Dvinosaurus* do Permiano superior da Rússia, o qual implicaria na existência de um evento de dispersão deste táxon até o Gondwana, provavelmente no Permiano Tardío. A comparação da Fauna de Colonia Orozco com outras asociaciones Permo-Triássicas, indica que a fauna uruguaya poderia ser equivalente a Comunidade de Vyazniki do Permiano mais superior da plataforma russa, y que poderia ostentar um status bastante próximo às associações presentes na porção mais basal da Zona de *Lystrosaurus* da África do Sul e na Formação Arcadia, na Austrália. Por outro lado, a Fauna Local de Colonia Orozco seria mais antiga que a Fauna Local de Catuçaba registrada na Formação Sanga do Cabral, bacia do Paraná (Brasil), considerada de idade Triássico inferior.

Palavras-chave: Temnospondyli, Fauna Local de Colonia Orozco, Formação Buena Vista, Permiano superior, Triássico inferior.

INTRODUCTION

The Buena Vista Formation crops out in north-eastern Uruguay (Figure 1) and was deposited under continental fluvial conditions, thus revealing an important environmental change from the brackish epicontinental sea that dominated the underlying Permian succession. The Buena Vista Formation consists of red brownish sandstones, intercalated with thin layers of red brownish mudstones and

intraformational conglomerates (Bossi & Navarro, 1991; Goso *et al.*, 2001; Piñeiro & Ubilla, 2003), which provided most of the known fossil specimens of the unit (Figure 2).

Although there is a general consensus among authors about the fluvial environmental characterization of the Buena Vista Formation, its age has remained contentious. For a long time, only one fossil specimen has been found in this formation (Marsicano *et al.*, 2000), thus precluding good correlations with other fossiliferous Permo-Triassic

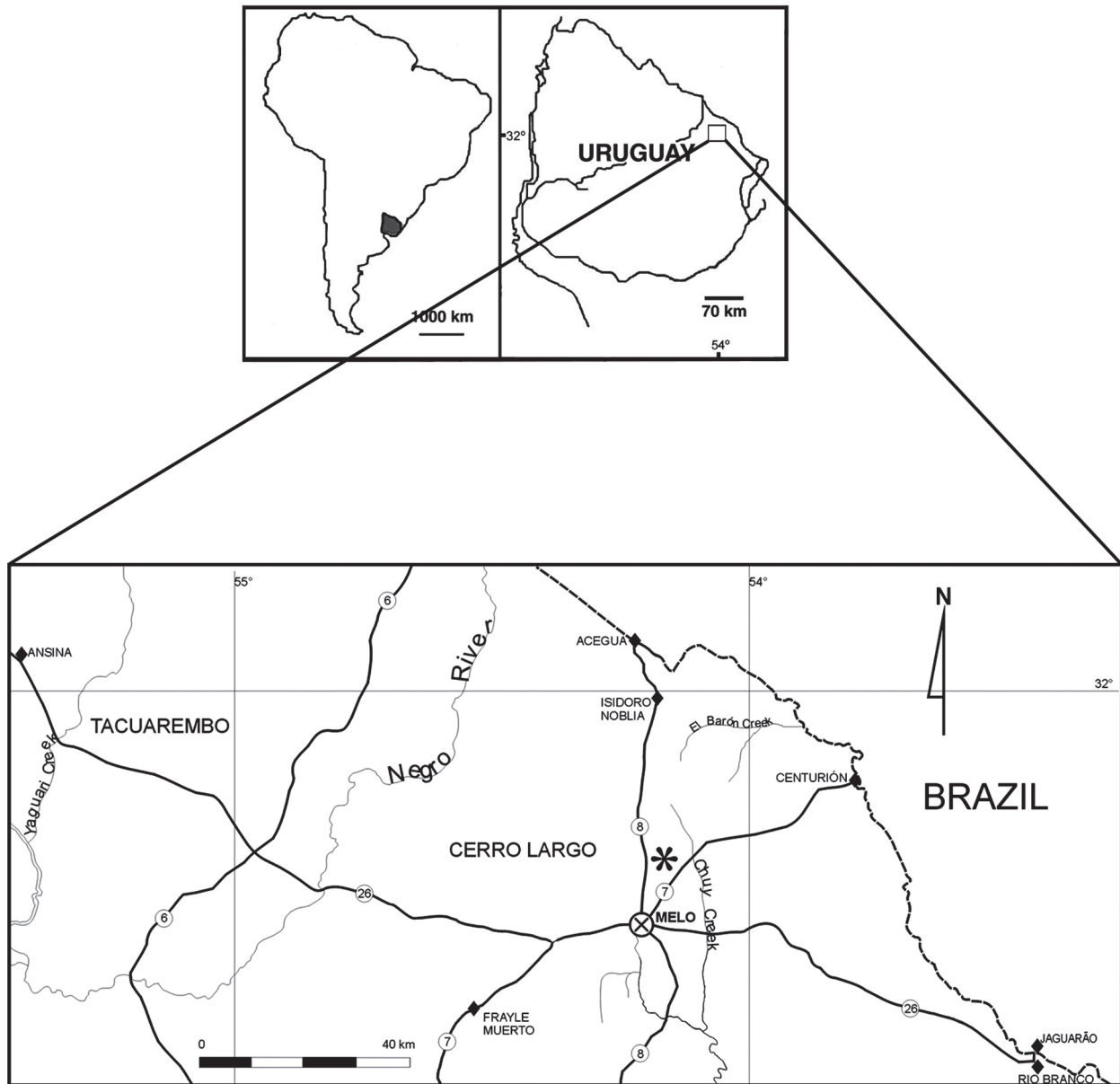


Figure 1. Detailed area at the Cerro Largo County, northeastern Uruguay, showing the location of the fossiliferous outcrop (asterisk) of the Buena Vista Formation.

