

A NEW LATE TRIASSIC VERTEBRATE ASSEMBLAGE FROM NORTHWESTERN ARGENTINA

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A NEW LATE TRIASSIC VERTEBRATE ASSEMBLAGE FROM NORTHWESTERN ARGENTINA

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Abstract. The Quebrada del Barro Formation (QBF) is part of the continental Marayes-El Carrizal Basin, in NW Argentina. Here we report a diverse faunal assemblage recently discovered in the Quebrada del Barro Formation, along with a preliminary discussion of the taxonomic status and affinities of numerous vertebrate specimens found at two localities where this unit is exposed. The new vertebrate association includes remains of at least 12 different new species related to six major vertebrate groups: Cynodontia, Testudinata, Sphenodontia, Pseudosuchia, Pterosauria, and Dinosauromorpha. The most abundant specimens in this faunal assemblage are opisthodontian sphenodonts, tritheledontid cynodonts and basal sauropodomorph dinosaurs, but the assemblage also includes diagnostic remains of lagerpetid dinosauromorphs, theropods, pterosaurs, basal crocodylomorphs, and stem testudinatan. Several of these groups have also been reported for the Los Colorados Formation (LCF), although the two units differ in their taxonomic content at the species level and in the relative abundance of different taxonomic groups. A comparison of these two faunal assemblage suggest the fauna of QBF is younger than that of LCF and we tentatively assess a late Norian–Rhaetian age for the QBF. Some of the specimens reported here are known from well-preserved specimens and yield important new information for understanding the evolution of these groups, which underscores the relevance of the QBF fauna for assessing the dynamics of the major groups of vertebrates that dominated the terrestrial ecosystems during the early Mesozoic in Pangea.

Key words. Triassic. late Norian. Vertebrate assemblage. Quebrada del Barro Formation.

Resumen. UNA NUEVA ASOCIACIÓN DE VERTEBRADOS DEL TRIÁSICO TARDÍO DEL NOROESTE DE ARGENTINA. La formación Quebrada del Barro (QBF) es parte de la Cuenca continental Marayes-El Carrizal, en el noroeste de Argentina. Acá reportamos una diversa asociación faunística recientemente descubierta en la Formación Quebrada del Barro, junto con una discusión preliminar del estado taxonómico y afinidades de los numerosos especímenes de vertebrados encontrados en dos localidades de esa unidad. La nueva asociación de vertebrados incluye restos de al menos 12 diferentes nuevas especies relacionadas a seis grupos mayores de vertebrados: Cynodontia, Testudinata, Sphenodontia, Pseudosuchia, Pterosauria, and Dinosauromorpha. Los especímenes más abundantes en esta asociación faunística son esfenodontes opisthodontes, cinodontes tritheledontidos y dinosaurios sauropodomorfos basales, pero la asociación también incluye restos diagnósticos de dinosauriomorfos lagerpétidos, terópodos, pterosaurios, crocodylomorfos basales y *stem* testudinales. Varios de estos grupos han sido reportados también para la Formación Los Colorados (LCF), aunque las dos unidades difieren en su contenido taxonómico a nivel específico y en la abundancia relativa de los diferentes grupos taxonómicos. La comparación de estas dos asociaciones faunísticas sugiere que la fauna de QBF es más joven que la de LCF y tentativamente asignamos una edad Noriano–Retiano para QBF. Algunos de los especímenes reportados acá son conocidos por especímenes bien preservados y cuentan con importante nueva información para el entendimiento de la evolución de esos grupos, que pone de manifiesto la relevancia de la fauna de QBF para evaluar la dinámica de grupos de vertebrados mayores que dominaron los ecosistemas terrestres durante el Mesozoico Temprano de Pangea.

Palabras clave. Triásico. Noriano tardío. Asociación de vertebrados. Formación Quebrada del Barro.

THE Upper Triassic Marayes-El Carrizal Basin crops out along southeastern San Juan and northwestern San Luis provinces, NW Argentina between latitudes 31° 21' S and 32° 01' S (Fig. 1). This continental basin holds the Marayes Group (Bossi *et al.*, 1975) which is subdivided, from bottom to top, into four formations: Esquina Colorada, Carrizal,

Quebrada del Barro, and an unnamed unit (Bossi *et al.*, 1975; Colombi *et al.*, 2014).

Since the works of Bossi and collaborators (1975; Bossi, 1976) most research conducted in this Basin was mainly focused on the stratigraphy of the southern outcrops (Rivarola *et al.*, 2002) or on the sedimentology and paleoflora of the

Carrizal Formation (Spalletti *et al.*, 2011; Lutz and Arce, 2013). The first vertebrate record reported for the basin came from the Quebrada del Barro Formation (Bossi and Bonaparte, 1978). This record consists of an incomplete articulated right pes (PVL 4087) of a basal sauropodomorph dinosaur. The cited authors referred PVL 4087 to *Riojasaurus* Bonaparte, 1967, based on its similarities with *Riojasaurus incertus* (Bonaparte, 1967, 1972) from the Norian Los Colorados Formation of the neighbouring Ischigualasto-Villa Unión Basin. In addition, this assignation also allowed them to suggest a Norian age for the Quebrada del Barro Formation (Bossi and Bonaparte, 1978).

