



Original article

Tetrapod association and palaeoenvironment
of the Los Colorados Formation (Argentina):
a significant sample from Western Gondwana at the end of the Triassic

Association de tétrapodes et paléoenvironnement
de la Formation Los Colorados (Argentina):
un échantillon significatif de l'ouest du Gondwana à la fin du Trias

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Abstract

The Los Colorados Formation constitutes a continuous continental succession deposited in Western Argentina during the Late Triassic, a time period that is crucial to the record of the faunistic turnover at the Triassic–Jurassic boundary. Many authors have pointed out that its rich tetrapod fauna represents a unique transitional assemblage with elements typical of both Late Triassic and Early Jurassic. However, the possibility that the fauna represented a mixture of Triassic and Jurassic horizons was also proposed. Recently, stratigraphic control of the fossiliferous levels was developed in order to correlate the different localities of the extense Los Colorados outcrops, and a revision of the taxonomic status of most tetrapods recovered is currently undergoing. Preliminary results confirm previous assumptions about the transitional nature of the assemblage where typical Triassic taxa are associated with dinosaur groups known from Early Jurassic levels in other Gondwanan areas. The fossiliferous levels of the upper third of the sequence included several basal archosaurs (aetosaurus, rauisuchids, sphenosuchians), protosuchian crocodiles, dinosaurs (sauropodomorphs, tetanuran theropods), derived therapsids and primitive chelonians. New evidence about tetrapod ichnites of chirotheroid affinities is added to the fossiliferous association.

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Résumé

La Formation Los Colorados constitue une succession continentale continue déposée à l'ouest de l'Argentine pendant le Trias terminal, et une période cruciale pour l'enregistrement des changements faunistiques à la limite Trias–Jurassique. De nombreux auteurs ont établi que cette faune riche en tétrapodes représente un assemblage unique de transition avec des éléments typiques à la fois du Trias terminal et du Jurassique inférieur. Cependant, il a été aussi proposé que la faune représentée soit un mélange d'éléments du Trias et du Jurassique. Plus récemment, il a été établi un contrôle stratigraphique des niveaux fossilifères pour établir la corrélation entre les différentes localités du grand affleurement de Los Colorados ainsi qu'une révision du statut taxonomique de la plupart des tétrapodes rencontrés. Les résultats préliminaires confirment les hypothèses sur la nature transitionnelle de l'ensemble dans lequel les taxa typiques du Trias sont associés avec des groupes des dinosaures connus au début du Jurassique en d'autres régions du Gondwana. Les niveaux fossilifères du tiers supérieur de la séquence contiennent

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différents archosauriens (aetosauriens, raiusuchides, sphénosuchiens), des crocodiles protosuchiens, des dinosaures (prosauropodiens et tetanuriens), des tétrapsides dérivés et des chéloniens primitifs. De nouvelles données sur des pistes de tétrapodes (à affinités chirothéroïde) s'ajoutent à l'association fossile.

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Mots clés : Trias terminal ; Archosauriens ; Los Colorados ; Paléoenvironnements ; Pistes de chirothéroïdes

1. Introduction

Between the end of the Paleozoic and the beginning of the Triassic, several extensional depocenters were formed along the western margin of southern South America related to events associated with the pre-breakup of Gondwana (Uliana and Biddle, 1988). One of these depocenters, the Triassic Ischigualasto-Villa Unión Basin (Stipanovic and Bonaparte, 1972), is located in central-western Argentina (San Juan and La Rioja Provinces) and was filled by a thick entirely non-marine and predominantly fluvial and lacustrine succession. The uppermost part of the succession are redbeds deposited by fluvial systems during the Late Triassic, and it is included in the Los Colorados Formation.

The importance of the Los Colorados levels, as some of the underlying units (Ischigualasto and Chañares formations), is their exceptional tetrapod record represented by both body fossils and tracks. The vertebrate association includes several basal archosaurs (aetosaurus, raiusuchids, sphenosuchians), protosuchian crocodiles, derived dinosaurs (sauropodomorphs, tetanuran theropods), primitive chelonians and therapsids (Bonaparte, 1960, 1966b, 1971, 1980; Rougier et al., 1995; Arcucci and Coria, 1998; Caselli et al., 2001).

Some authors have pointed out that this rich tetrapod fauna represents a unique transitional assemblage with elements typical of both Late Triassic and Early Jurassic. However, the possibility that the fauna represents a mixture of horizons of different age was also proposed (Olsen and Sues, 1986; Shubin and Sues, 1991; Lucas, 1998). This rich association contrasts with previous interpretations of the depositional setting as ephemeral rivers and dunes developed in an arid climate and supported by a poor paleofloristic record (Lopez Gamundi et al., 1989; Milana and Alcober, 1994; Bracco et al., 1996; Cladera et al., 1998).

In the present paper, the stratigraphy of the Los Colorados unit is analyzed in order to correlate the different tetrapod-bearing levels along its widespread exposures. Thus, previous assumptions about the transitional nature of the assemblage (or if it represents a mixture of horizons of different age) are discussed. Moreover, a new interpretation of the depositional setting of the Los Colorados Formation and the climatic conditions during deposition from both sedimentological and paleontological data is presented.

2. Geological setting

The Ischigualasto-Villa Unión Basin was interpreted as growth-fault half-graben model (Milana and Alcober, 1994) and up to 4000 m of non-marine Triassic rocks are preserved within the basin. They are well exposed along the border between the San Juan and La Rioja Provinces and the best-known outcrops are those located in the Ischigualasto Provincial Park (San Juan Province) and Talampaya National Park (La Rioja Province). At the base, the red beds of the Early? Triassic Talampaya and Tarjados formations (Romer and Jensen, 1966) unconformably overlie Palaeozoic deposits. This sequence is overlain at a regional unconformity by the Agua de La Peña Group (Rogers et al., 2001), which it is divided into five units. The lower Chañares Formation is dominated by tuffaceous sandstones and siltstones deposited in a fluvial-lacustrine environment that grades upward into the lacustrine black shales and deltaic sandstones of Ischichuca/Los Rastros formations. This sequence passes upward into the sandstones, mudstones and tuffs of Ischigualasto Formation deposited by a moderate- to high-sinuosity river system. Finally, the succession culminates with the red beds of the Los Colorados Formation. The Triassic sequence is unconformably covered by the Cerro Rajado Formation (?Cretaceous) and Miocene rocks (Stipanovic and Bonaparte, 1979; Parker, 1974; Malizzia, 1989).

