



South American Crocodylomorphs (Archosauria; Crocodylomorpha): A review of the early fossil record in the continent and its relevance on understanding the origins of the clade

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ARTICLE INFO

Keywords:

South America
Pangea
Archosauria
Crocodylomorpha
Crocodyliformes
Late Triassic

ABSTRACT

Crocodylomorpha is a clade that has its origins during the Late Triassic and attained a global distribution early in their radiation. In this context, although limited to few geological units, the South American record has been relevant in the understanding of the origins of the clade. Additionally analyzing the South American crocodylomorph record and comparing it with the one in the rest of Pangea is relevant as, in recent years, provincialism has been proposed for different faunal assemblages. In this contribution we review the crocodylomorph Triassic record in South America by analyzing three units that have yielded fossils of the clade: the Santa María Supersequence in Brazil; and, the Ischigualasto and Los Colorados formations in Argentina. Our review does not support previous assignments of the taxon *Barberenasuchus* from the Santa María Supersequence as a non-crocodyliform crocodylomorph, as it displays traits that are absent in all known crocodylomorphs and are present in other earlier branching archosaurs. On the other hand, the Argentinian stratigraphic units remain as the only ones that have crocodylomorphs in the subcontinent. Here we report for the first time the occurrence of “large-bodied” crocodylomorphs in the Ischigualasto Formation, represented by a new yet undescribed taxon. The Los Colorados Formation has a diverse crocodylomorph record being represented by a non-crocodyliform crocodylomorph (*Pseudhesperosuchus*) and two crocodyliforms (*Hemiprotosuchus* and *Coloradisuchus*). Here we present a putative new non-crocodyliform crocodylomorph taxon from Los Colorados Formation. When compared with other crocodylomorph bearing formations around Pangea, the Ischigualasto Formation bears similarities with the crocodylomorphs assemblages of North America due to the presence of early branching crocodylomorphs (*Trialestes*) including “large-bodied” taxa. The Los Colorados Formation reveals a transitional composition corresponding to Norian and Early Jurassic assemblages of Pangea, as it shares the presence of basal crocodyliforms (i.e., protosuchids) typical of Early Jurassic units (e.g., Upper Elliot) and basal non-crocodyliform crocodylomorphs, widely present in Norian assemblages.

1. Introduction

Crocodylomorphs are a highly successful clade of archosaurs that originated in the Late Triassic (late Carnian) and greatly diversified later in the Mesozoic (e.g., Young et al., 2010; Pol and Leardi, 2015; Bronzati et al., 2015; Manion et al., 2019). Today it is only represented by fewer than 30 (23–27) species restricted to the amphibious Crocodylia

(Brochu, 2003; Grigg and Kirshner, 2015). Crocodylomorphs have long been considered highly autapomorphic when compared with other archosaurs, in particular due to the presence of several cranial (e.g., elongated posterodorsal process of the premaxilla; jugal excluded of the antorbital fossa/fenestra; quadrate contacting the braincase) and postcranial (e.g., presence of an elongated postglenoid process; elongated proximal carpals; long preacetabular process of the ilium; reduction of

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<https://doi.org/10.1016/j.jsames.2020.102780>

Received 1 April 2020; Received in revised form 13 July 2020; Accepted 20 July 2020

Available online 28 August 2020

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pedal digit V) synapomorphies that are unique among pseudosuchians (Walker, 1970, 1990; Clark, 1986; Benton and Clark, 1988). The origins of crocodylomorphs among paracrocodylomorphs (formerly known as “rauisuchians”, but this term has been restricted in the past years [Nesbitt, 2011]) has attracted the attention of several archosaur specialists due to the markedly different “bauplans” among the different taxa. Non-crocodylomorph paracrocodylomorphs were animals with large skulls relative to their body, high body masses, short anterior limbs and pillar-erect hindlimbs that occupied the role of apex predators in Late Triassic ecosystems (Gower, 2000; Nesbitt, 2011; Nesbitt et al., 2013). In contrast, crocodylomorphs have been historically regarded as small, cursorial, terrestrial predators (Clark et al., 2000, 2004). However, in recent years, new but fragmentary specimens were reported from North America that display typical crocodylomorph features but have body sizes that are larger (estimated femoral length > 300 mm) than those of other early crocodylomorphs (Nesbitt et al., 2005; Nesbitt, 2011; Zanno et al., 2015). This led to the recognition of a series of basal taxa informally known as “large-bodied crocodylomorphs” which have

been interpreted as taxa filling the ecological gap of large predators in their respective faunal assemblages (Nesbitt et al., 2005; Zanno et al., 2015).

The early record of Crocodylomorpha is well documented when compared to other archosaur lineages, as the taxa known are represented by specimens composed by both cranial and postcranial remains in most cases (Irmis et al., 2013). However, previous contributions noted that the rarity of crocodylomorph specimens is related to the difficulty of recognition of diagnostic characters that allow identification of taxa based on isolated remains (Nesbitt, 2011; Irmis et al., 2013). This is not reflected in phylogenetic datasets; for example, the data matrix with the most complete taxonomic sampling among basal crocodylomorphs (Leardi et al., 2017) has only 36% of postcranial characters. However, the issue relies on which parts of the anatomy of basal crocodylomorphs have been sampled in search of phylogenetically informative characters, as highly repeated elements on the vertebrate skeleton (i.e., vertebrae) are underrepresented in these studies (4 of 138 characters), unlike the diversity of vertebral features seen in basal dinosaurs (e.g., 21 of 139 in