successions like those of Brazil, South Africa, Australia and Russia. Therefore, the Triassic age previously assigned to the Buena Vista Formation was only based on lithostratigraphic similarities with the Sanga do Cabral Formation of southern Brazil (Bossi & Navarro, 1991). Nevertheless, a significant tetrapod assemblage has recently been recovered from several localities of the Buena Vista Formation at Cerro Largo County. This assemblage appears to be different from that recovered in the Sanga do Cabral Formation, mainly in the presence of pelycosaurian-grade synapsids in the Uruguayan beds (Piñeiro *et al.*, 2003; Piñeiro, 2004). In addition, the Buena Vista Formation has yielded procolophonoid and prolacertiform reptiles (Piñeiro *et al.*, 2004; Piñeiro, 2004), and temnospondyl amphibians (Piñeiro, 2004; Piñeiro *et*

al., 2007a,b), taxa which are also components of the Brazilian Catuçaba Local Fauna of the Sanga do Cabral Formation (Lavina, 1983; Barberena *et al.*, 1985a; Cisneros & Schultz, 2002; Abdala *et al.*, 2002; Dias-da-Silva *et al.*, 2005; 2006), although the Uruguayan fauna apparently represents an older assemblage (Piñeiro & Ubilla, 2003; Piñeiro, 2004; Piñeiro *et al.*, 2007a,b).

The aim of this paper is to provide an overview of the taxonomic composition of the temnospondyl fauna produced by the intraformational conglomerates of the Buena Vista Formation and to compare it to those described for other Pangaeian regions, particularly South Africa, Brazil, Australia and Russia. In addition, the biostratigraphic and paleobiogeographic implications of the Uruguayan temnospondyls are discussed.

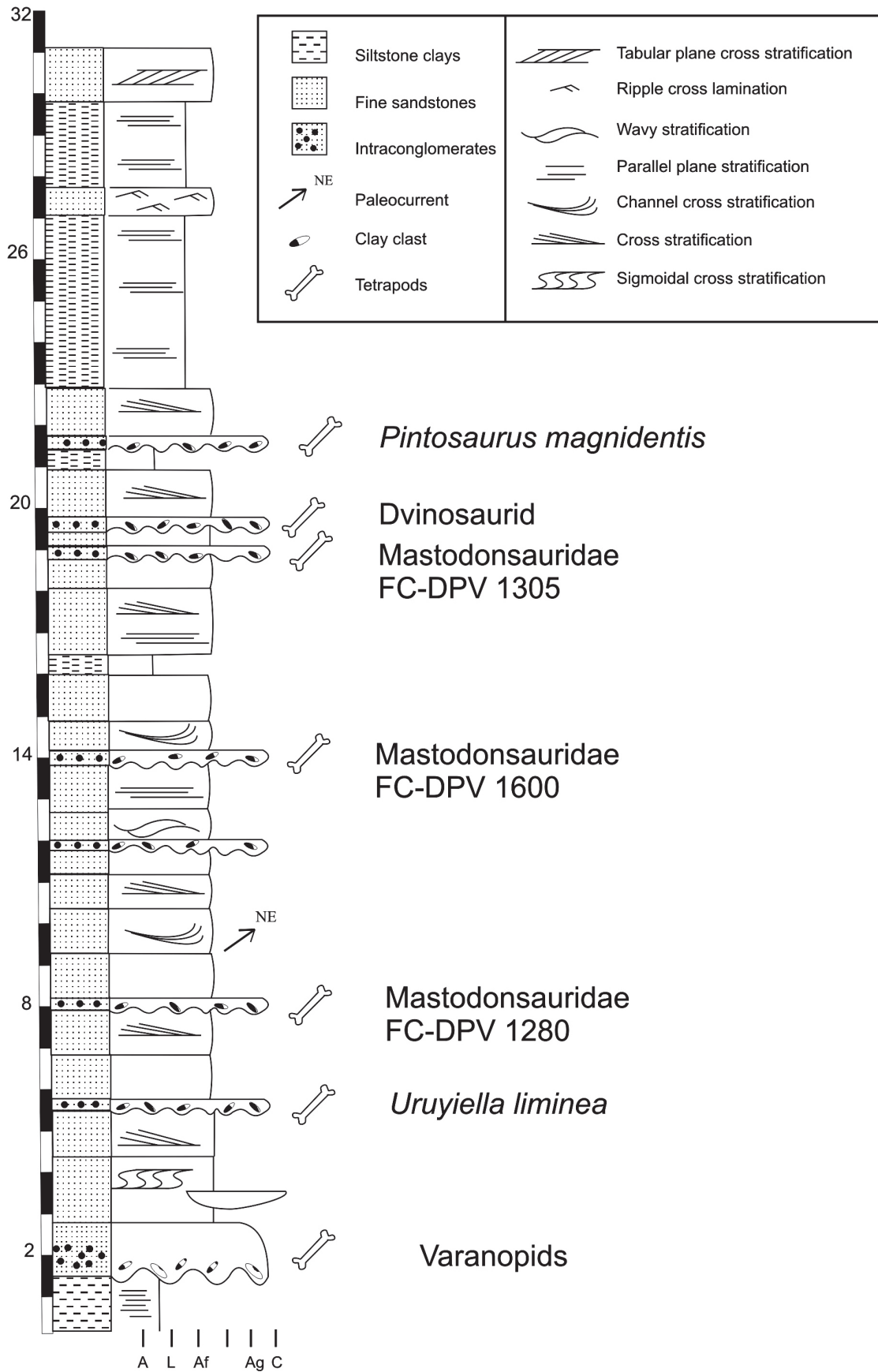


Figure 2. Combined profile of the Buena Vista Formation, including the stratigraphic sections present near the Colonia Orozco town, those along the Ruta N° 7, and those around the Tres Boliches area, along the Ruta N° 8.