Two decades later, during a brief expedition to the uppermost layers of the Quebrada del Barro Formation several specimens of a basal sauropodomorph were discovered showing affinities with the Early Jurassic basal sauropodomorph *Massospondylus* Owen, 1854 (Martínez *et al.*, 2004). A detailed study of the new sauropodomorph confirmed the presence of a new dinosaur species, *Leyesaurus marayensis* (Apaldetti, Martínez, Alcober and Pol, 2011). Based on the close affinities of *Leyesaurus* with the basal sauropodomorph *Adeopapposaurus* Martínez, 2009, as well as with the Early Jurassic *Massospondylus* from South Africa, the authors suggested an Early Jurassic age for the Quebrada del Barro Formation. However, a revision of the southern outcrops of the Quebrada del Barro Formation allowed recognizing that all specimens of *Leyesaurus* found to date were collected from another stratigraphic unit, different from the Quebrada del Barro Formation (Fig. 1.2). This new lithostratigraphic unit, probably of Early Jurassic age, conformably overlies the Quebrada del Barro Formation and is separated by an erosive unconformity from the Cretaceous El Gigante Group (Colombi *et al.*, 2013, 2014). Therefore, the main argument against the Norian age of the Quebrada del Barro Formation originally held by Bossi and Bonaparte (1978) –the presence of *Leyesaurus*, a taxon with Early Jurassic affinities–was no longer valid; thus knowledge of the vertebrate paleontology and age of the Quebrada del Barro Formation still remained unclear.

Recent new discoveries in the Quebrada del Barro Formation have provided an abundant and varied vertebrate fauna that dramatically changed our knowledge and interpretations about the taxonomic content and biostratigraphy of this unit. The new discoveries evidence a vertebrate

association that includes remains of at least 12 different new species related to six main vertebrate groups: Cynodontia, Testudinata, Sphenodontia, Pseudosuchia, Pterosauria, and Dinosauromorpha.

We preliminary report herein the taxonomic content of the Quebrada del Barro Formation. Although a detailed study of each taxon is beyond the scope of this contribution, we briefly report the groups discovered and summarize the relevance of this new, abundant, and diverse vertebrate fauna within the context of currently known Late Triassic vertebrate faunal assemblages from South America.

GEOLOGICAL SETTING

The Marayes-El Carrizal Basin belongs to a series of extensional basins developed along the southwestern edge of Pangaea during the early Mesozoic (Spalletti, 1999) (Fig. 1). This basin was described by Bossi (1976), who defined the Marayes Group based on the previous studies of Borrello (1946), formally naming the (from base to top) Esquina Colorada, Carrizal, and Quebrada del Barro formations. As previously mentioned, a recent evaluation of this sequence revealed that another still unnamed lithostratigraphic unit should be included in the Marayes Group. This unit conformably overlies the Quebrada del Barro Formation (Colombi *et al.*, 2013, 2014). The Marayes Group rests unconformably on the crystalline basement of the Valle Fértil Group (Bossi, 1976), composed mainly by amphibolites and other low and mid-grade metamorphic rocks. In turn, this group is separated by an erosional unconformity from the Cretaceous El Gigante Group (Flores and Criado Roque, 1972).

The Esquina Colorada Formation (Middle Triassic) consists of a sequence of 450–550 m thick fine metamorphic conglomerates, mid-micaceous sandstones and massive diamictites, both red in color, interbedded with tuffaceous levels. This part of the sequence represents distal and partially proximal piedmont facies with anastomosed channels (Bossi, 1971; Bossi *et al.*, 1975). Borrello (1946) mentioned the presence of bone fragments, although this has not been further confirmed. The age was tentatively deemed to be Middle Triassic by correlation with the Chañares, Ischichuca and Los Rastros formations in the Ischigualasto - Villa Union Basin (Yrigoyen and Stover, 1970).