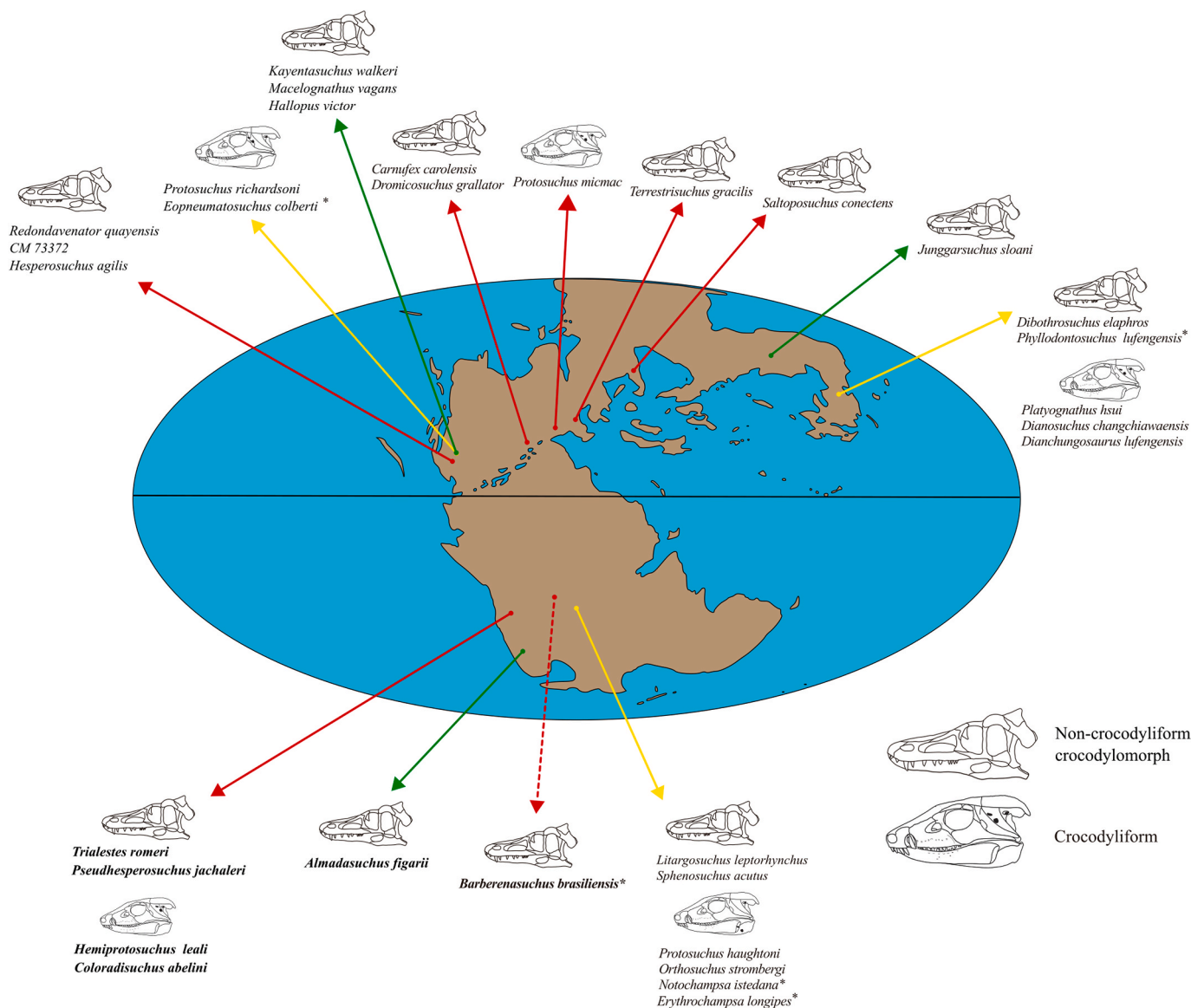


Fig. 1. Late Triassic paleogeographic map indicating occurrences of crocodylomorph taxa around the world. Arrows indicate the different localities in red, Late Triassic; in yellow, Lower Jurassic; and, in green, Upper Jurassic. Asterisks next to the name of some taxa indicate those of conflicting assignment (either to Crocodylomorpha, or the validity of the taxon itself). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Martínez et al., 2011; 33 of 256 in Cabreira et al., 2016). Furthermore, other postcranial elements (e.g., femora) display particular anatomic features (e.g., pseudointernal trochanter) that seem to diagnose some clades but not individual species, precluding the identification of the latter based on isolated remains.

The early record of Crocodylomorpha is relatively widespread in Pangea (Fig. 1; Irmis et al., 2013). The earliest undisputed record of Crocodylomorpha comes from the Ischigualasto Formation (upper Carnian) of Argentina, represented by the taxon *Triolestes romeri* (Reig, 1963; Bonaparte, 1982). However, the general acceptance by most researchers of the stem-based definition of the Crocodylomorpha excluding Rausuchidae (sensu Nesbitt, 2011) led to the recognition of the “large-bodied crocodylomorphs” (see above) as stem taxa to the classical “small-bodied crocodylomorphs” (Zanno et al., 2015). These forms, are restricted to Carnian–Norian localities of North America to date, with *Carnifex carolinensis* being the oldest record of the “large-bodied crocodylomorphs” (Zanno et al., 2015). On the other hand, the “small-bodied crocodylomorphs” attained a wide distribution by the latest Triassic (Norian–Rhaetian) with taxa known from the South America (*Pseudhesperosuchus* and the disputed *Barberenasuchus*), North America (*Hesperosuchus*, known from several specimens [see Leardi et al., 2017], and *Dromicosuchus*), and Europe (*Saltoposuchus* and *Terrestrisuchus*). Non-crocodyliform crocodylomorphs are reported from the Lower Jurassic in China (*Dibothrosuchus*), South Africa (*Sphenosuchus* and *Litargosuchus* from Upper Elliot) and United States (*Kayentasuchus* from Kayenta Formation) (Fig. 1). Non-crocodyliform crocodylomorphs are known up to the Upper Jurassic, represented by rare records scattered around Pangea (Walker, 1970; Clark et al., 2004; Pol et al., 2013; Leardi et al., 2017). These basal crocodylomorphs were contemporary with the first representatives of the crocodyliform radiation that took place during the Late Triassic and Early Jurassic (Clark, 1986; Martínez et al., 2018).

Even with the full amalgamation of Pangea in the Late Triassic, provincialism has been proposed for several faunal assemblages around the globe (Irmis et al., 2007; Ezcurra, 2010). Thus, although crocodylomorphs have a geographically wide distribution since their origins, the record of the clade should be analyzed considering each geological unit. Our objectives in the present contribution are to evaluate the early record of Crocodylomorpha and basal crocodyliforms in the Late Triassic of South America and to compare these faunal assemblages with other Triassic units in the world where the clade has been recognized. This is of relevance, considering the recent proposals of an equatorial origin for Crocodylomorpha (Zanno et al., 2015) or a South American origin and initial diversification of Crocodyliformes (Martínez et al., 2018).

2. Materials and methods

In order to evaluate the South American record in the context of the origin and early diversification of Crocodylomorpha our analysis will be focused on Late Triassic–Early Jurassic geological units from the subcontinent that bear crocodylomorph remains. Also, as other contributions did (e.g., Irmis et al., 2013), the crocodylomorph remains that will be considered are those that can actually be assigned to valid taxa. We are aware that fragmentary specimens provide important evidence of presence of the clade in certain locations (e.g., Martínez et al., 2015), but in many cases these remains preclude its comparisons with other, more complete, taxa. Also tentatively assigned taxa (i.e., Crocodylomorpha indet) are difficult to evaluate at specimen level.

In line with most recent contributions dealing with basal crocodylomorphs (e.g., Irmis et al., 2013; Zanno et al., 2015; Lecuona et al., 2016; Leardi et al., 2017, 2020) we use the stem-based definition of Crocodylomorpha (Nesbitt, 2011) and the node-based definition of Crocodyliformes (Sereno et al., 2001). In this context, we also apply the terminology coined by Zanno et al. (2015) and Drymala and Zanno (2016) when referring to the basal members of Crocodylomorpha that have large body masses as “large-bodied crocodylomorphs”. On the

other hand, the smaller and classical forms will be referred as “small-bodied crocodylomorphs” throughout this review.

Institutional Abbreviations: CRILARPV, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Anillaco, Argentina; PVL, Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; PVSJ, División de Paleontología, Museo de Ciencias Naturales de la Universidad Nacional de San Juan, San Juan, Argentina; MCP, Museu de Ciêncian e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil.

3. South American crocodylomorph assemblages

In order to review and discuss the South American crocodylomorph diversity we will analyze them considering the formations that yielded any records of the clade in South America. Then, the crocodylomorph record of each unit (i.e., assemblage) will be discussed in detail. As mentioned previously (see Introduction), our analysis will be focused on the Triassic record, as the present contribution is focused on the origins of the clade and its early history in South America.

The South American Triassic continental record is recognized by its abundance and the key role its faunal components play in understanding the Triassic ecosystems, especially on the Late Triassic (e.g., Arcucci et al., 2004; Martínez et al., 2011; Mancuso et al., 2014). However, Triassic crocodylomorph findings are currently restricted to three stratigraphic units (Fig. 1): a putative record from the Santa María Supersequence (*Barberenasuchus brasiliensis*) from southern Brazil; and, four taxa from the Ischigualasto-Villa Unión Basin in Argentina recovered from the formations that cap the Triassic sequence on it (Ischigualasto and Los Colorados formations).