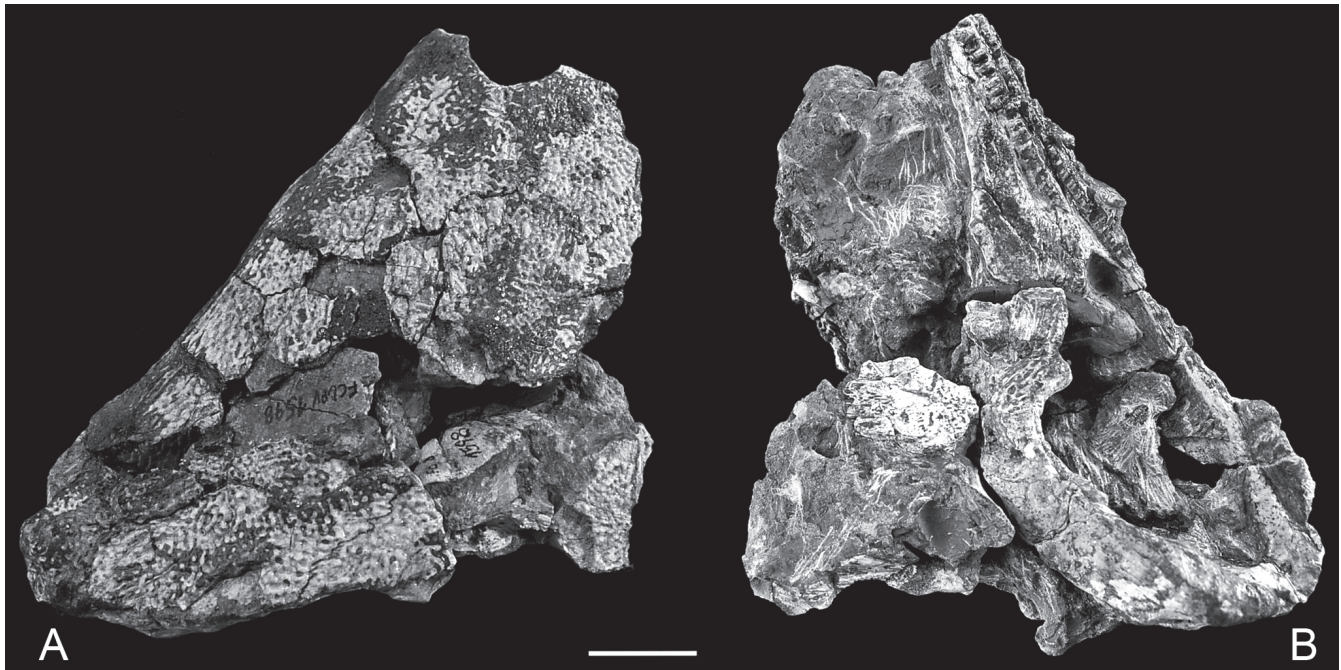


Figure 3. FC-DPV 1598, holotype of the laidleriid *Uruyiella liminea* from the lowermost intraformational conglomerates of the Buena Vista Formation (northeastern Uruguay), in dorsal (A) and ventral (B) views. Scale bar = 10 mm.

MATERIALS AND METHODS

The materials on which we based this contribution are deposited in the Colección de Vertebrados Fósiles de la Facultad de Ciencias of Montevideo (FC-DPV), Montevideo (Uruguay). The comparative materials examined are from the Bernard Price Institute for Palaeontological Research of South Africa, examined by Claudia Marsicano, and from the Museu de Paleontologia, Fundação Zoobotânica do Rio Grande do Sul and the Instituto de Geociencias, Universidade Federal do Rio Grande do Sul (UFRGS) of Brazil, studied by Graciela Piñeiro and Claudia Marsicano.

SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI LAIDLERIIDAE

Uruyiella liminea Piñeiro, Marsicano & Lorenzo

Material. FC-DPV 1598 (Figure 3), a partial skull from the lowermost intraformational conglomerates of the Buena Vista Formation at Colonia Orozco Town, Cerro Largo County, Uruguay.

Remarks. According to both anatomical and phylogenetic studies, *Uruyiella* appears to lie close to the Lower or Middle Triassic species *Laidleria gracilis* of South Africa, due to the triangular shape of the skull, the ornamentation of the dermal bones and the lateral position of the orbits in both taxa (Piñeiro *et al.*, 2007b). However, *Uruyiella* displays several autapomorphic characters which are not

observed in any Triassic taxa. For instance, all the postorbital bones in *Uruyiella* are remarkably large and anteroposteriorly elongated, being almost twice as long as they are wide. This arrangement is observed in *Trucheosaurus major* from Australia (Marsicano & Warren, 1998), the only known Permian rhytidosteid. Moreover, the palatine ramus of the pterygoid in *Uruyiella* extends well anteriorly, thus excluding the ectopterygoid and at least the posterior part of the palatine from the interpterygoid vacuity, a condition which is only comparable to that present in Palaeozoic temnospondyls (*e.g.* Watson, 1962; Gubin, 1991; Schoch & Milner, 2000). On the other hand, the presence of a trough on the ventral surface of the quadratojugal which forms an ‘overhang’ in occipital view in *Uruyiella* and *Laidleria*, is a characteristic that they share with the plagiosaurids. It is important to note that the phylogenetic affinities of both *Laidleria* and the plagiosaurids have been the subject of controversy among authors. *Laidleria* was alternatively considered as a trematosaurid by Kitching (1957), a laidleriid within the superfamily Rhytidosteioidea (Cosgriff, 1965, 1974), or as a member of a different family (Laidleriidae) within Temnospondyli (Cosgriff & Zawiskie, 1979). The plagiosaurids in turn have been recognized as stem Lissamphibia close to *Peltobatrachus* (Milner, 1990). A recent comprehensive study of temnospondyl relationships showed that *Laidleria* and the plagiosaurids are closely related taxa within the Stereospondyli (Yates & Warren, 2000); however, a new analysis including *Uruyiella* indicated that all these taxa form a clade related to the Dvinosauria, and that they fall outside the Stereospondyli (Piñeiro *et al.*, 2007b).