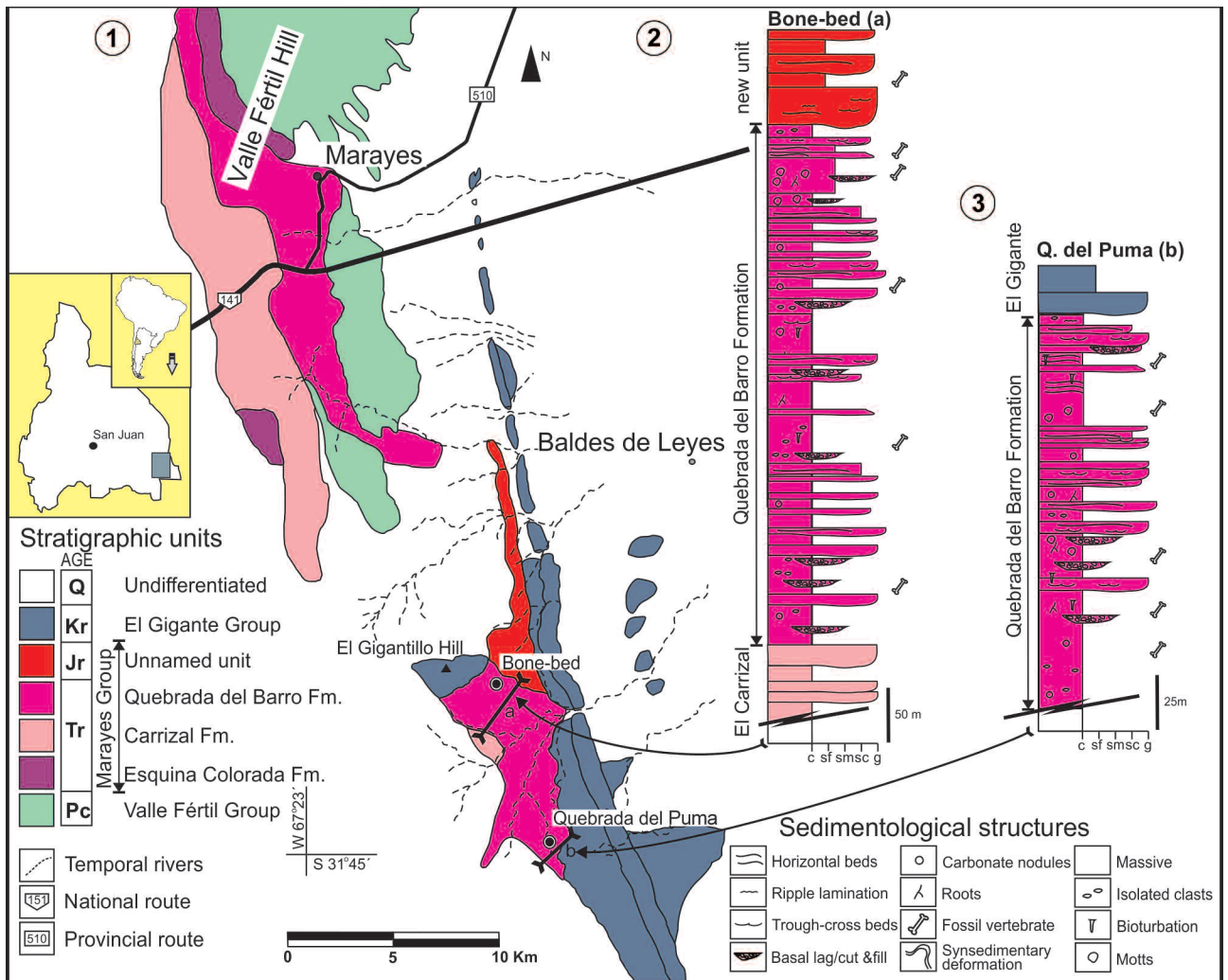


Figure 1. 1–3, Location and geological map of the Marayes-El Carrizal Basin and stratigraphic sections of fossil localities; 1, geological map of the Marayes-El Carrizal Basin; 2, stratigraphic section of the Quebrada del Barro Formation at the “Bone-bed” locality; 3, stratigraphic section of the upper levels of the Quebrada del Barro Formation at the “Quebrada del Puma” locality. Circles indicate the fossil localities sites, (a) Bone bed, and (b) Quebrada del Puma.

The Carrizal Formation (late Carnian–early Norian; Lutz and Arce, 2013) consists of 100 to 350 m of carbonaceous sandstones, conglomeratic sandstones and conglomerates interbedded with siltstone and coal. This unit has been interpreted as a fluvial environment dominated by bed load sediment in the lower portion and mixed river system towards the top (Spalletti *et al.*, 2011). Within this unit, abundant paleofloristic remains corresponding to the *Dicroidium* Flora have been found; these allowed biostratigraphic correlation with the Cortaderitas and Potrerillos formations in the Cuyo Basin (Lutz and Arce, 2013).

The Quebrada del Barro Formation, the focus of this study, has a variable thickness ranging between 600 and

1400 m, and consists of coarse sandstones and conglomerates interbedded with sandy-claystone with sabulitic clasts (Fig. 1). The depositional paleoenvironment has been interpreted as an alluvial fan (Bossi *et al.*, 1975), and as a braided fluvial system (Rivarola *et al.*, 2002). Nevertheless, discrepancies about the interpretation of the facies associations has led to re-interpret the depositional environment as a distributive fluvial system, in which fluvial channels with a large range of sinuosity form a complex deposit with mudflow-dominated floodplains, and terminal splay that are formed by heterolithic sandstone and mudstone accumulations (Colombi *et al.*, 2014). The fossiliferous localities described here include a facies associa-

tion interpreted as deposited by gravel-sand meandering rivers with lateral overflows of mudflow dominating the floodplain formation.

The previously mentioned new unnamed unit that overlies the Quebrada del Barro Formation (Fig. 1.2) consists of a 130 m thick section of channel and floodplain deposits (Colombi *et al.*, 2013, 2014). The sequence is composed of reddish brown coarse sandstone and conglomerate channels interlaid with fine clay-rich mudstones characterized by the development of calcisol. The new unit has been interpreted as the source area of a megafan (Martínez *et al.*, 2013; Colombi *et al.*, 2014). The age of the unit is

suggested to be Early Jurassic based on the presence of the massospondylid sauropodomorph dinosaur *Leyesaurus* (Martínez *et al.*, 2013).

Institutional Abbreviations. PVL, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina; PVSJ, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina.

VERTEBRATE ASSEMBLAGE

The specimens reported here were found during the 2012 and 2014 expeditions to the Quebrada del Barro Formation. A total of 75 specimens of vertebrates were col-

TABLE 1. Vertebrate fossil record of the Quebrada del Barro, Upper Los Colorados, and Caturrita (Faxinal do Soturno) formations.

Group	Number of specimens		
	Q. del Barro Formation	Los Colorados Formation	Faxinal do Soturno
<i>Procolophonidae</i>	—	—	2
<i>Lepidosauriformes</i>	—	—	1
<i>Sphenodontia</i>	84	1	15
<i>Cynodontia</i>	36	4	52
<i>Testudinata</i>	2	3	—
<i>Pseudosuchia</i>	8	18	—
<i>Aetosauria</i>	—	8	—
<i>Ornithosuchidae</i>	—	4	—
"Rauisuchid"	5	1	—
<i>Crocodylomorpha</i>	1	2	—
<i>Protosuchidae</i>	2	3	—
<i>Basal Ornithodira</i>	—	—	2
<i>Pterosauria</i>	2	—	1
<i>Dinosauromorpha</i>	1	—	—
<i>Basal Saurischia</i>	—	—	4
<i>Sauropodomorpha</i>	33	87	—
<i>Theropoda</i>	4	1	—

Record from Quebrada del Barro Formation based on all specimens collected to date. Record from Los Colorados Formation based on data published by Bonaparte (1972, 1980, 1981); Rougier *et al.* (1995); Arcucci and Coria (2003); and specimens collected during the 2003 and 2005 expeditions of the Instituto y Museo de Ciencias Naturales. Record from Faxinal do Soturno based on data published by Bonaparte *et al.* (2010a, 2010b); Arantes *et al.* (2009); Soares *et al.* (2011); Oliveira *et al.* (2010); Langer *et al.* (2010).

lected during the 2012 fieldwork season; 14 of them were found isolated at different stratigraphic levels, and the rest were found concentrated in a stratigraphically and laterally reduced small area of approximately 200 m² –informally called “Bone-bed” locality (Fig. 1.2)– and recently interpreted as a microfossil bone-bed (Colombi *et al.*, 2014). All these specimens belong to four main groups of vertebrates: Sphenodontia, Cynodontia, Dinosauria, and Pseudosuchia. Subsequently, during the 2014 fieldwork a new highly fossiliferous locality was discovered 8 km from the “Bone-bed” locality. This locality, informally known as “Quebrada del Puma” (Fig. 1.3), spreads over 2 km² approximately, exposing the uppermost levels of the Quebrada del Barro Formation. From this area, 113 specimens were collected corresponding to at least six major groups of vertebrates: Cynodontia, Testudinata, Sphenodontia, Pseudosuchia, Pterosauria, and Dinosauromorpha.