3.1. Santa María assemblage

The Santa María crocodylomorph assemblage comprises a single taxon, *Barberenasuchus brasiliensis* Mattar (1987). The only known specimen was recovered from the lower levels of the Santa María Supersequence, particularly to what has been named as the Pinheiros-Chiniquá Sequence by Horn et al. (2014) (Pinheiro local fauna sensu Barberena et al., 1985). The lower levels of the Santa María Supersequence consist of clast-supported conglomerates and cross-bedded sandstones that are overlain by laminated mudstones. These were interpreted as fluvial deposits that transition to shallow lacustrine deposits (Zerfass et al., 2003). The specific temporal range of the outcrops of this sequence is not known, as most of the temporal correlations have been done using biostratigraphic comparisons with other Triassic basins. Fortunately, the upper parts of the Santa María supersequence have recently been dated using detrital zircon by Langer et al. (2018) obtaining ages of 233.23 ± 0.61 Ma (late Carnian) for the Santa María Formation and 225.42 ± 0.37 Ma for the Caturrita Formation (early Norian). However, there are still no dates for the lower levels of the Santa María Supersequence, which are currently regarded as late Ladinian–early Carnian based on the recognition of the *Dinodontosaurus* Assemblage Zone (Soares et al., 2011). Therefore, this would imply that *Barberenasuchus* is the oldest known crocodylomorph currently recognized.

Barberenasuchus brasiliensis was studied by Mattar (1987) and Mattar and Barberena (1987). In these contributions, the only known specimen, consisting of a poorly preserved skull and an isolated axis, was assigned to “Sphenosuchia” (sensu Bonaparte, 1972). *Barberenasuchus* was also compared with members of Proterochampsidae/Proterochampsia (known then as Cerritosauridae), as these were considered closely related to crocodylomorphs at that time (Sill, 1967; Walker, 1970). This assignment has been challenged recently by Clark et al. (2000) and Irmis et al. (2013), based on the incompleteness of the only known specimen and the lack of crocodylomorph synapomorphies on it. Furthermore, Irmis et al. (2013) could not recognize further characters other than the presence of an antorbital fenestra, which is a synapomorphy of

Archosauriformes (Gauthier et al., 1988) (Fig. 2 A and D).

Mattar and Barberena (1987) assignment of *Barberenasuchus* to “Sphenosuchia” was mostly based on perceived similarities with *Pseudhesperosuchus jachaleri*. It should be noted (Fig. 2A) that the only specimen (MCP 3844 PV), which includes is very a poorly preserved skull and an isolated axis, evidences ventral crushing and distortion towards its right side (Fig. 2B). As previously noted (Clark et al., 2000), most of the sutures are very difficult to observe and heavily rely on the observer’s interpretation. This is evidenced on Mattar and Barberena (1987) illustration of *Barberenasuchus*, where the sutures between different cranial elements are represented by dotted lines (Mattar and Barberena, 1987: Figs. 1 and 2). One of the most notable features observed in that contribution is the presence of an expansion of the dorsolateral region of the squamosal forming an otic overhang (Mattar and Barberena, 1987: pp. 87). Personal observation (JML) revealed that the preserved region of the squamosal does not display a lateral projection, and it is located medially to the lateral border of the body of the quadrate (Fig. 2 C). What could be considered as a posterior wall of the otic overhang (as in *Pseudhesperosuchus* [PVL 3830]) is, in fact, the paroccipital processes of the opisthotics. Thus, there is no otic overhang in *Barberenasuchus*. Furthermore, the presence of an otic overhang of the squamosal is not unique to crocodylomorphs, as it has also been noted in some basal pseudosuchians such as *Gracilisuchus* (although it was considered absent by Nesbitt, 2011). In addition, Mattar and Barberena (1987: pp. 87) noted an unusual orientation of the main axis of the quadrate, which is inclined posteriorly, and in the general shape of the infratemporal fenestra, which is anteroposteriorly compressed (Fig. 2 C). These traits are not observed in any other currently recognized crocodylomorph (JML, pers. obs).

Finally, an additional feature that helps elucidating *Barberenasuchus* affinities is the general configuration of the elements of the snout (Fig. 2 D). *Barberenasuchus* has a large triangular antorbital fenestra surrounded by a deep antorbital fossa. In accordance with the original interpretations (Mattar and Barberena, 1987: Figs. 1 and 2) the antorbital fossa has participation of the anterior process of the jugal, a feature not present in crocodylomorphs (Clark et al., 2000). In addition, most basal crocodylomorphs have a long and rounded posterodorsal process of the

premaxilla that is not firmly sutured to the anterodorsal region of the snout, between the maxilla and the nasal (Pol et al., 2013), which is later lost in Crocodyliformes as in these taxa the premaxilla is firmly sutured to the maxilla (Clark, 1986; Benton and Clark, 1988). Although it is badly preserved, the premaxilla of *Barberenasuchus* lacks such a posterodorsal process (Fig. 2 D).

In conclusion, none of the anatomical features present in the only known specimen of *Barberenasuchus* (MCP 3844 PV) support its assignment to Crocodylomorpha. In particular, the participation of the jugal into the antorbital fenestra is a feature absent in crocodylomorphs, thus excluding *Barberenasuchus* from this clade. A detailed review and analysis of this specimen will be crucial to understand its affinities, although with the data at hand, its inclusion among Crocodylomorpha is not supported.

3.2. Ischigualasto assemblage

The Ischigualasto Formation represents the second-youngest stratigraphic unit of the Mesozoic succession of the Ischigualasto-Villa Unión Basin, overlying the deposits of the Los Rastros Formation (Rogers et al., 1993, 2001; Milana and Alcober, 1994; Currie et al., 2009; Mancuso and Caselli, 2012; Marsicano et al., 2016; Colombi et al., 2017). It is dominated by fluvial and volcanoclastic deposits represented by channel and overbank sandstones, siltstones, and mudstones. The depositional environment was characterized as a fluvial system with shallow channels and ephemeral lakes, in a seasonal climatic regime (Rogers et al., 1993; Currie et al., 2009; Colombi et al., 2012). The age of the Ischigualasto Formation is constrained by two $^{40}\text{Ar}/^{39}\text{Ar}$ radioisotopic datings that have yielded an age of 231.4 ± 0.3 Ma near the bottom of the unit and an age of 225.9 ± 0.9 Ma near its top (Rogers et al., 1993; Martínez et al., 2011). The age constraints suggest that the Ischigualasto Formation was deposited during a period of approximately 6 million years during the Carnian to early Norian (Martínez et al., 2011).