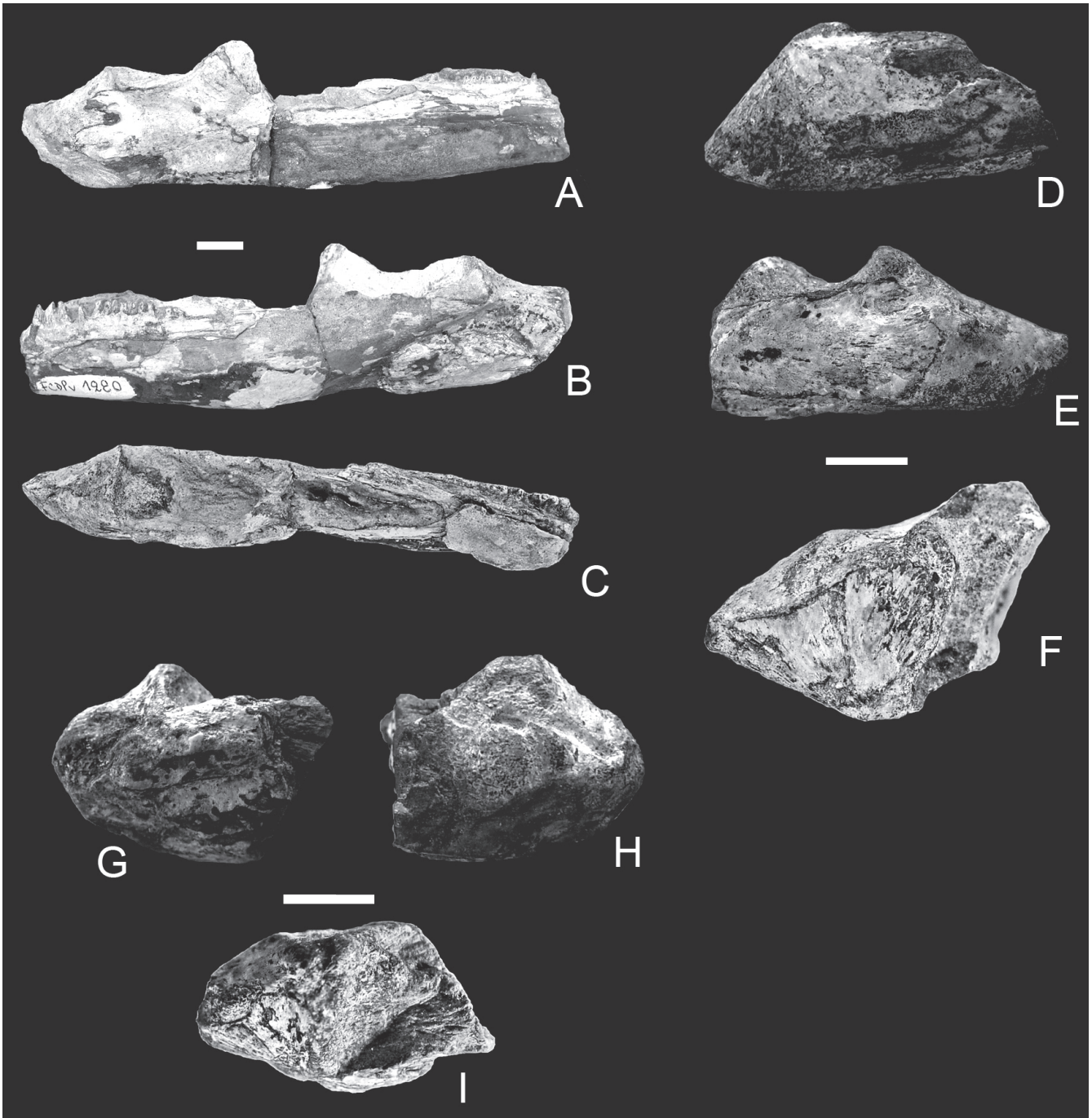


Figure 4. Mastodontosaurid mandibles from the intraformational conglomerates of the Buena Vista Formation (northeastern Uruguay): **A-C**, FC-DPV 1280, partial left mandible in labial (**A**), lingual (**B**) and dorsal (**C**) views; **D-F**, FC-DPV 1600, post glenoid area (PGA) of a right mandible in labial (**D**), lingual (**E**) and dorsal (**F**) views; **G-I**, FC-DPV 1305, PGA of a left mandible in labial (**G**), lingual (**H**) and dorsal (**I**) views. Scale bars = 10 mm.

TEMNOSPONDYLI
MASTODONSAURIDAE

Materials. FC-DPV 1280, 1305, 1600 (Figure 4); partial mandibles preserving the post-glenoid area (PGA), from middle and upper conglomerate levels of the Buena Vista Formation at Colonia Orozco town, Cerro Largo County, Uruguay.