Here we review the materials of the six main vertebrate groups collected from both the “Bone-bed” and “Quebrada del Puma” localities of the Quebrada del Barro Formation:

Cynodontia

A total of 36 specimens of cynodonts were collected at both localities, comprising 21% of all findings (Table 1). Most of them are partial skulls, but one of the specimens includes a complete skull with lower jaws and partial postcranial skeleton (PVSJ 901; Fig. 2.1). Some of the cranial and dental features of these specimens (*e.g.*, posterior portion of the secondary palate at the level of the tip of postcanines; middle and posterior lower postcanines with four aligned cusps that decreases in size posteriorly) suggest a close affinity to Tritheledontidae, a group of derived non-mammalian cynodonts closely related to the origin of Mammaliaformes. Preliminary comparative study resulted in the recognition of two different morphotypes or taxa among the collected material, one gracile morph with a short rostrum (PVSJ 901, Fig. 2.1), and another robust one with a long-snout (PVSJ 902, Fig. 2.2). Both morphotypes –or taxa– bear up to 9 upper postcanines and a diastema between the incisors and canine, traits different from those in *Chalimnia musteloides* Bonaparte, 1980 (Martinelli and Rougier, 2007) from the Norian Los Colorados Formation in the neighboring Ischigualasto-Villa Unión Basin. The upper postcanines with a high central bulbous cusp and two smaller cusps on the

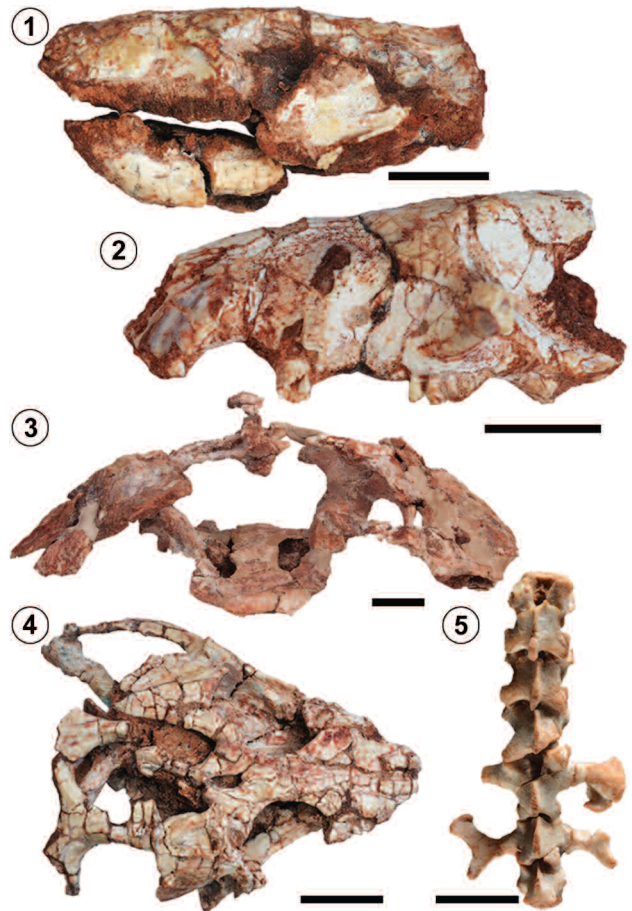


Figure 2. Cynodonts, turtle, and sphenodont from the Quebrada del Barro Formation. 1–2, skull of tritheledontid cynodonts in lateral view; 1, PVSJ 901, short snout specimen; 2, PVSJ 902, long snout specimen; 3, PVSJ 904, articulated pelvis and partial carapace of a stem turtle in anterior view; 4–5, *Sphenotitan leyesi*, PVSJ 900, dorsal view; 4, skull; 5, last three dorsal vertebrae and articulated sacrum. Scale bars= 10 mm (in 1–2 and 5), and 30 mm (in 3–4).

mesiolingual and distolingual edges are similar to *Irajatherium hernandezii* Martinelli, Bonaparte, Schultz and Rubert, 2005, but in the new specimens the cusps B and C are smaller and the roots are not constricted. The absence of lingual and labial cingula on the postcanines also differentiates it from more derived forms such as *Pachygenelus monus* Watson, 1913, and *Tritheledon riconoi* Broom, 1912.

Testudinata

Two partial skeletons and carapaces (PVSJ 903 and PVSJ 904) of turtles were found in different stratigraphic beds of the “Quebrada del Puma” locality. PVSJ 903 includes a partial dorsal carapace and plastron, sacral vertebrae and both scapula-coracoids, whereas PVSJ 904 includes a partial dor-