The vertebrate fauna of the Ischigualasto Formation includes one of the oldest dinosaur assemblages known to date, non-archosauriform archosauromorphs, pseudosuchians, synapsids, and temnospondyls (Bonaparte, 1982b; Rogers et al., 1993; Brusatte et al., 2010; Martínez

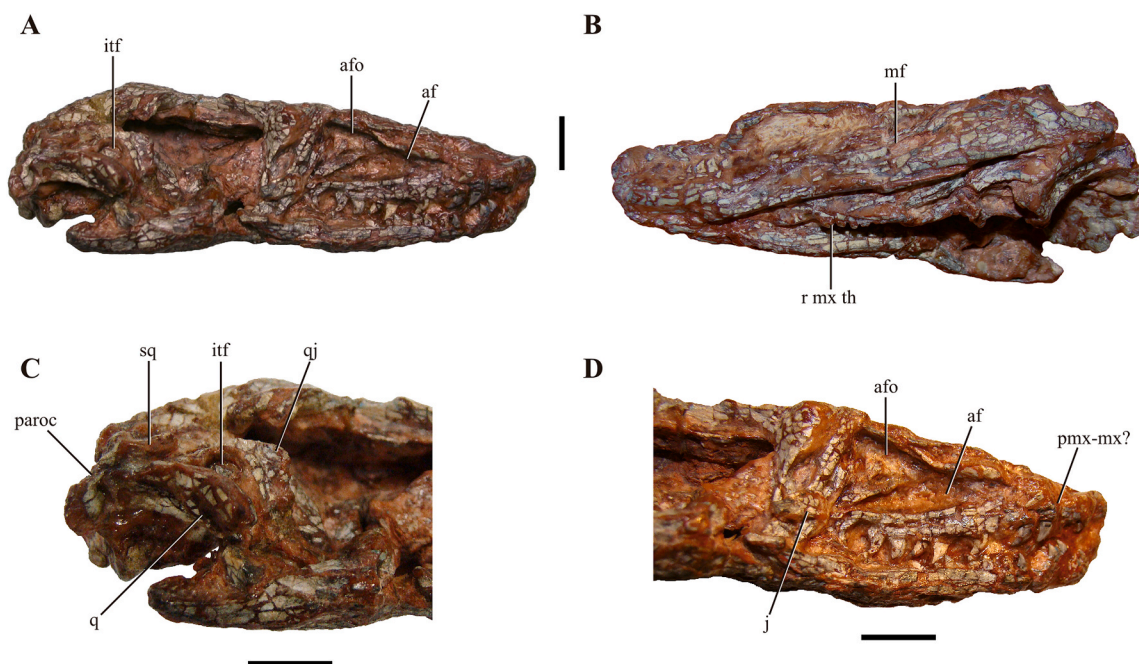


Fig. 2. Skull of *Barberenasuchus brasiliensis* (MCP 3844 PV) in A, right lateral view; B, left lateral view; C, detail of right suspensorium and temporal region; and, D, right view of the snout. Abbreviations: af, antorbital fenestra; afo, antorbital fossa; itf, infratemporal fenestra; j, jugal; mf, mandibular fenestra; r mx th, right maxillary teeth; paroc, paroccipital processes; pmx-mx? premaxillary-maxillary suture? q, quadrate; qj, quadratojugal; sq, squamosal. Scale bars equal 10 mm.

et al., 2012). The dinosaurian and pseudosuchian components of this fauna are taxonomically diverse but less abundant than the rhynchosaur *Hyperdaperodon* which accounts for nearly 60% of all the recovered specimens (Martínez et al., 2012). Valid taxa of pseudosuchians described so far includes: the ornithosuchid *Venaticosuchus rusconii* (Bonaparte, 1970; von Baczko et al., 2014), the aetosaur *Aetosauroides scagliai* (Casamiquela, 1960; Desojo and Ezcurra, 2011), the poposaurid *Sillosuchus longicervix* (Alcober and Parrish, 1997), the non-crocodylomorph loricatan *Saurosichus galilei* (Sill, 1974; Alcober, 2000; Trotteyn et al., 2011) and the non-crocodyliform crocodylomorph *Trialestes romeri* (Reig, 1963; Bonaparte, 1978; Lecuona et al., 2016). Currently, *Trialestes romeri* represents one of the oldest members of Crocodylomorpha known to date (Irmis et al., 2013; Lecuona et al., 2016), although its taxonomic identity has historically been controversial due to the poor preservation and incompleteness of the holotype (PVL 2561) and the referral to this taxon of two materials (PVL 2559 and PVL 3889) without proper anatomical justification. In this sense, the specimen PVL 2559 was studied by Novas (1989, 1994) who removed it from the hypodigm and assigned it to Herrerasauridae indet. More recently, Lecuona et al. (2016) redescribed the specimens PVL 2561 and PVL 3889 and concluded that: “there is a strong similarity of the elements preserved in both specimens, specially the scapulae, humeri, ulnae, radii and pubes”. These authors recognized the presence of a strong lateral acromial ridge of the scapula (Fig. 3 A–C) as an autapomorphy of *Trialestes romeri*, uniting both specimens in the same hypodigm (Lecuona et al., 2016), in agreement with Bonaparte (1978).

Trialestes romeri was recently retrieved within Crocodylomorpha in two independent phylogenetic analyses (Lecuona et al., 2016; Leardi et al., 2017), in which was recovered as either forming a clade with *Pseudhesperosuchus jachaleri* near the base of Crocodylomorpha (Leardi et al., 2017), or well-nested within non-crocodyliform crocodylomorphs (Lecuona et al., 2016). *Trialestes romeri* has some traditional synapomorphies of Crocodylomorpha including elongated proximal carpals (Fig. 3E), a closed ectepicondylar groove, and a short and blunt

postglenoid process on the coracoid (Fig. 3E) (*sensu* Nesbitt, 2011; Leardi et al., 2017). The basal position recovered for *Trialestes romeri* in the analysis by Leardi et al. (2017) is due to the presence of an elongated anterior part (anterior to the antorbital fenestra) of the facial lamina of the maxillae, considered as a retention of a plesiomorphic character state when compared with more derived crocodylomorphs. On the other hand, the more crown-ward phylogenetic position recovered by Lecuona et al. (2016) for *Trialestes romeri* is due to the presence of a scapula less than 75% the length of the humerus length, a condition also shared with *Terrestriusuchus gracilis*, *Litargosuchus leptorhynchus*, *Junggarsuchus sloani*, and *Protosuchus richardsoni* (Lecuona et al., 2016).

Since the discovery of *Trialestes romeri*, more than half a century ago (Reig, 1963), no other valid crocodylomorph taxa has been formally described from the Ischigualasto Formation. However, Ezcurra et al. (2011) reported two specimens (PVSJ 846 and PVSJ 890) from the Cancha de Bochas Member of the Ischigualasto Formation and regarded them as a new medium-sized species of non-crocodyliform crocodylomorph with a lightly built axial skeleton. PVSJ 846 is the smaller specimen of the two and is represented by several cranial and postcranial elements, whereas PVSJ 890 is an isolated relatively large posterior cervical vertebra (maximum height of 13.2 cm; Ezcurra et al., 2011). These authors assigned both specimens to the same taxon based on the presence of a very deep fossa on the lateral surface of the mid-posterior cervical centra (among other unique combination of features) and recovered this putative new taxon nested within Crocodylomorpha and as the sister taxon to *Trialestes romeri* in a preliminary phylogenetic analysis (Ezcurra et al., 2011). The character states that would support the inclusion of the taxon (at least of specimen PVSJ 846) in Crocodylomorpha are the presence of a maxillary palatal process of the maxilla and an ilium with a preacetabular process that extends beyond the anterior acetabular margin. Furthermore, the new species was found as the sister taxon of *Trialestes romeri* based on the presence of a highly developed acromial process of the scapula and elongated anterior cervical vertebrae (Ezcurra et al., 2011). The authors also