Remarks. The fragmentary nature of the materials and the

absence of associated skulls preclude a more precise taxonomic assignation. The placement of these specimens within Mastodontosauridae is supported by the distinctive morphology of the PGA, the nature of its dorsal muscular crests, and by the presence of a well developed hamate process. Although their general morphology is consistent with that described for most basal members of Mastodontosauridae (*sensu* Damiani, 2001), the Uruguayan mandibles may represent new taxa that display some

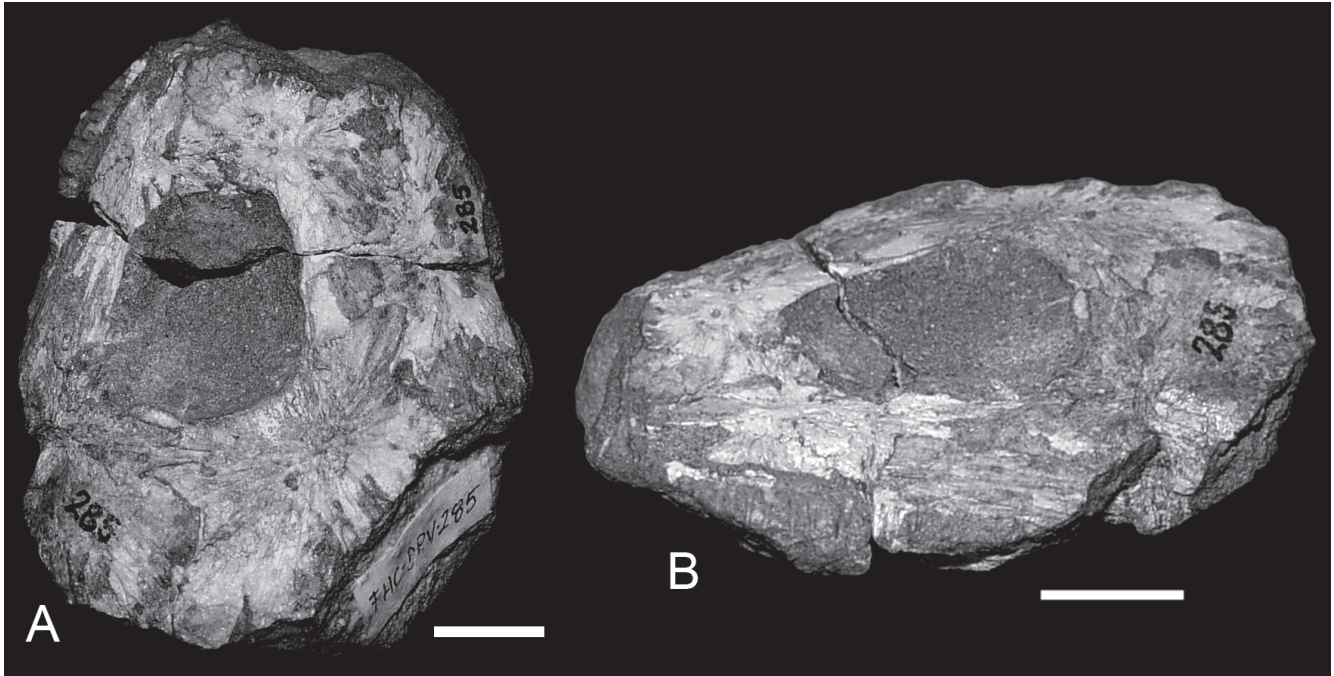


Figure 5. FC-DPV 285, dvinosaurid skull fragment including the left orbit, from the uppermost intraformational conglomerates of the Buena Vista Formation, in dorsal (A) and lateral (B) views. Scale bar = 10 mm.

characters not previously described in Mesozoic temnospondyls. Among them, the presence of a continuous tooth row on at least the posterior and middle coronoids appears to be convergent with the Late Permian rhinesuchids of southern Brazil (personal observation, Piñeiro *et al.*, 2007a).

TEMNOSPONDYLI

DVINOSAURIA (*sensu* Yates & Warren, 2000)

Material. FC-DPV 285 (Figures 5, 6). A partial skull, preserving part of the skull table at the level of the left orbital region. It comes from intraformational conglomerates of the Buena Vista Formation exposed at the wedge of Ruta N° 7, Cerro Largo County, Uruguay.

Remarks. This skull fragment was the first specimen discovered in the Buena Vista Formation and for a long time it was the only known fossil from this unit (Marsicano *et al.*, 2000). The fragmentary nature of the specimen precludes a precise taxonomic assignment, but regarding its short and broad skull and the presence of a bone which forms the anterolateral margin of the orbit in the position of the lacrimal or the lateral exposure of the palatine (LEP) (Figure 6), the material was related to the *Dvinosaurus*-Tupilakosauridae clade (Marsicano *et al.*, 2000). The poor preservation of the skull hamper a secure identification of that bone as the lacrimal. On the one hand, it displays the same ornamentation of the other preserved skull table elements as occurs in those taxa where the lacrimal is present. Tupilakosaurids display the unusual condition among temnospondyls of a large postorbital that contacts both the frontal (Milner & Sequeira 2004) and the parietal

(Warren, 1999) because of the unusually small size of the postfrontal. This condition is not observed in FC-DPV 285, which in turns shows a large postfrontal in contact with the prefrontal, thus precluding the frontal from contacting the postorbital and also excluding it from the orbital margin (Figures 5A, 6). The absence of a postorbital-parietal contact can be also inferred because the postorbital is laterally displaced by the large postfrontal, and thus does not contact the parietal. Among brachyopids, which also have a short and parabolic skull, the lacrimal and the LEP are absent in most cases, and only the Russian *Batrachosuchoides lacer* and the Australian *Xenobrachyops allos* have a LEP (Shishkin, 1967; Damiani & Warren, 1996). As the only known specimen of *Batrachosuchoides* consists of an antorbital area of a skull, the configuration of the postorbital bones cannot be compared to that present in FC-DPV 285. Along with the presence of a LEP, *Batrachosuchoides* shares some other characters with dvinosaurians (see Warren, 1999; Warren and Marsicano, 2000; Marsicano *et al.*, 2000), thus its affinities will remain unclear until more complete specimens can be discovered. Therefore, we consider the skull bone configuration present in FC-DPV 285 as more consistent with that described for the Permian *Dvinosaurus* (Bystrów, 1938) than for tupilakosaurids and brachyopids.