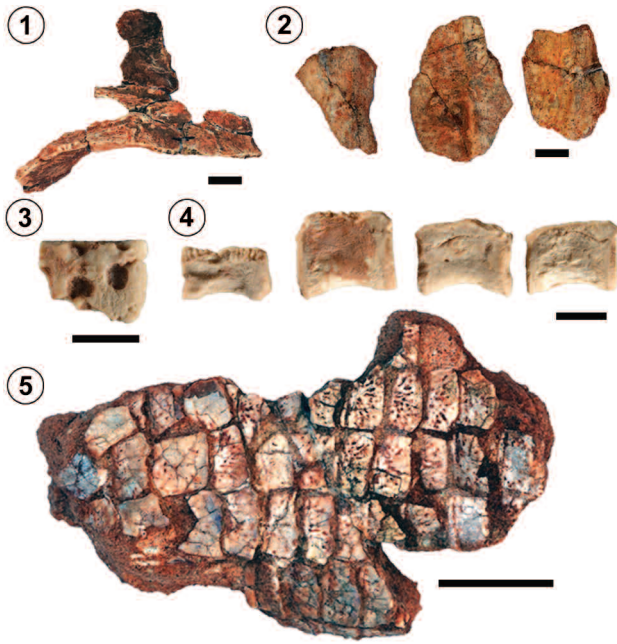


Figure 3. Pseudosuchia remains from the Quebrada del Barro Formation. 1–2, PVSJ 909, bones of putative “rauisuchid” pseudosuchian; 1, fragments of the skull; 2, three partial scutes; 3–4, PVSJ 912, remains of a putative “sphenosuchid” pseudosuchian; 3, fragment of dorsal scute in dorsal view; 4, a cervical and three dorsal body vertebrae in right lateral view; 5, PVSJ 910, partial articulated armor of a crocodyliform in ventral view. Scale bars= 20 mm (in 1–2), and 10 mm (in 3–5).

sal carapace, sacrum, and a fully articulated pelvis (Fig. 2.3). The similarity between carapaces and size suggests both specimens belong to the same species. The plesiomorphic morphological features of the scapula–coracoid of PVSJ 903 (e.g., short acromial process of scapula, almost closed coracoid foramen) suggest that the new specimens from the Quebrada del Barro Formation may belong to a basal stem turtle. These specimens differ from *Palaeochersis talampayensis* Rougier, De La Fuente and Arcucci, 1995 (Sterli *et al.*, 2007) from the Los Colorados Formation, which has a more plesiomorphic configuration of the scapular girdle (closed coracoid foramen and shorter acromial process of scapula).

Sphenodontia

The specimens of this group are the most abundant component at the two fossil localities, comprising 50% of all findings (Table 1). All specimens collected in 2012 were fragmentary skulls and jaws, although with enough

information to nominate a new taxon, *Sphenotitan leyesi* (Martínez, Apaldetti, Colombi, Praderio, Fernández, Santi Malnis, Correa, Abelin and Alcober 2013). *Sphenotitan* is a basal opisthodontid sphenodontian and represents the only species from the Quebrada del Barro Formation that has been formally described to date. During the 2014 fieldwork season, new sphenodontian materials were found, including a complete skull and a partial postcranial skeleton (PVSJ 900; Fig. 2.4–5). The skull features (e.g., large supratemporal fenestra, large quadrate–quadratojugal foramen, straight orbital border of the maxilla, long posterior maxillary teeth, wide dentary additional teeth) allow us assigning PVSJ 900 to the basal opisthodontian *Sphenotitan*. The well-preserved and fully articulated skull, as well as the postcranial remains of this new specimen, complete previous knowledge of the morphology of *Sphenotitan* and will provide a better understanding on the origin of herbivory in Sphenodontia.

Pseudosuchia

Several pseudosuchian specimens were collected at both localities (Fig. 3). Due to the fragmentary nature of the material, they can only be tentatively assigned to two different groups or grades: “rauisuchid” and Crocodylomorpha.

“Rauisuchid”. Few fragments including a partial skull and three partial osteoderms (PVSJ 909) were found at the “Quebrada del Puma” locality (Fig. 3.1–2). Although incomplete, the morphology (asymmetrical, roughly leaf-shaped, dorsally located keel) of the osteoderms are similar to that observed in “rauisuchids” (e.g., *Saurosuchus gallei* Reig, 1959; *Rauisuchus tiradentes* Huene, 1938; Lautenschlager and Rauhut, 2015). The size of the osteoderms is much smaller than in those of *Fasolasuchus* Bonaparte, 1981, from the Los Colorados Formation, but the scarce and poorly preserved material does not show enough details for a more precise taxonomic identification.

Crocodylomorpha. Three specimens of crocodylomorphs have been collected from both localities. One of the specimens, recovered from the “Bone-bed” locality, consists of a partial dorsal osteoderm and several centra of cervical and dorsal vertebrae (PVSJ 912; Fig. 3.3–4). The morphology of the vertebrae (e.g., cervical centra with anterior articular surface more concave than the posterior one, and ventrally keeled) resemble the condition observed in *Pseudhesperosuchus jachaleri* Bonaparte, 1972. The ornamentation of the

only preserved osteoderm (evenly distributed circular pits) is similar to that present in an unpublished specimen of a putative “sphenosuchid” (PVSJ 2003 20) from the Los Colorados Formation, although closer affinities with more derived crocodyliforms may also be suggested for this specimen. The other two specimens were collected at the “Quebrada del Puma” locality. Both specimens correspond to small animals and consist of an articulated partial armor with bones inside (PVSJ 910; Fig. 3.5) and fragments of vertebrae, armor, and few long bones (PVSJ 911). The size and morphology of the armor, with six? rows of small and sub-square ventral scutes and two rows of large and rectangular dorsal scutes are concordant with those of protosuchids, although more preparation and detailed study are necessary to confirm the accuracy of this assignation, or its affinity with *Hemiprotosuchus leali* Bonaparte, 1972, from the Los Colorados Formation.

Ornithodira

Two pterosaurian specimens and several dinosauromorphs were collected at both localities (Fig. 4). The dinosauromorph remains belong to a non-dinosauriform dinosauromorph, four specimens of theropods and several specimens of basal sauropodomorph dinosaurs.

Pterosauria. Two pterosaur specimens were found; a rostral portion of a small skull with the anterior end of both maxillae and posterior end of both premaxillae, and an isolated and fragmentary long bone (PVSJ 914 and PVSJ 913, Fig. 4.1–2). The specimens were collected at the “Quebrada del Puma” and “Bone-bed” localities, respectively. PVSJ 913 is tentatively assigned to a proximal end of a right ulna (Fig. 4.2). The other specimen is part of an elongated snout (PVSJ 914, Fig. 4.1) characterized by trabeculate bone section, parallel lateral borders of maxillae and premaxillae, medial fusion of maxillae and premaxillae, presence of premaxillary crest, and regular separation between the teeth. This suite of characters allows us to identify PVSJ 914 as a pterosaur, although the absence of diagnostic characters at this point precludes reaching a more accurate taxonomic identification.