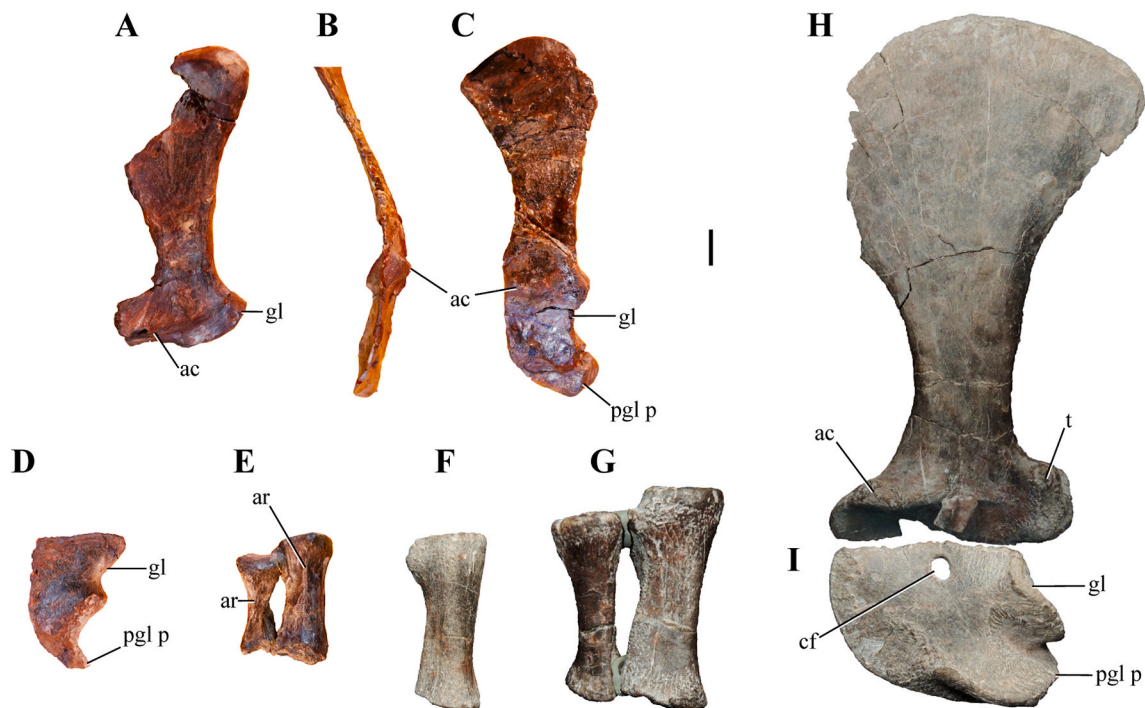


Fig. 3. Pectoral girdles and proximal carpals of crocodylomorph specimens from the Ischigualasto Crocodylomorph Assemblage. A, left scapula of PVL 2561 in lateral view; B, left scapulocoracoid of PVL 3889 in anterior view; C, left scapulocoracoid of PVL 3889 in lateral view; D, right coracoid of PVL 3889 in lateral view; E, right radiale and ulnare of PVL 2561 in anterior view; F, right radiale of PVSJ 1078 in anterior view; G, right radiale and ulnare of PVSJ 1088 in anterior view; H, right scapula of PVSJ 1090 in lateral view (reversed for comparison); I, left coracoid of PVSJ 1090 in lateral view. Abbreviations: ac, acromial process; ar, anterior ridge; cf, coracoid foramen; gl, glenoid; pgl p, postglenoid process; t, tuber. Scale bars equal 10 mm.

indicate that the new taxon differs from *Trialestes romeri* in the presence of a lateral process on the posterolateral surface of the scapula and the deeply excavated cervical vertebrae (Ezcurra et al., 2011). Following a formal description of PVSJ 846 and PVSJ 890, and if further studies confirm the identification of Ezcurra et al. (2011), the new taxon would become the second crocodylomorph species from the Ischigualasto Formation and one of the largest non-crocodyliform crocodylomorphs known to date.

In the last twenty years, the Instituto y Museo de Ciencias Naturales (IMCN) has been conducting field trips to the type locality of the Ischigualasto Formation in San Juan Province, Argentina. Among the many finds, there are four specimens (PVSJ 1078, PVSJ 1088, PVSJ 1089, and PVSJ 1090; Fig. 3F–I, Fig. 4) that have been assigned to Crocodylomorpha based on the presence of elongated proximal carpals. Currently, these specimens are under study for the doctoral thesis of one of the authors (IY). In the following lines we will introduce for the first time in the literature several elements of these specimens, briefly comment on their osteology, and discuss their taxonomic relevance. PVSJ 1078, 1088, 1089 and, 1090 come from the Hoyada de Ischigualasto (type locality of the Ischigualasto Fm.) in the Ischigualasto Provincial Park and were recovered from the lower third of the unit in the

Cancha de Bochas Member. The specimens were found mostly disarticulated but closely associated to each other in a bonebed. Three of the specimens (PVSJ 1078, 1088, and 1089) are represented by several cranial and postcranial bones, while PVSJ 1090 is only represented by postcranial bones (but awaits further preparation). Specimens PVSJ 1078 (humeral length 243 mm; femoral length 358 mm) and PVSJ 1090 (scapular length 186 mm) belong to two medium-sized individuals, whereas PVSJ 1088 (estimated humeral length 313 mm; femoral length 451 mm) and PVSJ 1089 (estimated femoral length 415 mm) belong to two larger individuals (see Table 1 for further measurements of the specimens). The difference in size between the larger and medium-sized individuals is about 26% (358 mm v. 451 mm femoral length of PVSJ 1078 and PVSJ 1088, respectively). In contrast, *Trialestes romeri* is a small-bodied crocodylomorph (PVL 2561 estimated scapular length 107 mm; PVL 2561 humeral length 160 mm; PVL 3889 femoral length 204 mm; Table 1; Lecuona et al., 2016). This implies that there is a difference in size between *Trialestes romeri* and the new specimens of around 75%–120% (based on femoral length). At the time of this publication there are no current features that distinguish between the new specimens and are tentatively considered as belonging to the same taxon. Differences between the new specimens and *Trialestes romeri* will be discussed in the



Fig. 4. Appendicular elements of crocodylomorph specimens from the Ischigualasto Crocodylomorph Assemblage. A, proximal head of left humerus of PVSJ 1088 in anterior view; B, right humerus of PVSJ 1078 in anterior view; C, detail of ectepicondyle of the right humerus of PVSJ 1078 in lateral view; D, right femur of PVSJ 1078 in anterior view; E, left femur of PVSJ 1088 in anterior view; F, distal head of left femur of PVSJ 1089 in distal view; G, right calcaneum of PVSJ 1088 in proximal view (anterior to left); H, right calcaneum of PVSJ 1088 in medial view (anterior to left); I, left humerus of PVL 2561 in anterior view (with diaphyseal segment removed since Lecuona et al., 2016); J, left humerus of PVL 3889 in anterior view ("probable" according to Lecuona et al., 2016); K, Left femur of PVL 3889 in anterior (top) and distal (bottom) views; L, right calcaneum of PVL 3889 in proximal view (anterior to left); M, right calcaneum of PVL 3889 in medial view (anterior to left). Abbreviations: alt, anterolateral tuber; cc, calcaneal condyle; cs, calcaneal socket; ct, calcaneal tuber; dp, deltopectoral crest; ec, ectepicondyle; en, entepicondyle; fc, fibular crest; lc, lateral condyle; mc, medial condyle; mp, medial process on calcaneum; pf, plopital fossa. Scale bars represent 10 mm.