Los Colorados Formation is well exposed along the eastern side of the Sierra Morada range, Cerro Rajado and Cerro Bola (Fig. 1), with an average thickness of 700 m (Bracco et al., 1996; Bossi, 1970). The basal contact of Los Colorados unit with the Ischigualasto Formation was interpreted both as an angular unconformity (Lopez Gamundi et al., 1989) and as an concordant erosive unconformity (Yrigoyen and Stover, 1970; Stipanovic and Bonaparte, 1979; Milana and Alcober, 1994). The Los Colorados Formation is unconformably overlain by the fluvial conglomerates and sandstones of the putative Cretaceous Cerro Rajado Formation (Bossi, 1977; Stipanovic and Bonaparte, 1979; Lopez Gamundi et al., 1989). Nearby to Cerro Rajado locality, Los Colorados unit is directly overlain by Tertiary sandstones in angular unconformity (Malizzia, 1989).

The red beds of Los Colorados Formation are composed by successive thinning-upward cycles characterized by coarse- to medium-grained sandstones and fine-grained sandstones intercalated with siltstones, which progressively

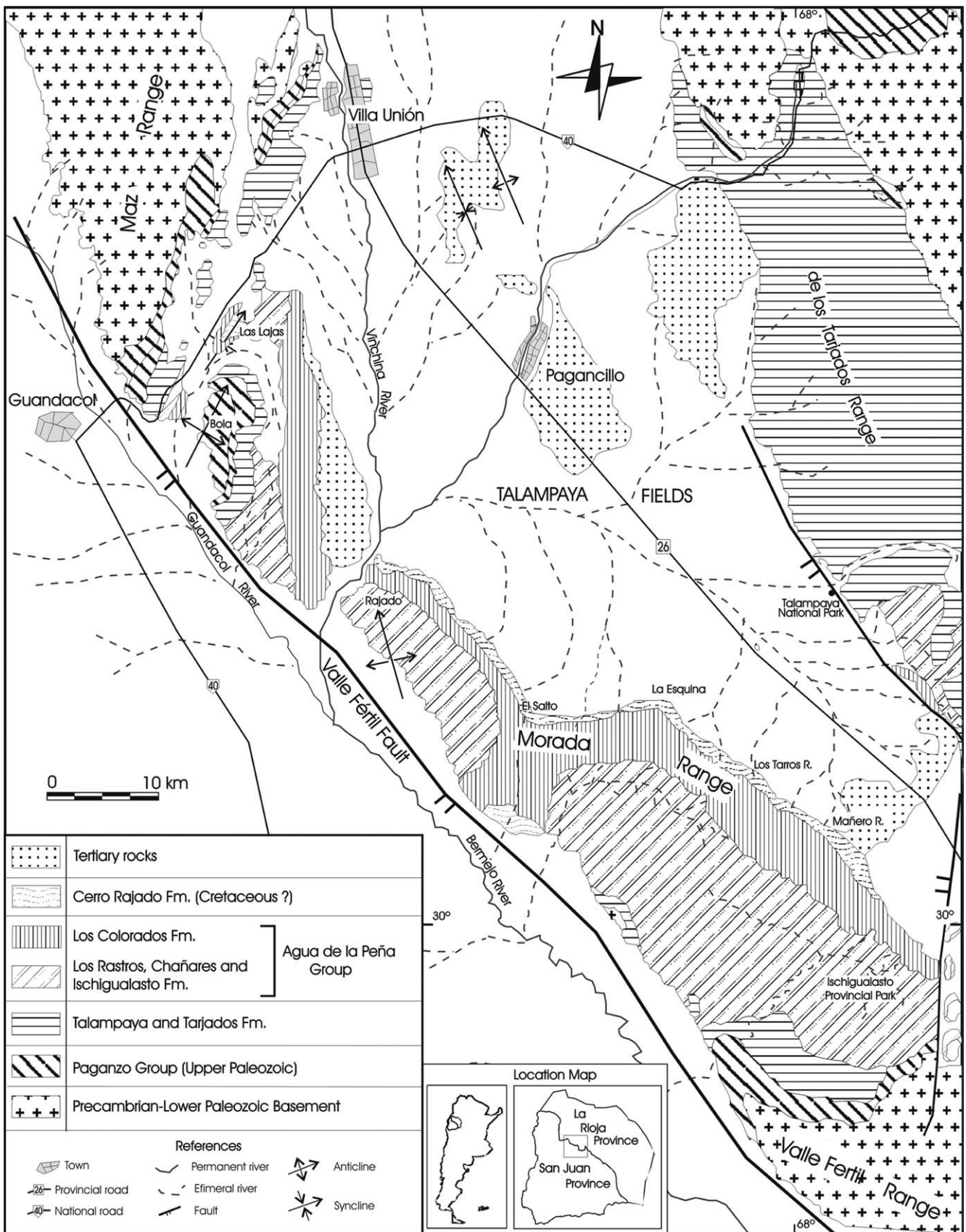


Fig. 1. Geological map of the Ischigualasto-Villa Union Basin outcrops, San Juan and La Rioja Provinces, NW Argentina.

Fig. 1. Carte géologique des affleurements du bassin Ischigualasto-Villa Union, provinces de San Juan et de La Rioja, NW Argentine.