DISCUSSION

Geological overview of the Buena Vista Formation

Currently, the succession that includes the end of the Permian and probably the beginning of the Triassic in Uruguay is represented by two units, the Yaguarí and the

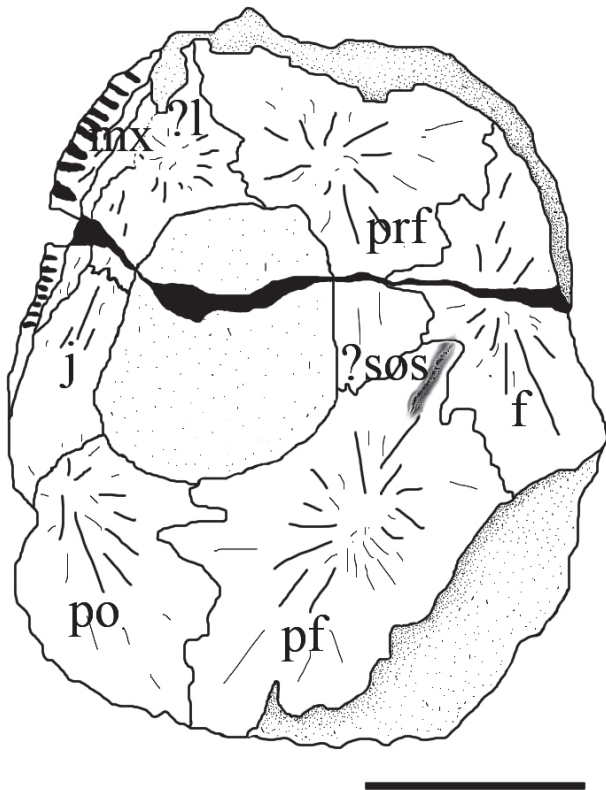


Figure 6. Interpretive drawing of FC-DPV 285 in dorsal view, showing the presence of a probable lacrimal and also the morphology of the preserved prefrontal, postfrontal and postorbital (see text). **Abbreviations:** f, frontal; j, jugal; l, lacrimal; mx, maxilla; pf, postfrontal; prf, prefrontal; po, postorbital; sos, supraorbital sulcus.

Buena Vista formations. For a long time both the characterization and the age of these units have been the subject of controversy among authors (see Falconer, 1937; Delaney & Goñi, 1963). The difficulty in establishing the boundary between the Yaguarí Formation and the overlying Buena Vista Formation lead some geologists to consider them as a single unit, assigned to the Upper Permian (e.g. Falconer, 1937; Bossi, 1966; Elizalde *et al.*, 1970). Other authors, in turn, differentiated the red, mostly arenaceous upper portion of the succession as an independent and well defined unit, the Buena Vista Formation, which was considered to represent the Lower Triassic in Uruguay (Caorsi & Goñi, 1958; Ferrando & Andreis, 1986; Bossi & Navarro, 1991), although no fossils were yet discovered from it.

At present, local and regional stratigraphic studies support the recognition of the Buena Vista Formation as a separate unit from the Yaguarí Formation (Goso *et al.*, 2001; de Santa Ana, 2005), but the tetrapod assemblage recently found in the Buena Vista Formation, designated the Colonia Orozco Local Fauna by Piñeiro & Ubilla (2003) and Piñeiro (2004), points to an older age than that previously recognized, closer to the Permian-Triassic boundary (Piñeiro *et al.*, 2003; Piñeiro & Ubilla, 2003; Piñeiro, 2004; Piñeiro *et al.*, 2004; Piñeiro *et al.*, 2007b).

Biostratigraphic relations of the Colonia Orozco Local Fauna with other Pangaeian communities

The Catuçaba Local Fauna of the Brazilian Sanga do Cabral Formation. The lithological similarities observed between the Uruguayan Buena Vista and the Brazilian Sanga do Cabral formations, in addition to the fact that both are part of the infilling of the Paraná Basin, strongly suggested that they could be stratigraphic equivalents. Nevertheless, the Uruguayan Colonia Orozco Local Fauna does not seem to be contemporaneous with the Catuçaba Local Fauna of the Brazilian Sanga do Cabral Formation. In particular, their temnospondyls and procolophonoid reptiles show important differences (Piñeiro & Ubilla, 2003; Piñeiro *et al.*, 2004). Thus, *Pintosaurus magnidentis*, at present the only described procolophonoid from the Buena Vista Formation, is more closely allied to the basal representatives known from the Lower Triassic of South Africa and Russia (Piñeiro, 2004; Piñeiro *et al.*, 2004) than to *Procolophon*, the most common taxon in the Catuçaba Local Fauna (Lavina, 1983; Barberena *et al.*, 1985a; Cisneros & Shultz, 2002; Dias-da-Silva *et al.*, 2006; Cisneros, in press).