Non-dinosauriform dinosauromorph. One specimen including a proximal and a distal end of the left femur (PVSJ 898) was collected at the “Quebrada del Puma” locality (Fig. 4.3). This specimen was recently interpreted as a new lagerpetid

taxon (Martinez *et al.*, in press) and depicted in a phylogenetic analysis as more derived than *Lagerpeton chanarensis* Romer, 1971, nested within the genus *Dromomeron* (previously known only from Norian beds of North America; Irmis *et al.*, 2007 and Nesbitt *et al.*, 2009).

Theropod dinosaur. Four theropod specimens were collected at the “Quebrada del Puma” locality. The specimens are represented by a partial series of articulated cervical vertebrae (from the 2nd to the 10th; Fig. 4.4), several dorsals, and sacrum articulated to the pelvis (PVSJ 906), a partial sacrum (PVSJ 1013), a sacrum and articulated pelvis (PVSJ 899; Fig. 4.5), and proximal end of a right tibia (PVSJ 1004). The absence of any difference among the overlapping material suggests the four specimens may belong to the same species, and several features (*e.g.*, long cervical vertebrae with pleurocoels, long cervical ribs, sacrum with 5 fused vertebrae) suggest it may represent a new coelophysoid theropod. Unfortunately, these specimens lack equivalent bones to those of the putative coelophysoid from the Los Colorados Formation, *Zupaysaurus rougieri* Arcucci and Coria, 2003 (Ezcurra and Novas, 2007), precluding a comparison with this taxon. Nevertheless, all the coelophysoid specimens from the Quebrada del Barro Formation are significantly smaller than *Zupaysaurus*.

Sauropodomorph dinosaurs. Several sauropodomorph specimens were collected at both fossil localities, all of them represented by partial skeletons without skulls. Most sauropodomorph specimens collected at both localities show anatomical features related to basal forms (*e.g.*, short neural arches, subrectangular astragalus in proximal view; Fig. 4.8–9). These materials (PVSJ 907, PVSJ 959) however show differences with *Riojasaurus* from the Los Colorados Formation, such as the protruding anteromedial corner of the astragalus (Fig. 4.8–9), larger pubic foramen (Fig. 4.7), and taller ilium (Fig. 4.6). One of the most complete specimens consists of cervical and dorsal vertebrae, humerus, radio, ulna, manual phalanges, femur, partial tibia, astragalus and a complete pes (PVSJ 908, Fig. 4.10–14). Several anatomical features such as tall neural arches (Fig. 4.11), fourth trochanter located at mid-shaft of the femur (Fig. 4.12), sub-triangular astragalus in proximal view (Fig. 4.13), highly reduced manus and pes (Fig. 4.10, 14) indicate affinities with basal sauropods. The last two traits mentioned above are features more derived than *Lessemsaurus*