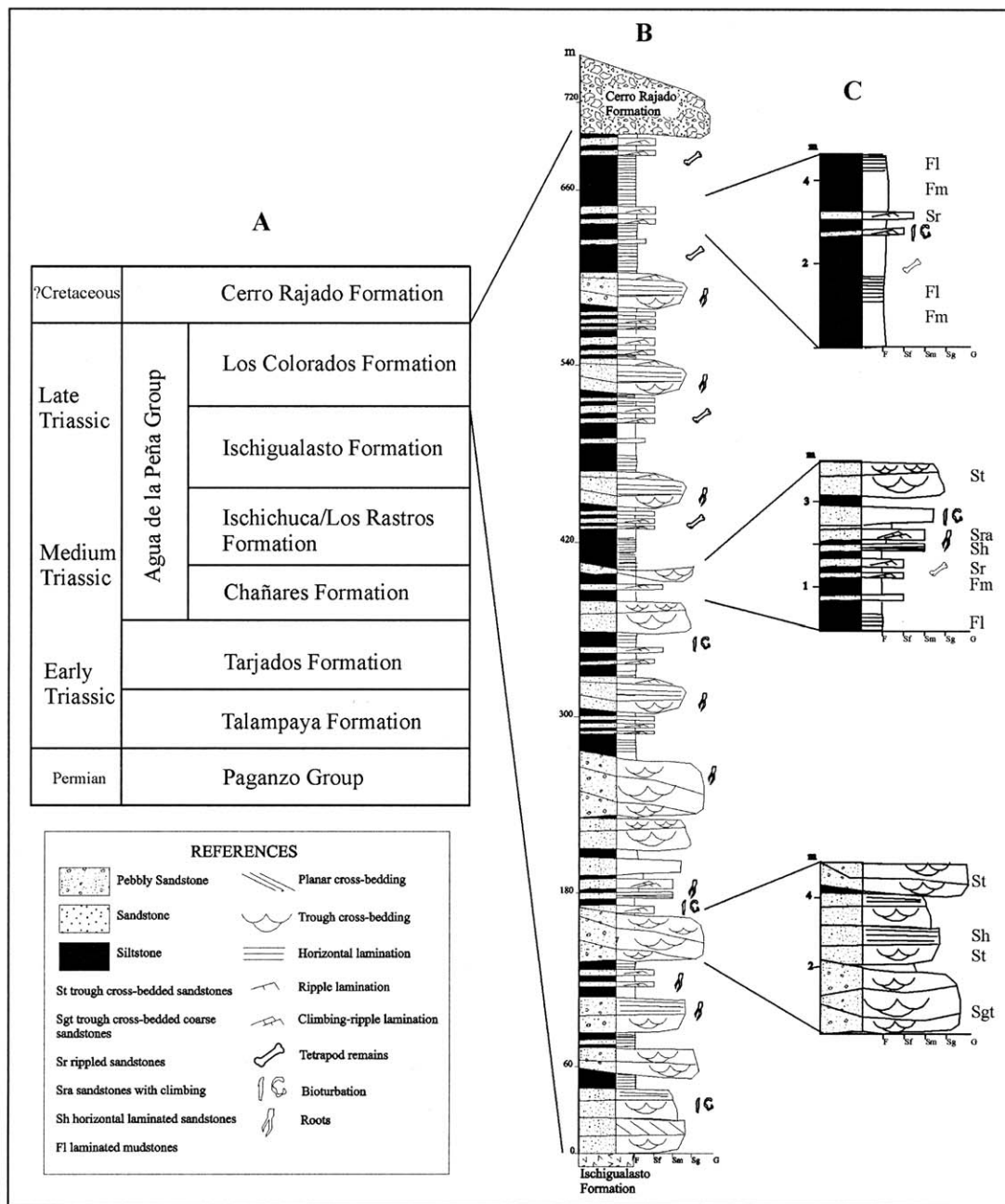


Fig. 2. (A) Lithostratigraphy of the Ischigualasto-Villa Unión Basin. (B) Generalized sedimentological section of Los Colorados Formation. (C) Detail of the facies recognized in the sequence.

Fig. 2. (A) Lithostratigraphie du bassin d'Ischigualasto-Villa Unión. (B) Coupe sédimentologique schématisée de la Formation de Los Colorados. (C) Détails des faciès reconnus dans la séquence.

dominate to the upper part of the unit (Fig. 2). Coarse-grained sandstone beds are generally tabular in geometry, cross stratified (large-scale trough and tabular cross-bedding) and locally display horizontal lamination. Rounded pebbles and cobbles of chert, quartzite and metamorphic rocks commonly mantle set boundaries. Massive and horizontal laminated siltstones interfinger with rippled lamination fine-grained sandstones forms the uppermost portion of the cycles (Caselli et al., 2001).

The sequence was interpreted as deposited by moderately sinuous fluvial systems, which laterally interfinger with

and grade into horizontally bedded flood-plain deposits. To the top of the sequence, thin-bedded sandstones and siltstones dominate and were deposited in ponds and as crevasse splays in overbank settings (Caselli et al., 2001). Previously, other authors indicated that Los Colorados succession was deposited by both sand dominated fluvial system with alluvial plains (Bossi, 1971; Stipanovic and Bonaparte, 1979) and ephemeral stream sandstones with intercalated aeolian dunes (Lopez Gamundi et al., 1989; Cladera et al., 1998) under arid climatic conditions (Milana and Alcober, 1994).

3. Paleontology of the Los Colorados Formation

The first description of floral fossil remains from Los Colorados Formation were poorly preserved trunks from the basal levels of the sequence, identified as “araucarioid like” (Brett, 1968). Posteriorly, the presence of putative *Cladophlebis* impressions (Stipanovic and Bonaparte, 1979) and “*Rhexoxylon*” remains (Bonaparte, 1997) were only mentioned in the literature. Recently, numerous vertical tubes in fine sandstones (with approximately 1.5 m deep and 0.30 m diameter) were tentatively attributed to roots traces of medium sized trees (Caselli et al., 2001).

The vertebrate record of the Los Colorados unit is, until now, restricted to tetrapods (Table 1; Fig. 3), which were exhumated generally as isolated skeletons, partially or completely articulated. The preservation of the material is not particularly good, but the light gray-white color of the bone

easily distinguished it from the red sediments. Most of the findings come from the upper levels of the sequence, but there are a few records from the basal part from two different localities, La Chilca’s Creek near El Salto, and from the most southern outcrops in the Hoyada de Ischigualasto, NW of Cerro Morado. There is just one record of an indeterminate archosaur from the “medium levels” in the same area (Bonaparte, 1997).