Table 1

Selected measurements of the specimens from the Ischigualasto Formation. All measurements are the maximum measurable and in mm. (r) and (l) indicate right or left side element, respectively. *Incomplete element. PVL 2561 and PVL 3889 data taken from [Lecuona et al. \(2016\)](#). Abbreviations: **APL**, anteroposterior length; **DVH**, dorsoventral height; **LDC**, length of the deltopectoral crest; **LMW**, lateromedial width; **LSC**, length of scapulo-coracoid; **MPPH**, major posterior proximodistal height; **MWN**, minimum width of neck; **MWS**, minimum width of shaft; **WDB**, width of distal end of blade; **WDE**, width of the distal end; **WPE**, width of the proximal end.

	PVSJ 1078	PVSJ 1088	PVSJ 1089	PVSJ 1090	PVL 2561		PVL 3889	
					Right	Left	Right	Left
Scapula								
Length	–	–	–	186(r)	–	107.2*	84.8*	–
LSC	–	–	–	–	–	–	–	132.4
WDB	–	–	–	107.6*(r)	–	44.9*	45.1	49.7*
WPE	–	–	–	87.2(r)	–	44.6*	24.3*	30.7*
MWN	–	–	–	35.6(r)	–	19.8	20.2	21.2
Coracoid								
APL	–	–	–	66.1(l)	–	–	38.9*	34.8*
DVH	–	–	–	50.7(l)	–	–	37.4*	–
Humerus								
Length	243(r)	78.8*(l)	–	–	–	160	–	160
WPE	82.9(r)	97.6(l)	–	–	–	31.3*	–	37.6*
WDE	51.7(r)	–	–	–	–	31.1	–	35.3*
LCD	71.6(r)	74.2*(l)	–	–	–	76.0	–	–
Radiale								
Length	52.2(r)	68(r)	–	–	36.8	35.0	–	–
WPE	23.3(r)	31.7(r)	–	–	19.2	17.5*	–	–
WDE	18.8(r)	27.3(r)	–	–	15.6	18.2	–	–
MWS	14.5(r)	18.4(r)	–	–	12.2	13.1	–	–
Ulnare								
Length	–	55.6(r)	–	–	27.8	19.2*	–	–
WPE	–	19.8(r)	–	–	12.3	11.9	–	–
WDE	–	22(r)	–	–	12.3	9.8	–	–
MWS	–	12.3(r)	–	–	6.2	–	–	–
Femur length	358(r)	–	82*(l)	–	–	–	184*	204
Calcaneum								
APL	–	54.8(r)	–	–	–	–	28.7	–
LMW	–	36.8(r)	–	–	–	–	20.0	–
MPPH	–	36.1(r)	–	–	–	–	15.1	–

following lines.

As mentioned before, the new taxon possesses elongated proximal carpals. The right radiale is preserved in PVSJ 1078 (Fig. 3F), and both right radiale and ulnare are preserved in PVSJ 1088 (Fig. 3G). The radiale is longer and stouter than the ulnare. Both elements are proximodistally elongated, twice as long as their maximum proximal width (Table 1), a ratio that is similar to that present in other early crocodylomorphs (e.g., *Pseudhesperosuchus*, *Terrestriusuchus*, and *Dibothrosuchus*). The overall morphology of the proximal carpals is similar to that of the holotype of *Trialestes romeri* (PVL 2561; Fig. 3E), but they lack a ridge present on the anterior surface of both elements of the latter (Fig. 3E–G; [Lecuona et al., 2016](#)). The scapula of the new taxon, as represented by PVSJ 1090, is relatively complete, only lacking the anterodistal corner of the blade and a fragment of the proximal articular surface for the coracoid (Fig. 3H). The scapula possesses a lateromedially thin, fan-shaped, scapular blade that is also very similar to that of *Trialestes romeri*, although there is a size difference of about 73% (Fig. 3A, C, H; Table 1). PVSJ 1090 shares with *Trialestes romeri* the presence of a laterally well-developed acromial process that projects posteriorly towards the glenoid as a ridge. Nevertheless, the acromial process of PVSJ 1090 is dorsoventrally thicker than in *Trialestes romeri* and has a subtriangular outline in anterolateral view (Fig. 3H), whereas the acromial process in *Trialestes romeri* tapers laterally (Fig. 3A–C). Moreover, the scapula of PVSJ 1090 bears a lateral tuber on the posterolateral surface of the scapular body, just dorsolateral to the glenoid (Fig. 3H). A similar tuber is present in *Batrachotomus kupferzellensis* ([Gower and Schoch, 2009](#)) and in *Rauisuchus tiradentes* ([Lautenschlager and Rauhut, 2015](#)) and is interpreted as the origin site of the scapular head of M. triceps ([Meers, 2003](#); [Gower and Schoch, 2009](#)). This tuber is absent in both specimens of *Trialestes romeri* (Fig. 3 A, C) and other

non-crocodyliform crocodylomorphs (*Hesperosuchus agilis*, *Pseudhesperosuchus jachaleri*, *Dibothrosuchus elaphros*). However, it is noteworthy that this tuber is present on the scapula of PVSJ 846 ([Ezcurra et al., 2011](#); *iy pers. obs.*). The scapula of PVSJ 1090 and PVSJ 846 are practically indistinguishable from one another and are almost the same size, rendering this element as a taxonomic link between both specimens and a potentially diagnostic feature of this taxon.

The coracoid of the new taxon (PVSJ 1090, Fig. 3I) is subcircular in outline, its medial surface is markedly concave whereas the lateral surface is convex and possesses a well-developed coracoid foramen near the center of the articular margin with the scapula. The postglenoid process is separated from the glenoid by a narrow and posteriorly concave margin in lateral view. The postglenoid process is short and posteriorly directed, unlike the long and posteroventrally directed postglenoid process of most “small-bodied” crocodylomorphs (e.g., *Pseudhesperosuchus*, *Hesperosuchus*, *Sphenosuchus*). The coracoid of PVSJ 1090 has a strong ridge on its ventrolateral surface that starts immediately below the coracoid foramen and reaches the posterior end of the short postglenoid process (Fig. 3I). The coracoid of PVSJ 1090 greatly differs from that of *Trialestes romeri* (PVL 3889) in the absence of a postglenoid process that extends beyond the posterior margin of the glenoid as is typical in crocodylomorphs (e.g., *Terrestriusuchus gracilis*, *Pseudhesperosuchus jachaleri*, *Sphenosuchus acutus*). In that sense, the coracoid of PVSJ 1090 is more similar to that of non-crocodylomorph loricatans as *Batrachotomus kupferzellensis* and *Prestosuchus chiniquensis*.