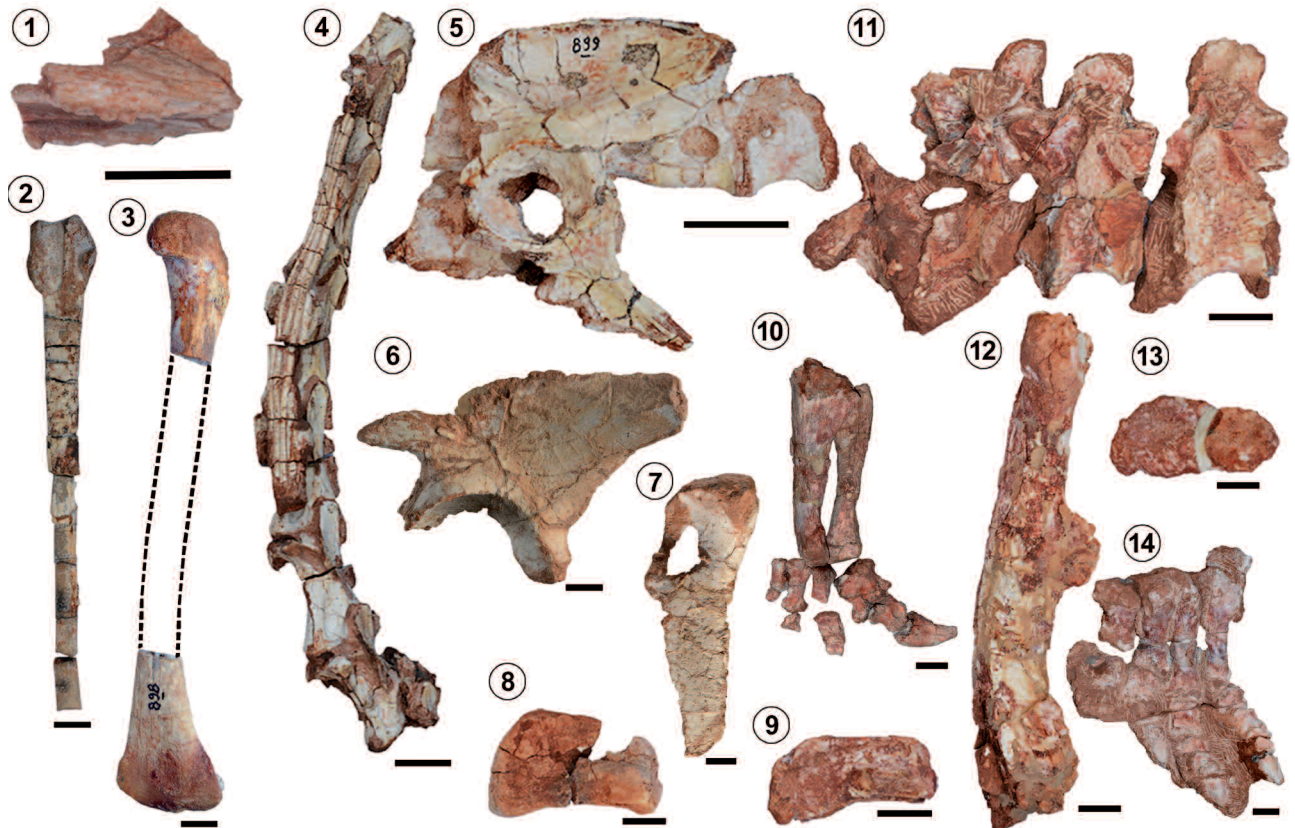


Figure 4. Ornithodira remains from the Quebrada del Barro Formation. 1–2, bones of putative pterosaur; 1, PVSJ 914, fragment of snout in right lateral view; 2, PVSJ 913, proximal half of a right ulna, medial view; 3, PVSJ 898, proximal and distal ends of the left femur of a lagerpetid dinosaur, anterolateral view; 4–5, theropod dinosaurs; 4, PVSJ 906, articulated anterior cervical vertebrae, right lateral view; 5, PVSJ 899, articulated sacrum and pelvis, left lateral view; 6–9, basal sauropodomorphs; 6–7, PVSJ 959, 6, left ilium, lateral view; 7, left pubis, anteromedial view; 8, PVSJ 907, right astragalum, proximal view; 9, PVSJ 980, left astragalum, proximal view; 10–14, PVSJ 908, basal sauropod; 10, right forelimb, anterodorsal view; 11, articulated mid-dorsal vertebrae, left lateral view; 12, right femur, anteromedial view; 13, astragalum, proximal view; 14, left pes, anterodorsal view. Scale bars= 10 mm (in 1–3) and 30 mm (in 4–11).

sauropoides Bonaparte, 1999, from the Los Colorados Formation. Although in *Lessemsaurus* the phalanges are shorter than in other more basal sauropodomorphs, in PVSJ 908 the phalanges are significantly shorter. The reduced manus of PVSJ 908 is a feature similar to that of *Melanorosaurus readi* Haughton, 1924 (Bonnan and Yates, 2007) and the pes is short as is that of *Blikanasaurus cromptoni* Galton and van Heerden, 1985.

DISCUSSION

Age of the Quebrada del Barro vertebrate assemblage

The specimens listed above indicate a typical faunal assemblage from the Late Triassic, showing particular similarities to the Norian “La Esquina” fauna of the Los Colorados Formation in the neighboring Ischigualasto-Villa Unión Basin (Bonaparte, 1972, 1973). Nevertheless, the

available data reveals that both formations –Quebrada del Barro and Los Colorados– share the presence of five out of the six major vertebrate groups, but their taxonomic composition and the relative abundance of these groups differ in both faunas.

Although the incompleteness and lack of diagnostic characters in some specimens (*i.e.*, the crocodylomorphs, “rauisuchid”) preclude comparing the faunas at the species level in some of the groups, other specimens bear diagnostic features (*e.g.*, cynodonts, turtles, sauropodomorph dinosaurs) that clearly distinguish the taxa from both formations. For example, the tritheledontid specimens found in the Quebrada del Barro Formation differ from *Chalimnia* from the Los Colorados Formation (Bonaparte, 1980; Martinelli and Rougier, 2007) by having up to 9 upper postcanines and the presence of a diastema between incisive

and canine. The stem turtle (PVSJ 903, PVSJ 904) shows a more derived pectoral girdle than *Palaeochersis* from the Los Colorados Formation (Sterli *et al.*, 2007) because it has a slightly longer acromial process and an open coracoid foramen. The basal sauropodomorph (PVSJ 907) is different from *Riojasaurus* (*i.e.*, the former specimen has larger pubic foramen, taller ilium, and protruding anteromedial corner of the astragalus). The other sauropodomorph specimen (PVSJ 908), tentatively interpreted as a basal sauropod, has very reduced manus and pes (Fig. 4.10–14), traits that are more derived than those of *Lessemsaurus* (Pol and Powell, 2007).

Further distinctions between the two faunal assemblages are centered on the presence/absence of some specific major clades or their relative abundance. Some of the new taxa discovered in the Quebrada del Barro Formation belong to clades so far unknown (*e.g.*, pterosaurs, lagerpetid dinosauromorphs) in the Los Colorados Formation. The absence of some vertebrate groups in the latter unit is not surprising considering the rarity and overall poor fossil record of pterosaurs and lagerpetid dinosauromorphs. Conversely, aetosaurs are present in the Los Colorados Formation but absent in the Quebrada del Barro Formation.

Furthermore, a striking difference is found in the relative abundance of different taxonomic groups (Table 1; Fig. 5). Sphenodontians and coelophysoid theropods are remarkably scarce in the Los Colorados Formation (one specimen of each group) but are abundant in the Quebrada del Barro Formation (84 specimens of sphenodontians and four specimens of coelophysoids). In the Quebrada del Barro Formation the most abundant component are the sphenodontians (50%) followed by the tritheledontids (21%) and sauropodomorphs (19%), whereas in the Los Colorados Formation sauropodomorphs represent more than 76% of the recorded specimens, followed by aetosaurs (7%), and tritheledontids are rare (2%) (Figs. 5.1–2).