Tetrapod records from the basal part of the sequence include a complete skull of the dicynodont *Jachaleria* (Bonaparte, 1966), a medium sized quadruped herbivorous, and it is probably related with *Ischigualastia*, another dicynodont taxon well known from the Ischigualasto Formation (Bonaparte, 1997). *Jachaleria* represents the youngest record of dicynodonts in South America. Additional disarticulated skeletons of dicynodonts and archosaurs (probably

Table 1

List of tetrapods collected from Los Colorados Formation. The material mentioned is housed in the collections of the National University of Tucuman (Fac. De Cs Naturales e Instituto Miguel Lillo: PVL), the National University of La Rioja (Museo de Cs. Naturales: PULR) and the National University of San Juan (USJ) Liste des tetrapods récoltés dans la Formation de Los Colorados. Le matériel décrit se trouve dans les collections de: National University of Tucuman (Fac. De Cs Naturales e Instituto Miguel Lillo: PVL); National University of La Rioja (Museo de Cs. Naturales: PULR); National University of San Juan (USJ)

TAXA	LOCALITY	ORIGINAL REFERENCE
Anapsida		
Chelonia		
<i>Paleochersis talampayensis</i>	NW of La Esquina and SE of El Salto (La Rioja)	Rougier et al. (1995)
Archosauria		
Archosauria indet.	Heads of La Sepultura river, Hoyada de Ischigualasto (San Juan)	Bonaparte (1960)
Archosauria indet.	Heads Los Tarros river (La Rioja)	Inedit
Archosauria indet.	Hoyada de Ischigualasto, NW Cerro Morado (San Juan)	Martinez et al. (1998)
Archosauria indet.	Agua del Colorado, Hoyada de Ischigualasto (San Juan)	Inedit
Crocodylomorpha		
<i>Hemiprotosuchus leali</i>	Qda. de los Jachaleros, El Salto (San Juan)	Bonaparte (1971)
<i>Pseudohesperosuchus jachaleri</i>	Qda. de los Jachaleros, El Salto (San Juan)	Bonaparte (1971)
Crurotarsi		
Aetosauria		
Aetosauria indet.	NW of La Esquina and SE of El Salto (La Rioja)	Inedit
Aetosauria indet.	Heads Los Tarros river (La Rioja)	Inedit
Aetosauria indet.	Heads of the Mañero river (La Rioja)	Inedit
Aetosauria indet.	Qda. de los Jachaleros, El Salto (San Juan)	Inedit
<i>Neoaetosauroides engaeus</i>	Qda. de los Jachaleros, El Salto (San Juan)	Bonaparte (1971)
<i>Riojasuchus tennuiseps</i>	Qda. de los Jachaleros, El Salto (San Juan)	Bonaparte (1971)
<i>Fasolasuchus tenax</i>	La Esquina (La Rioja)	Bonaparte (1981)
Dinosauria		
Sauropodomorpha		
Sauropodomorpha indet.	Heads Los Tarros river (La Rioja)	Inedit
Sauropodomorpha indet.	Heads of the Mañero river (La Rioja)	Inedit
Sauropodomorpha indet.	Cerro de Las Lajas (La Rioja)	Arcucci and Coria (1996)
<i>Riojasaurus</i> sp.	Heads of the Mañero river (La Rioja)	Inedit
<i>Riojasaurus incertus</i>	La Esquina (La Rioja)	Bonaparte (1971)
<i>Coloradisaurus brevis</i>	E of Cerro Rajado (La Rioja)	Bonaparte (1978)
Theropoda		
Theropoda indet.	Qda. de los Jachaleros, El Salto (San Juan)	Bonaparte (1971)
<i>Zupaysaurus rougieri</i>	NW of La Esquina and SE of El Salto (La Rioja)	Arcucci and Coria (2003)
Therapsida		
Anomodontia		
<i>Jachaleria colorata</i>	Qda. de la Chilca (San Juan)	Bonaparte (1960, 1966)
Eucynodontia		
<i>Chalimnia musteloides</i>	E of Cerro Rajado (La Rioja)	Bonaparte (1980)