The temnospondyl composition at the Brazilian Sanga do Cabral Formation includes probable lydekkerinids and rhytidosteids (Lavina & Barberena, 1985; Dias-da-Silva *et al.*, 2005; 2006) which are absent in the Buena Vista fauna. Both groups are widely represented in Early Triassic successions in Gondwana (e.g. Yates & Warren, 2000; Damiani, 2001; Damiani & Yates, 2003) and there is an isolated record of Rhytidosteidae from Upper Permian deposits of Australia (Marsicano & Warren, 1998). This evidence, in addition to the presence of *Procolophon* in the Sanga do Cabral beds, strongly suggest an Early Triassic age for this unit. This is in concordance with the ‘impoverished zone’ or *Procolophon* subzone *sensu* Neveling *et al.* (1999) recognized in the South African Permo-Triassic succession (Cisneros & Shultz, 2002; Dias-da-Silva *et al.*, 2006).

In contrast, the Uruguayan Colonia Orozco fauna includes some temnospondyl taxa that although related to essentially Triassic groups (e.g. Laidleriidae and Mastodontosauridae), they possess several features that locate them in basal positions within those groups (Piñeiro *et al.*, 2007a,b). In addition, the presence in the Colonia Orozco fauna of a temnospondyl probably related to the Russian taxon *Dvinosaurus*, an exclusively Late Permian taxon, indicates that the age of that assemblage is older than the Brazilian fauna and might be placed in the Late Permian or close to the Permian-Triassic boundary.

The chronological hypothesis discussed above is also corroborated by recent radiometric studies on bentonite ashes from the Yaguarí Formation (de Santa Ana *et al.*, 2006), which place this unit in the Middle Permian (269.8 ± 4.7 Ma). Considering its conformable contact with the Buena Vista Formation, an Early Triassic age for the latter unit becomes improbable.

It is important to remark that recent radiometric data from the Upper Paleozoic Brazilian succession revealed older

ages for the constituent units than those previously assigned to them. For instance, zircons from the Irati Formation indicate an Early Permian (Cisuralian) age for this unit (Ventura-Santos *et al.*, 2006) which is significantly older than the Late Permian (old Guadalupian) age traditionally assigned to it (e.g. Daemon & Quadros, 1970). This has resulted in a new stratigraphic scheme where the Rio do Rasto Formation (the unit that stratigraphically underlies the Sanga do Cabral Formation) is placed mostly within the Guadalupian (268.0 ± 0.7 Ma, Middle Permian) (Ventura-Santos *et al.*, 2006), thus contrasting with most previous studies which placed the Rio do Rasto Formation entirely within the Late Permian (e.g. Barberena *et al.*, 1985a; Barberena *et al.*, 1985b; Langer, 2000). The contact between the Rio do Rasto and Sanga do Cabral formations was described as conformable by some authors (Gamermann, 1973; Faccini, 1989), but in more recent studies it has been regarded as not conformable (Scherer *et al.*, 2000; Zerfass *et al.*, 2003). However, this disagreement may be because of 'missing' stratigraphy in some places where the contact is described (Faccini, 1989).

Most of the fossils recovered from both the Sanga do Cabral Formation in Brazil and from the Buena Vista Formation in Uruguay come from intra-formational conglomerate levels present in both units. Two bodies of conglomerates separated by a thin mudstone layer have been described for the Sanga do Cabral Formation by Zerfass *et al.* (2003), correlating the upper body with the fossiliferous *Procolophon* Range Zone from South Africa. Taking into account the differences in faunal composition between the Uruguayan and the Brazilian units, it seems possible that the fossiliferous conglomerates present in the Buena Vista Formation correspond to the lower body, therefore explaining the older age suggested by its tetrapods. As the mapped area of the Sanga do Cabral Formation suggests topographic highs to the west (Zerfass *et al.*, 2003), it is possible that the upper body of conglomerates is not present in Uruguay (César Schultz, pers. comm. 2007). In fact, the isopachic map that includes the Buena Vista Formation shows that it increases its thickness to the northwest portion of the basin, where it attains more than 600 meters thickness (de Santa Ana *et al.*, 2006), contrasting with the sharply erosive processes that can be seen near the Colonia Orozco town, at the eastern part of the basin. That erosion is related to the late Hercynian tectonic activities produced in the inner cratonic Gondwana (Cobbold *et al.*, 1992).

***Lystrosaurus* Assemblage Zone of South Africa.** Permian and Triassic terrestrial strata are represented in the South African Karoo Basin and their fossil vertebrates were the subject of several recent papers (Ward *et al.*, 2000, 2005; Smith & Ward, 2001; Steiner *et al.*, 2003; Smith & Botha, 2005; Botha & Smith, 2006). According to these studies, the uppermost Permian strata (*Dicynodon* Assemblage Zone; Lower Palingkloof Member of the Balfour Formation) have yielded non mammalian therapsids (e.g. *Dicynodon*,