The differences noted above between the faunal assem-

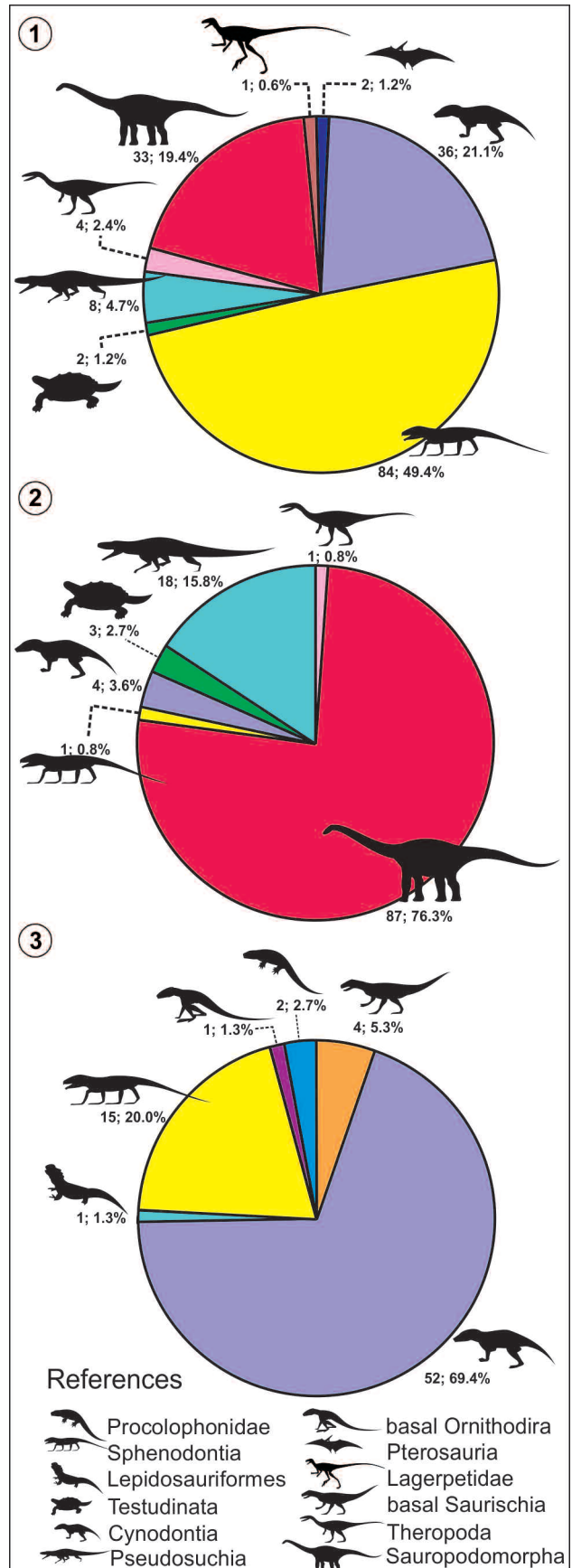


Figure 5. 1–3, Comparative pie charts summarizing relative abundance of specimens for each major group of vertebrates in three South American Norian faunal assemblages; 1, Quebrada del Barro Formation assemblage; 2, Upper Los Colorados Formation assemblage; 3, Caturrita Formation at Faximal do Soturno locality assemblage.

blages of the Los Colorados and Quebrada del Barro formations suggest that they do not seem to be contemporary. The absence of aetosaurs and the presence of basal sauropods and more derived forms of turtles could indicate that the faunal assemblage of the Quebrada del Barro Formation may be younger than that one from the Los Colorados Formation.

In a regional context, the other Late Triassic vertebrate assemblage in which the most abundant components are sphenodontians and cynodonts is the fauna of Faxinal do Soturno (Bonaparte *et al.*, 2010b) from middle beds of the Caturrita Formation in Brazil. Based on the vertebrate components, Bonaparte *et al.* (2010b) suggested this fauna was early Norian in age –younger than the Ischigualasto but older than the upper Los Colorados faunas. Although cynodonts and sphenodontians are abundant in both faunas, the relative abundance of each group is different (Fig. 5). In fact, several aspects of the Faxinal do Soturno assemblage are quite different: 1) in Faxinal do Soturno, cynodonts are the most abundant specimens (69%), followed by the sphenodontians (20%), while in Quebrada del Barro the most abundant are sphenodontians followed by cynodonts and sauropodomorphs; 2) absence of derived basal sauropodomorphs; 3) presence of scarce basal saurischian dinosaurs and absence of more derived coelophysoid theropods; 4) presence of procolophonids and lepidosauriforms; 5) the sphenodontians are basal forms rather than the derived opisthodontid sphenodontians from the Quebrada del Barro Formation (Martínez *et al.*, 2013); and 6) absence of turtles, “rauisuchids”, and crocodylomorphs. Some of the aforementioned differences (items 2, 3, and 5) clearly support the older age proposed by Bonaparte *et al.* (2010b) for the Faxinal do Soturno fauna in comparison with the Los Colorados fauna, which also evidences that the Faxinal do Soturno faunal association is older than the Quebrada del Barro Formation assemblage. Consequently, we propose here that the new findings support the late Norian–Rhaetian age for the Quebrada del Barro Formation.

Significance of the new faunal assemblage

The new faunal assemblage from the Quebrada del Barro Formation is significant given the relative rarity of latest Triassic vertebrate continental assemblages, especially as it shows a taxonomic composition that differs from

previously known South American assemblages. Furthermore, the new fauna has a major biogeographic importance for some taxonomic groups. For instance, (i) the lagerpetid dinosauiromorph (PVSJ 898) is the first record of a non-dinosauriform dinosauiromorph from the Norian in the Southern Hemisphere; (ii) the coelophysoid theropod specimens (PVSJ 899, 1013, 906, 1004) increase our limited knowledge on the abundance of this group in South America, and finally, (iii) the pterosaur presented here (PVSJ 913, 914) is the first Triassic record for the Southern Hemisphere, except for the putative pterosaur *Faxinalipterus minima* (Bonaparte *et al.*, 2010a) from the Caturrita Formation (southern Brazil), which has been reconsidered as a non-pterosaur in recent studies (Dalla Vecchia, 2013; Soares *et al.*, 2013).

Summarizing, the specimens listed here represent new cynodont, archosaur, and lepidosauriform taxa that will provide additional information on the diversity of these three major groups of vertebrates during the Late Triassic in South America. This underscores the importance of the Quebrada del Barro Formation fauna for understanding the evolution of the major groups of vertebrates that dominated terrestrial ecosystems during the Early Mesozoic across Pangea.

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