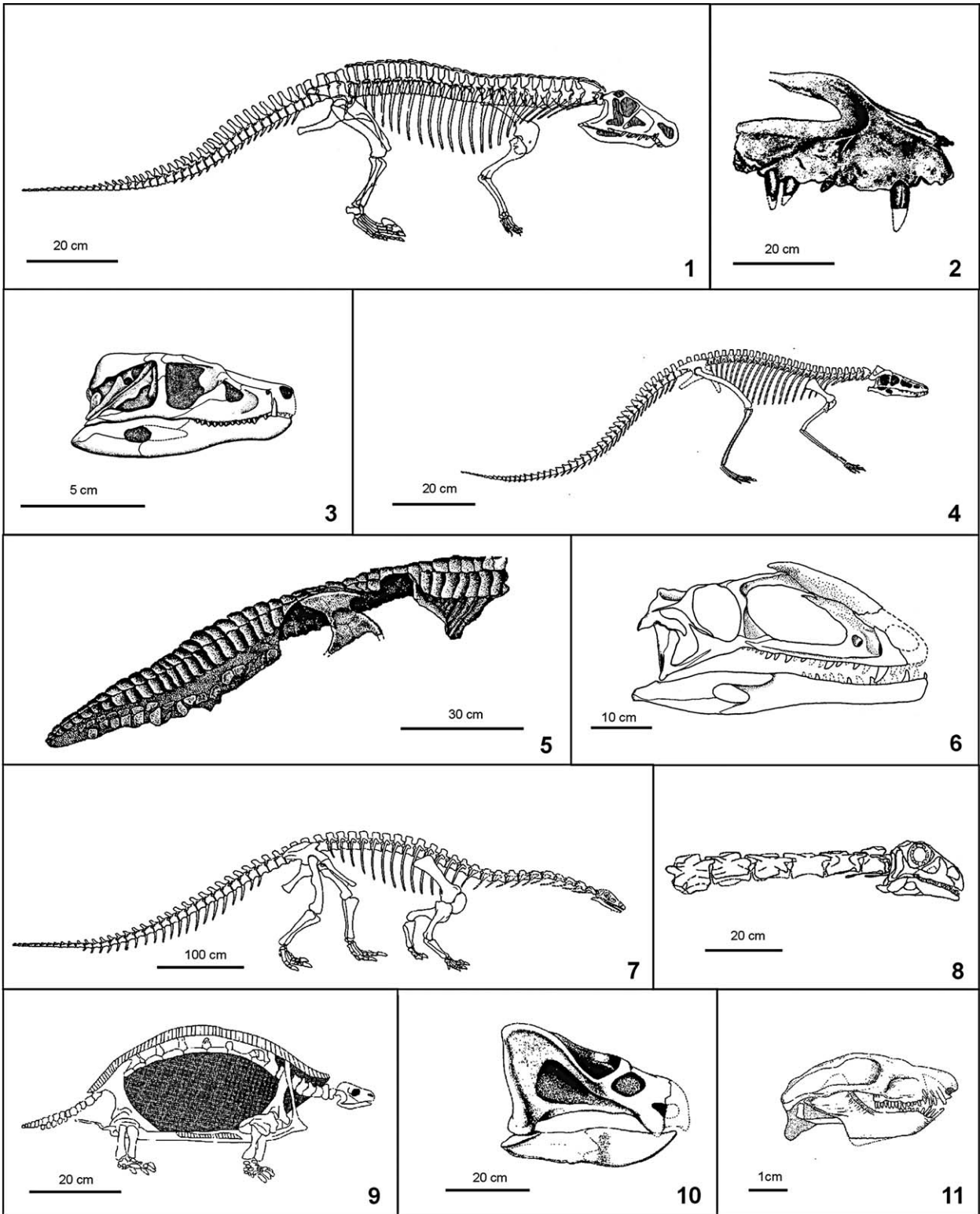


Fig. 3. Tetrapod fauna of Los Colorados Formation: (1) *Riojasuchus tenuiceps* ornithomimid. (2) *Fasolasuchus tenax*, rauisuchid. (3) *Hemiprotosuchus lealli*, crocodylid. (4) *Pseudohesperosuchus*, spenosuchid. (5) *Neoaetosauroides*, aetosauroid. (6) Tetanuran teropod. (7) *Riojasaurus incertus*, prosauropod. (8) *Coloradia brevis*, prosauropod. (9) *Palaeochersis talampayensis*, chelonian. (10) *Jachaleria colorata*, dicynodont. (11) *Chalimnia musteloides* derived cynodont. (1, 3, 4, 5, 7, 11, from Bonaparte, 1972; 2, from Bonaparte, 1982; 6 from Arcucci and Coria, 2003; 8 and 10 from Bonaparte, 1978; 9, from Rougier et al., 1998).

Fig. 3. Faune de Tétrapodes de la Formation de Los Colorados : (1) *Riojasuchus tenuiceps*, ornithomimidé. (2) *Fasolasuchus tenax*, rauisuchidé. (3) *Hemiprotosuchus lealli*, crocodylidé. (4) *Pseudohesperosuchus*, spénosuchide. (5) *Neoaetosauroides*, aetosauure. (6) Téropepe tétanuren. (7) *Riojasaurus incertus*, prosauropode. (8) *Coloradia brevis*, prosauropode. (9) *Palaeochersis talampayensis*, chélonien. (10) *Jachaleria colorata*, dicynodonte. (11) *Chalimnia musteloides*, cynodonte. (1, 3, 4, 5, 7, 11: Bonaparte, 1972; 2: Bonaparte, 1982; 6: Arcucci et Coria, 2003; 8 et 10: Bonaparte, 1978; 9: Rougier et al., 1998).

prosauropods), from the same basal levels, remain still undescribed (Martinez et al., 1998).

The tetrapod association recorded in the upper part of the sequence is diverse and many groups are known by a high number of specimens. The association is dominated by archosaurs, including a variety of both carnivorous and herbivorous forms with a wide range of sizes. The non-predatory forms, that are represented by a large number of specimens, include both basal archosaurs such as the medium sized aetosaur *Neoaetosauroides* (Bonaparte, 1971), and derived groups, and the prosauropod dinosaurs *Riojasaurus* and *Coloradisaurus* (Bonaparte, 1971, 1978). These prosauropods were attributed to the South African family Melanosauridae and the European family Plateosauridae, but their precise phylogenetic affinities are still uncertain. Although, they have undoubtedly a basal position in the evolution of the Sauropodomorpha clade (Upchurch, 1997). The prosauropods from Los Colorados include specimens from medium to large size, with a body length between 3 and 10 m. Carnivorous archosaurs are also represented in the upper part of Los Colorados sequence by basal groups, such as rauisuchids and crocodylomorphs (sphenosuchids and protosuchids). Crocodylomorphs were small sized quadrupeds, like *Pseudohesperosuchus* and *Hemiprotosuchus* (Bonaparte, 1971) both with long and slender limbs, and presumably terrestrial habits. The rauisuchids are represented by fragmentary remains of the huge *Fasolasuchus*, a carnivore with a skull almost 1 m long (Bonaparte, 1981, 1997). The ornitosuquid *Riojasuchus* (Bonaparte, 1971) is a medium size carnivore with close phylogenetic relationships with *Venaticosuchus*, a ornitosuchid taxon known from the Ischigualasto Formation (Bonaparte, 1970, 1997). Both taxa are related with *Ornithosuchus*, from the Triassic of England (Walker, 1964). Finally, carnivorous archosaurs are represented by derived forms, the theropods, which are strictly bipeds and include only two specimens. One is a small and very fragmentary postcranial skeleton assigned to a coelurosaur (Bonaparte, 1971). The other is a medium sized (approximately 3 m of body length) theropod dinosaur and the specimen includes a complete skull, vertebral series and hind limb, (Arcucci and Coria, 1998). The skull of this theropod is well preserved and displays several features that relate it with the tetanuran theropods, not known previously from South America.

Two other the tetrapod groups are present in the association (upper part of the Los Colorados Formation), the Therapsida and Chelonia, although comparatively with a low diversity and abundance (Caselli et al., 2001). Therapsids include two taxa of derived cynodonts (cf. *Tritylodon* and *Chalimonia*), each of them recorded by one single specimen, with a skull a few centimetres long and a herbivorous diet (Bonaparte, 1971, 1980). Both taxa are probably closely related with lower Jurassic South African forms (Bonaparte, 1997). The only quelonian group recorded is the Australochelidia, which is considered as the sister group of modern turtles (Rougier et al., 1995). The specimens are large (carapace length nearly 70 cm) with a small head and long tail

without osteoderms. The specimens exhumated are numerous, all belong presumably to one taxon, *Palaeochersis*, and come from the same site and stratigraphic level (Rougier et al., 1995).