Lystrosaurus maccaigi and *Moschorhinus*), but temnospondyl remains have not been found in that deposits at present. The Early Triassic is represented in several localities by the tetrapods of the *Lystrosaurus* Assemblage Zone (upper Palingkloof Member of the Balfour Formation and the overlying Katberg Formation) where the therapsid *Lystrosaurus* is the most common taxon (Botha & Smith, 2006). However, a lowermost Triassic locality at Barendskraal shows a different faunal composition (Damiani *et al.*, 2003), dominated by basal procolophonoids (Modesto *et al.*, 2001, 2003, Modesto & Damiani, 2007; Reisz & Scott, 2002) and other amniote taxa, but temnospondyls appear still to be absent. With the exception of the dissorophid *Micropholis*, which first record is in the upper Palingkloof Member and the lydekkerinid *Lydekkerina*, which is for the first time recorded in the basal Katberg Formation (Smith & Botha, 2005; Botha & Smith, 2006), the stratigraphic position of the remaining temnospondyl taxa in the Karoo (Rhinesuchidae, Tupilakosauridae, Rhytidosteidae, Mastodonsauridae and Trematosauridae) is poorly constrained (Damiani, 2004). Rhinesuchidae are characteristic in Permian strata, while lydekkerinids (particularly represented by *Lydekkerina huxleyi*) are a conspicuous component of the Lower Triassic beds (Rubidge *et al.*, 1995). None of these taxa have been found in the Colonia Orozco Fauna at present, neither other characteristic Triassic temnospondyls of the Karoo as rhytidosteids, tupilakosaurids and trematosaurids. Despite the Uruguayan mastodonsaurids display a similar morphology to that found in basal Triassic representatives of this group, they appear to be more plesiomorphic (Piñeiro *et al.*, 2007). Nevertheless, this hypothesis needs to be confirmed by the discovery of more complete specimens in the Uruguayan beds.

The Early Triassic Arcadia Formation of Australia. The Permo-Triassic succession in Australia is represented by the Rewan Group, which includes the Upper Permian-lowermost Triassic Sagittarius Sandstone conformably overlaid by the Lower Triassic Arcadia Formation (Warren *et al.*, 2006). The age of the Sagittarius Sandstone is supported by palinological and radiometric data (Foster, 1982; Archbald & Dickens, 1996 in Warren *et al.*, 2006) thus suggesting an earlier Triassic age than that previously proposed for the Arcadia Formation, closer to the P-T boundary (Warren *et al.*, 2006). Nevertheless and according to Warren *et al.*, (2006), the P-T boundary in Australia remains controversial. The recent discovery of the temnospondyl *Lydekkerina huxleyi* in the Arcadia Formation might help to constrain the age of this unit. In South Africa *Lydekkerina* has been recovered from the lower part of the *Lystrosaurus* Assemblage Zone, thus suggesting a probable correlation between the Arcadia Formation and the lower part of the Katberg Formation of South Africa (Warren *et al.*, 2006). This hypothesis is supported by the presence of taxa as the Lapillopsidae, which display a basal position in most recent temnospondyl phylogenies (Yates,

1999; Yates & Warren, 2000) and also by some plesiomorphic representatives of known Triassic groups (Warren *et al.*, 2006).

This situation could be comparable with that seen in the Colonia Orozco fauna, but it remains rather different if we consider that unambiguous Triassic fossil index are absent from the Uruguayan community.

The Vyazniki community from Russia. In Russia, the uppermost Permian is represented in the Vyazniki Community (Vyatkian Horizon) (Sennikov, 1996; Sennikov & Golubev, 2006), which seems to be different to other Late Permian continental faunas from Pangaea (Sennikov, 1996; Sennikov & Golubev, 2006). Tetrapods and other groups from Vyazniki include taxa that are characteristic in Late Permian communities, together with taxa known to be present in the Early Triassic, a feature that was used to infer a transitional status for this Russian assemblage (Sennikov, 1996; Sennikov & Golubev, 2006).

A similar condition is observed for the Colonia Orozco fauna, where a mixture of continental tetrapods including some putative Permian groups (e.g. varanopids and *Dvinosaurus*-type temnospondyls) and earlier components of well established Early Triassic taxa (e.g. Laidleriidae and Mastodontosauridae) are found. Although pareiasaurids have not yet been recovered from the Buena Vista levels, this might not be a relevant difference between both assemblages as this group is considered relictual in the Vyazniki Community, only represented by few elginiid taxa (see Sennikov & Golubev, 2006).

While *Dvinosaurus* is a typical taxon in the Russian Vyazniki Assemblage (Golubev, 2000; Sennikov & Golubev, 2006), it is not registered in the overlying Lower Veltuga Community, which represents the beginning of the Triassic in that area. Thus, the presence of a *Dvinosaurus*-like temnospondyl in the Buena Vista Formation of Uruguay could represent, as for the Russian Vyazniki community, the latest known record of this taxon close to the P-T boundary. It also suggests a dispersal event for dvinosaurians between Russian and South American areas at the end of the Permian, where they could have survived in refuges until the very end of the Permian or even until the beginning of the Triassic.

This biogeographic hypothesis was already established by several authors and largely documented by taxonomical similarities found between Russian and South African therapsids (Ochev & Shishkin, 1989; Milner, 1990; Warren, 1999; Yates & Warren, 2000; Battail, 2000; Sidor *et al.*, 2005; Surkov *et al.*, 2005; Smith *et al.*, 2006; Shishkin *et al.*, 2006).

CONCLUSIONS

Temnospondyls were a conspicuous and abundant component of the Uruguayan Colonia Orozco Fauna, thus contrasting with that observed in the lowermost Triassic of South Africa, where this group of tetrapods was not yet found.

Analyses of the Colonia Orozco temnospondyls show that they include Permian and Triassic lineages, thus suggesting a transitional status for this fauna, as also occurs in the latest Permian Russian Vyazniki Community. Therefore, the previously suggested Permo-Triassic age for the fossiliferous conglomerates of the Buena Vista Formation is also supported by its temnospondyl fauna.

Dvinosaurus-type temnospondyls seem to have been present in the Colonia Orozco Fauna representing the first record of this taxon in Gondwanan areas of Pangaea, and probably its latest known record. Considering both the presence of *Dvinosaurus* in Eastern Europe and *Dvinosaurus*-like temnospondyls in Gondwana, a probable faunal connection between these two geographically distant areas during the Permian is proposed, as it was also inferred by similar therapsid taxa present in both South African and Russian Permo-Triassic deposits.

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