A right humerus is fairly complete in PVSJ 1078, whereas PVSJ 1088 preserves only the proximal head of the left humerus (Fig. 4A and B). The humerus is a gracile bone with both proximal and distal ends mediolaterally expanded. The internal tuberosity is well-developed and proximomedially projecting in anterior view. The deltopectoral crest

originates just distal to the humeral head and strongly projects anteroventrally in lateral view, which confers it a triangular outline as in other crocodylomorphs (e.g., *Terrestrisuchus gracilis*, *Hesperosuchus agilis*, *Trialestes romeri*, and *Pseudhesperosuchus jachaleri*). At the distal end of the humerus, the lateral ectepicondylar surface lacks an ectepicondylar groove (Fig. 4C), as is the case in most “small-bodied” crocodylomorphs (Leardi et al., 2017), and unlike the condition in the “large-bodied” crocodylomorph *Carnufex* (Drymala and Zanno, 2016). In this regard, it is noteworthy that the humeral length of the new taxon (243 mm in PVSJ 1078) is larger than the humeral length of the holotype specimen of *Carnufex carolinensis* (210 mm; Zanno et al., 2015 Supplementary Information). The humeral size difference between *Trialestes romeri* (PVL 2561 and PVL 3889) and PVSJ 1078 is almost 52%, whereas with PVSJ 1088 there is almost a 95% size difference (Fig. 4A–B, I, J; Table 1). The humerus of PVSJ 1078 and PVSJ 1088 have a posteriorly expanded and hooked proximal head, which is also present in *Terrestrisuchus gracilis* (Crush, 1984), *Hesperosuchus agilis* (Colbert, 1952), *Sphenosuchus acutus* (Walker, 1990) and *Pseudhesperosuchus jachaleri* (Bonaparte, 1971). Moreover, the deltopectoral crest of PVSJ 1078 extends for less than 30% down the length of the humerus (Fig. 4B; Table 1) as in *Terrestrisuchus gracilis* (Crush, 1984), *Hesperosuchus agilis* (Colbert, 1952), and *Dibothrosuchus elaphros* (Wu and Chatterjee, 1993). On the other hand, the deltopectoral crest in the holotype of *Trialestes romeri* (deltopectoral crest not preserved in PVL 3889) extends for more than 30% down the length of the humerus (Fig. 4I; Table 1; Lecuona et al., 2016), a condition similar to that in *Sphenosuchus acutus* (Walker, 1990).

The femur of the new taxon is represented by a complete right element in PVSJ 1078 (Fig. 4D), although the anterior surface of the proximal half of the diaphysis is slightly crushed anteroposteriorly. Moreover, an almost complete left element is represented in PVSJ 1088, only lacking the distal end (Fig. 4E). Additionally, a distal end of a left femur is preserved in specimen PVSJ 1089 (Fig. 4F). The femur in PVSJ 1078 is around 47% longer than the humerus of the same specimen (Fig. 4B, D; Table 1). As mentioned before, there is roughly a 26% size difference between the femora of specimens PVSJ 1078 and PVSJ 1088 (Fig. 4 D–E; Table 1). The femur is a slender bone with a slightly sigmoidal shape in anterior view as in crocodylomorphs *Hesperosuchus agilis* (Colbert, 1952) and *Dromicosuchus grillator* (Sues et al., 2003). The femoral head is only barely anteroposteriorly compressed, slightly medially inturned, and transitions smoothly towards the femoral shaft. The femoral head bears on its anterior surface a well-developed anterolateral tuber (Fig. 4 D–E) as in many other loricatans (e.g., *Batrachotomus kupferzellensis*, *Postosuchus kirkpatricki*, *Hesperosuchus agilis*). The anterolateral surface of the femoral head possesses a very low and smoothly developed condylar fold. A similar development of this structure is seen in *Fasolasuchus tenax*, but contrasts with the condition of crocodylomorphs like CM 73372, *Hesperosuchus agilis*, *Dromicosuchus grillator*, and *Kayentasuchus walkeri*, in which the condylar fold is more pronounced (Nesbitt, 2011). Posteromedially, the femoral head of the new taxon bears both the anteromedial and posteromedial tubers. These tubers are equal in size, as is the case in most loricatans (e.g., *Batrachotomus kupferzellensis*, *Postosuchus kirkpatricki*, *Hesperosuchus agilis*) with the exception of *Prestosuchus chiniquensis* in which the posteromedial tuber is enlarged (Roberto-Da-Silva et al., 2018). The proximal surface of the femoral head possesses a transverse straight groove that is also present in some non-crocodylomorph loricatans (e.g., *Batrachotomus kupferzellensis*, *Saurosuchus galilei*, *Prestosuchus chiniquensis*; Nesbitt, 2011) but that is absent in *Fasolasuchus tenax*, *Postosuchus kirkpatricki* and crocodylomorphs (Nesbitt, 2011).

The femoral shaft is circular in cross-section and bears a dome-like longitudinally developed fourth trochanter on the posterior surface of the proximal half as in most crocodylomorphs like *Hesperosuchus agilis* (Colbert, 1952), *Dromicosuchus grillator* (Sues et al., 2003) and *Trialestes romeri* (PVL 3889; Lecuona et al., 2016). The distal end of the femur in the new taxon is slightly transversely expanded into two distinct condyles and the fibular crest. The medial condyle is the largest of the three

and is separated from the fibular crest by a well-developed popliteal fossa (Fig. 4F). The lateral condyle and the fibular crest form an obtuse angle in distal view (Fig. 4F). Among non-crocodyliform loricatans, the lateral condyle and the fibular crest form a right angle, except in *Prestosuchus chiniquensis* and *Saurosuchus galilei* in which they form an obtuse angle (Roberto-Da-Silva et al., 2018; Nesbitt, 2011).

Besides the previously mentioned size difference between the femur of *Trialestes romeri* (PVL 3889) and those of PVSJ 1078 and PVSJ 1088 (around 75% and 120%, respectively; Table 1), further comparison with *Trialestes romeri* becomes challenging because both referred femora are very poorly preserved and anatomical features in both proximal and distal ends have been removed by over preparation (Fig. 4K; Lecuona et al., 2016).

A right calcaneum is represented in PVSJ 1088. This heavily built element possesses the typical pseudosuchian morphology (Nesbitt, 2011). The calcaneum is anteroposteriorly longer than mediolaterally wide, with a posteriorly facing tuber and an anterior hemicylindrical calcaneal condyle for articulation with the fibula (Fig. 4G–F). Anterior to the hemicylindrical surface, a thin and smooth ridge of bone delimits the anterior end of the articular surface for the distal tarsal IV. The articular surface for the distal tarsal IV is separated from the calcaneal tuber by a well-developed fossa, a condition also shared with *Postosuchus kirkpatricki* (Weinbaum, 2013), *Batrachotomus kupferzellensis* (Gower and Schoch, 2009), *Prestosuchus chiniquensis* (Desojo et al., 2020) and *Dromicosuchus grillator* (Sues et al., 2003; Nesbitt, 2011). The calcaneal tuber is dorsoventrally flared in medial view (Fig. 4H) as in other loricatans (e.g., *Prestosuchus chiniquensis*, *Saurosuchus galilei*, *Postosuchus kirkpatricki*, *Dromicosuchus grillator*, *Trialestes romeri*; Fig. 4M). The calcaneal tuber projects posteriorly parallel to the horizontal plane (Fig. 4H), contrasting with the condition in *Postosuchus kirkpatricki* (Weinbaum, 2013) and *Macelognathus vagans* (Göhlich et al., 2005) in which the calcaneal tuber projects posterodorsally (posteroproximally), forming an acute angle with respect to the horizontal plane. Posteriorly, the calcaneal tuber has a subrectangular outline, is more taller than broad, and possesses a dorsoventrally aligned median depression (Fig. 4G), similar to *Prestosuchus chiniquensis* (Desojo et al., 2020) and *Postosuchus kirkpatricki* (Weinbaum, 2013), but contrasting with the condition in *Batrachotomus kupferzellensis* (Gower and Schoch, 2009) which possesses a rounded posterior calcaneal surface, and with *Trialestes romeri* (PVL 3889), which possesses a circular hollow on the same surface (Fig. 4L; Lecuona et al., 2016). The calcaneal tuber is mediolaterally broader at mid-shaft than the width of the calcaneal condyle (Fig. 4G). This condition is intermediate between that of *Saurosuchus galilei*, *Postosuchus kirkpatricki*, *Dromicosuchus grillator* or *Trialestes romeri* (PVL 3889; Fig. 4G) in which the shaft of the calcaneal tuber is about the same size or slightly broader than the width of the calcaneal condyle, but contrast with the condition in *Prestosuchus chiniquensis* and *Batrachotomus kupferzellensis* in which the calcaneal shaft is almost twice the mediolateral width of the fibular facer (Fig. 4 G–H, L–M; Desojo et al., 2020; Gower and Schoch, 2009; Nesbitt, 2011). The calcaneal socket is dorsoventrally tall, circular in outline and moderately deep (Fig. 4H). The posterior wall of the calcaneal socket continues onto a subtriangular, medially projecting process for articulation with the astragalus (Fig. 4G).