Besides the mentioned published material, there are still many undescribed body vertebrate fossils from the upper part of the Los Colorados Formation and they are included with a preliminary taxonomic identification in Table 1.

Tetrapod footprints from Los Colorados levels are known from three localities and, apparently, from different stratigraphic levels. They were mentioned in the literature several times but the material was never fully described (Leonardi and Oliveira, 1990; Leonardi, 1994; Bonaparte, 1997; Contreras and Bracco, 1998; Arcucci et al., 2000). Thus, Leonardi (1994) briefly described a collection of footprints founded in the water heads of Los Tarros river by Bonaparte in 1964. Posteriorly, this material was partially illustrated by Bonaparte (1997), who related it to “probable crocodylians” (Bonaparte, op. cit.). Posteriorly, a second lot of footprints was also collected by Bonaparte but in a different locality, (head waters of the Mañero river); this collection was never mentioned or figured. Both localities are apparently located where only the upper part of the Los Colorados sequence outcrops, in La Rioja province. Recently, a third group of footprints were briefly mentioned from the “middle-upper part” of the sequence without any location reference, and identified as “Cynodontia indet.” (Contreras and Bracco, 1998). This material remains still undescribed and was not located by the authors. Therefore, the footprints described herein from the Los Colorados Formation are only those collected by Bonaparte in the water heads of both Mañero and Los Tarros rivers, that come from the upper part of the sequence.

The material described below is housed in the collections of Paleontología de Vertebrados of the Instituto Miguel Lillo (PVL), Tucumán Province, Argentina.

Material: PVL 3438-3452: a collection of small slabs containing mainly isolated footprints and invertebrate trace fossils associated; the slabs PVL 3443-3447, invertebrate trace fossils are only preserved; the slab PVL 3452 records a right manus and the corresponding pes impressions, thus is the only one of the whole lot where more than one footprint is present.

Locality and Horizon: Head waters of Los Tarros river (approximately 29°55'S–67°57'W), Barrancas Coloradas, La Rioja province; Los Colorados Formation (Late Triassic).

Description: The footprints are preserved on small slabs of a fine-grained reddish sandstone and most of them are incomplete and poorly impressed. The specimen PVL 3452 (Fig. 4A) consists of the impression of a right hind foot and the corresponding front footprint impression. The pes is not complete but its outline corresponds to a pentadactyl footprint. The manus impression is apparently located in front to the pes one and the outline of the manus is nearly rounded with the digits not evident. The material PVL 3438, 3439 and 3442 preserves, each of them, a small manus, apparently

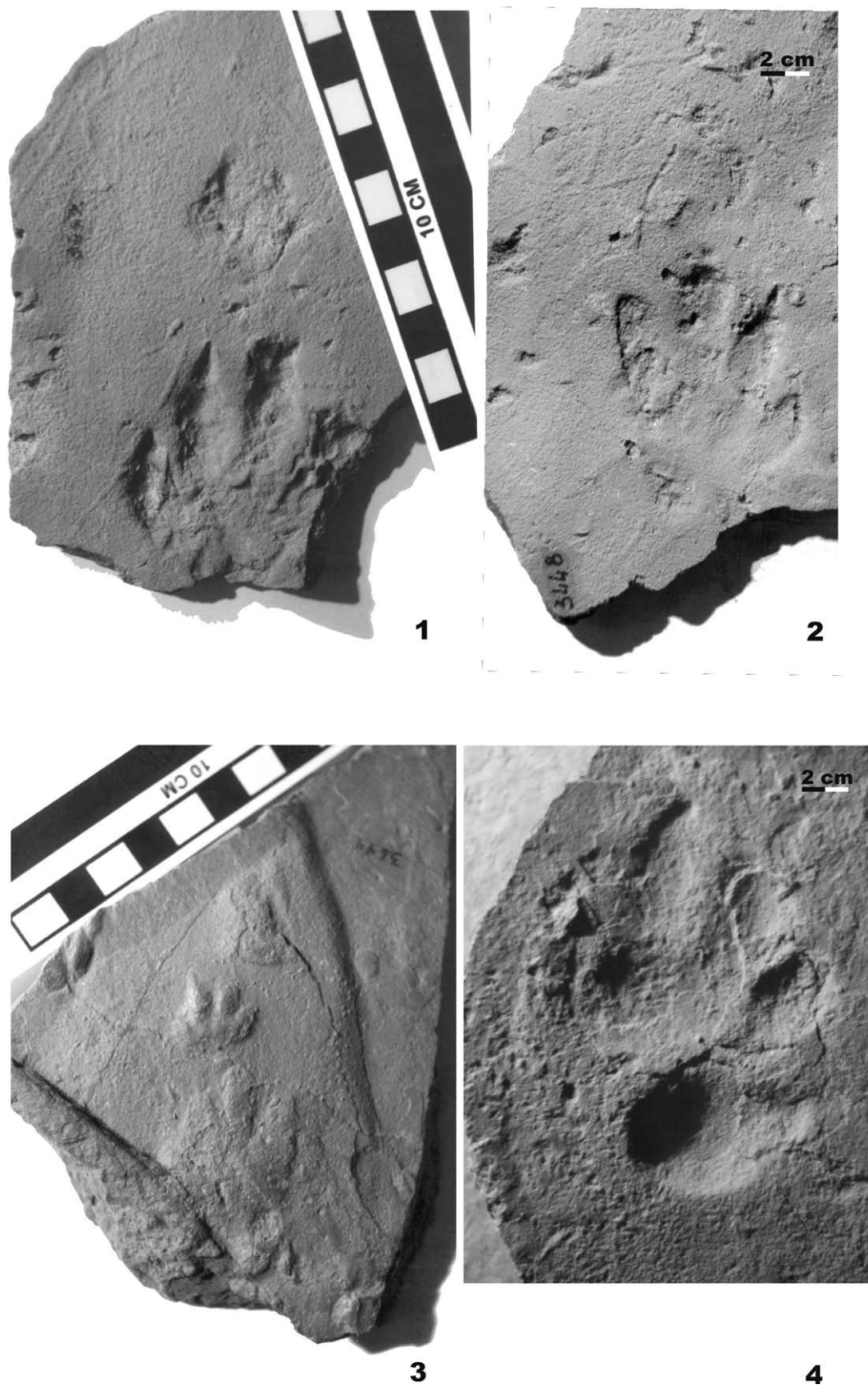


Fig. 4. Chirotheroid footprints from Los Colorados Formation. (1) Specimen PVL 3452. (2) Specimen PVL 3448. (3) Specimen PVL 3644. (4) Specimen PVL 3658.

Fig. 4. Empreintes de pas de chirothéroïdé de la Formation de Los Colorados.

pentadactyl impression. The digits are all directed to the same direction, with digit III slightly longer than II and IV, which are similar in length. The general size and shape of these manus impressions are very similar to that of PVL 3452, described above. Isolated hind footprints are present in slabs PVL 3440, 3441 and 3448, although, only in the specimen PVL 3448 (Fig. 4B) a complete outline of the footprint is visible. This pes is pentadactyl (anteroposterior length of approximately 6 cm) with digits I–IV directed in the same direction and with an average divarication angle of 30° between digit III–II and III–IV. Digits II and IV are nearly of equal size with the digit III slightly longer. Digit V is short, not everted, and, as the other digits, presents a claw mark. This pes impression is very similar to that of PVL 3452.

Material: PVL 3644–3661: small slabs containing isolated footprints, several footprints or pes impressions with the corresponding manus, but no trackways are present in the slabs.

Locality and Horizon: Head waters of Mañero River (approximately $29^\circ 59'S$ – $67^\circ 55'W$), Barrancas Coloradas, La Rioja Province; Los Colorados Formation (Late Triassic).

Description: The slabs containing the footprint material are brown-reddish mudstones with the tracks generally deeply impressed. The slabs PVL 3644, 3645, 3650, 3652, 3659 and 3660 preserve impression of pes with the corresponding manus. All front footprints are tetradactyl with digits II and III similar in length and I and IV slightly shorter than them. The hind footprint impressions are all pentadactyls and they are approximately of 5–6 cm in length. The digit III is slightly longer than II and IV, which are similar in length, and all digits are anteriorly directed. The average divarication angle is 20° between digit III–II and III–IV. In

the specimens preserved in slabs PVL 3645 and 3652, digit V is shorter than the remaining digits, but it is well developed and anteriorly directed. The specimen PVL 3644 (Fig. 4C) has the digit V very short and everted; the specimens PVL 3650, 3659 and 3660 are both poorly impressed thus the outline of digit V is not evident. All the specimens mentioned above have the manus impression apparently located in front to the pes; both manus and pes impressions in PVL 3652 lack claw marks, although they are clearly visible in PVL 3644, 3645, 3650, 3659 and 3660. The slabs numbered PVL 3647, 3648, 3653, 3654 and 3656 contain isolated manus impressions very similar to those described above, and PVL 3646, 3649, 3651, 3655, 3657 and 3661, only partially preserved pes impressions are visible, apparently not different to that described above. The specimen PVL 3658 (Fig. 4D) preserves a complete hind footprint impression, very close to that of PVL 3644, with digit V very reduced and everted. It is important to remark that in the specimen PVL 3652, the pes impression has the digit V covered by small rounded marks, that apparently corresponds to scale impressions (arrow in Fig. 5).

The material described above corresponds to small “chirotheroid” tracks. The size of the specimens is very similar and differences recognized are the position and development of digit V in the pes impressions, the presence of pentadactyl or tetradactyl manus impressions, and the presence or absence of well developed claw marks. Thus, apparently three different types are present in the described material: (1) “chirotheroid” footprints with pentadactyl manus impressions, (2) “chirotheroid” footprints with tetradactyl manus impressions and pes impressions with well developed digit V and not everted, and (3) “chirotheroid” footprints with tetra-

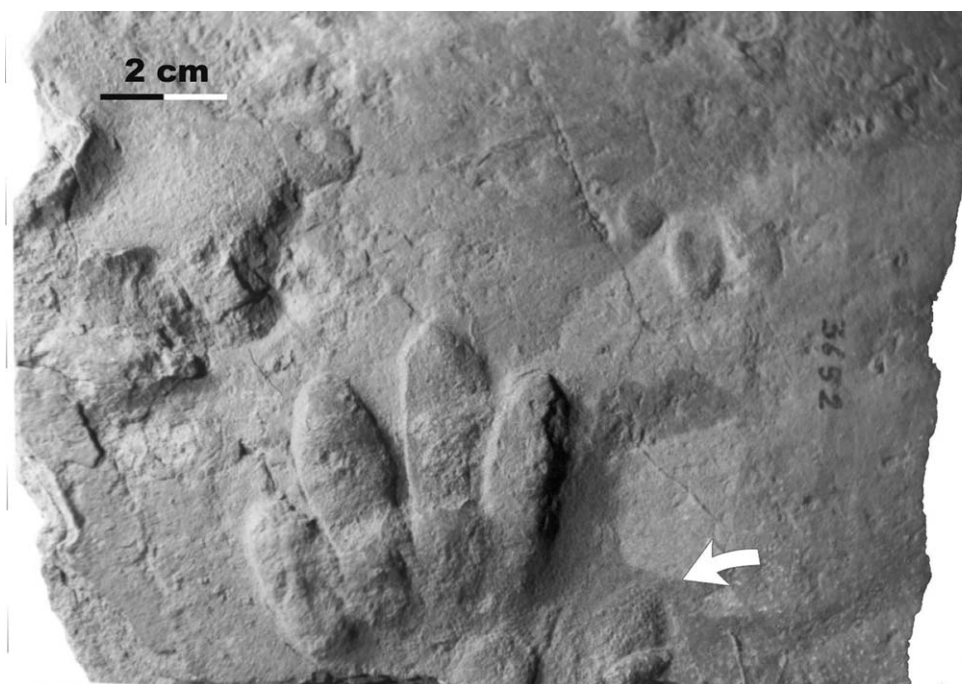


Fig. 5. Chirotheroid footprint (specimen PVL 3652) showing scales impressions on digit V (arrow).

Fig. 5. Empreintes de pas du spécimen PVL 3652 montrant des impressions en écailles sur le doigt V (flèche).

dactyl manus impressions and pes impressions with reduced and everted digit V.

“Chirotheroid” tracks with symmetric hand and feet has been allied to different groups of “crocodile-normal archosaurs” (Parrish, 1989), some of them already represented in Los Colorados Formation levels by skeletal remains (e.g. aetosaurs, rauisuchiids, crocodylomorphs). This type of tracks are an important component of the Middle-Late Triassic footprint assemblages in Pagea, and they are unknown after the Triassic–Jurassic boundary (Haubold, 1986; Courel and Demathieu, 1995; Parrish, 1989; Lockley and Hunt, 1995; Lockley and Meyer, 2000).

4. Discussion

4.1. Biostratigraphy and age

Since the faunal association of the Los Colorados levels were described as indicative of Late Triassic age in Southern South America (“La Esquina Local fauna” of Bonaparte, 1982), different authors have pointed out its outstanding nature. Thus, this rich and diverse association was interpreted as a unique combination of taxa including both typical elements from Late Triassic and Lower Jurassic faunas (e.g. Olsen and Sues, 1986; Shubin and Sues, 1991; Lucas, 1998). Nevertheless, a different hypothesis was proposed and such combination was suggested to be the result of a mixture of tetrapod-bearing horizons of different age (Shubin and Sues, 1991; Benton, 1994; Bracco et al., 1996). Recent stratigraphic analysis of the Los Colorados tetrapod-bearing levels (Caselli et al., 2001) confirmed the transitional nature of the association where typical Triassic taxa (e.g. aetosaurs) are found associated in the same beds with advanced theropod dinosaurs and cynodonts, known from Early Jurassic levels in other Gondwanan and Laurasian areas.

The age of Los Colorados Formation has been widely considered as Late Triassic (Norian) according to both the faunal content and the stratigraphic relationships (e.g. Stipanovic and Bonaparte, 1979; Bonaparte, 1982; Lopez Gamundi et al., 1989; Milana and Alcober, 1994; Benton, 1994; Spalletti, 1999). However recently, the deposition of the Los Colorados levels was considered to have occurred during Raethic times; this was justified by taxonomic comparisons with other Pangean areas and mainly based on aetosaur and prosauropod taxa (Lucas, 1998; Heckert and Lucas, 1998). Biostratigraphic correlations proposed on direct co-generic comparisons requires a thorough consideration of the phylogenetic relationships of the taxa involved, something not available in many Triassic tetrapod groups. Moreover, the recognizance of the Raethic Stage, a typical marine European stage at the end of the Triassic, poses the inconvenience of utilize marine standards in continental basins. It is important to remark that the Ischigualasto-Villa Unión Basin is an entirely non-marine depocenter without any lateral correlation with marine strata. As a matter of fact,

the use of the Norian Stage is not an exception to this problem. With this caveats and despite the lack of independent evidence for a precise age of these levels, there is a wide consensus about considering this unit as deposited during the latest Triassic based on both faunistic and stratigraphic data (Stipanovic and Bonaparte, 1979; Bonaparte, 1966, 1973, 1982, 1997; Stipanovic, 1983; Olsen and Sues, 1986; Lopez Gamundi et al., 1989; Milana and Alcober, 1994; Benton, 1994; Heckert and Lucas, 1998; Spalletti, 1999; Caselli et al., 2001).

4.2. Depositional environment and paleoclimate

Bossi (1970) suggested an alternation of arid and humid climatic conditions during the deposition of the Los Colorados Formation based on clay mineralogy analysis of the sequence. Posteriorly, several authors climatically interpreted the unit as increasingly arid in comparison with the conditions during the deposition of the underlying the Ischigualasto Formation (Lopez Gamundi et al., 1989; Milana and Alcober, 1994; Cladera et al., 1998). Moreover, Milana and Alcober (1994) discussed the evolution of the basin infilling and attributed the red color of the Los Colorados sediments to oxidation processes during deposition as in arid settings.

Recently, Caselli et al. (2001) made a detailed sedimentological analysis of the Los Colorados rocks and interpreted it as fluvial deposits of mixed charge (suspensive-tractional) with sand channels of moderate to high sinuosity, with well-developed flood plains. In the whole sequence, there were no evidence of aridity (e.g. intraclast breccias, desiccation cracks, eolian lenses, evaporite lenses). The presence of thick deposits of alluvial plains that represents episodic flows and high precipitation suggests humid or subhumid conditions. Moreover, petrographic analysis of the sandstones suggested that their red color is related to oxidation processes during early diagenesis (Caselli et al., 2001).

The tetrapod association recorded in the Los Colorados Formation includes a high abundance of herbivorous forms: dicynodonts, aetosaurs and prosauropods. Dicynodonts, represented by medium-to-large sized animals, are interpreted as browsers, with derived masticatory apparatus, and they probably foraged within 1 m of the ground (DiMichele and Hook, 1992); aetosaurs, that are also consider herbivorous forms (Wing and Sues, 1992; Parrish, 1994), are very abundant in the Los Colorados beds. Finally, prosauropod dinosaurs, which include quite large forms and are the major element in the Los Colorados faunal assemblage, are the first continental high-browsing herbivores and could have fed at heights up to 4 m above the ground (Wing and Sues, 1992). This herbivore fauna suggests the presence of an important vegetation cover in the area, probably composed both by a low-statured vegetation and a forest. It is important to point out that all tetrapod material in the Los Colorados levels was exhumated partially or completely articulated, thus suggesting that they were virtually not transported after death from a

nearby area with different environmental conditions. All these evidence supports the idea of a seasonally humid climate in the region during the Late Triassic. The lack of floral fossil record in the Los Colorados beds does not necessarily imply a poor vegetation cover owing to extreme arid conditions as it was previously suggested. Conversely, this absence of floral record was attributed to the taphonomic conditions in the Los Colorados setting, particularly during early diagenesis (Caselli et al., 2001).

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