Rigorous comparison between the calcaneum of PVSJ 1088 and that of *Trialestes romeri* (PVL 3889) is not straightforward because of the difficulty to discriminate between what actually are natural differences between them, and what are due to preservational or preparation artifacts, as extensively discussed by Lecuona et al. (2016). Nevertheless, there still are some differences in *Trialestes romeri* (PVL 3889) that can be pointed out, in addition to the previously mentioned ones. Unlike the calcaneum in PVSJ 1088, the ventral calcaneal surface in *Trialestes romeri* (PVL 3889) is continuously anteroposteriorly concave, lacking the distinct ventral fossa that separates the articular surface for distal tarsal IV from the calcaneal tuber (Lecuona et al., 2016). The posterior surface of the calcaneal tuber in *Trialestes romeri* (PVL 3889) has a deep

circular hollow (Fig. 4L) and not a dorsoventral depression as in PVSJ 1088 and other loricatans. Finally, the posteroventral (posterodistal) margin of the calcaneal tuber in *Trialestes romeri* possesses a posteriorly projected small process, just beneath the posterior hollow that is not present in any other loricatan (Lecuona et al., 2016).

3.3. Los Colorados assemblage

The Los Colorados Formation represents the top of the succession of the Ischigualasto-Villa Unión Basin, overlying the deposits of the Ischigualasto Formation (Caselli et al., 2001). The age of Los Colorados

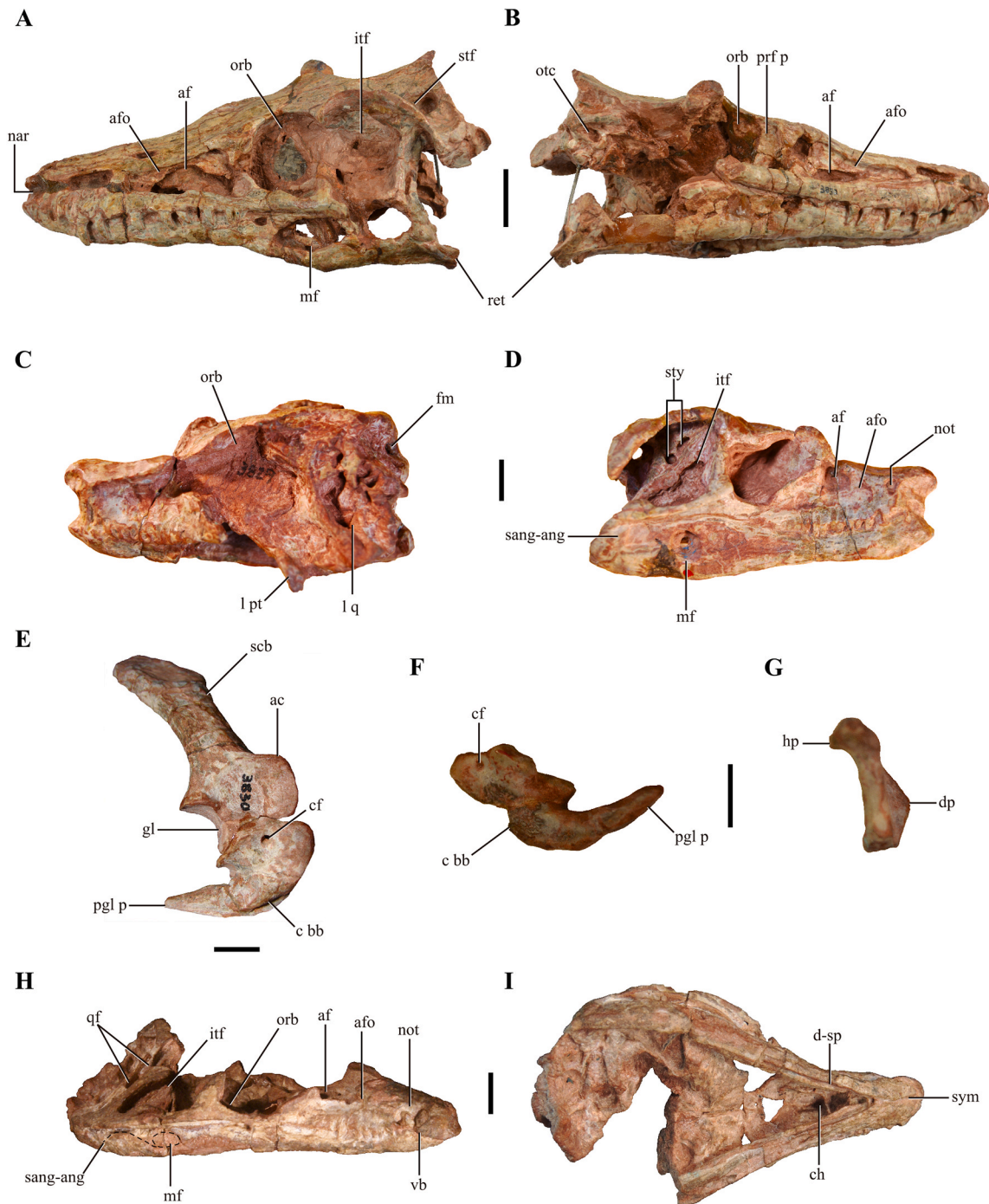


Fig. 5. Selected crocodylomorph remains from the Los Colorados Crocodylomorph Assemblage. Skull of *Pseudhesperosuchus jachaleri* (PVL 3830) in A, left lateral, and B, right lateral views. Skull of *Hemiprotosuchus leali* (PVL 3829) in A, left lateral, and B, right lateral views. E, Right pectoral girdle of *Pseudhesperosuchus jachaleri* (PVL 3830) in lateral view. Anterior appendicular elements of PVL 3842, F, left coracoid in lateral view; G, proximal end of the left humerus. Skull of *Coloradisuchus abelini* (CRILARPV 301) in H, right lateral view; and, I, ventral view. Abbreviations: ac, acromial ridge; af, antorbital fenestra; afo, antorbital fossa; c bb, crest related to the origin of the M. biceps brachii; ch, choana; cf, coracoid foramen; dp, deltopectoral crest; d-sp, dentary-splenic suture; fm, foramen magnum; gl, glenoid; hp, humeral hooked process; itf, infratemporal fenestra; l q, left quadrate; l pt, left pterygoid; mf, mandibular fenestra; nar, narial opening; not, notch for the hypertrophied mandibular tooth; orb, orbit; otc, otic capsule; pgl p, postglenoid process; prf p, prefrontal pillar; qf, quadrate foramina; ret, retroarticular process; sang-ang, surangular-angular suture; scb, scapular blade; sty, subtymppanic foramina; sym, mandibular symphysis; vb, ventral boundary of the notch for the hypertrophied tooth of the mandible. Scale bars equals 10 mm (A–E; H–I) or 5 mm (F–G).

Formation has long been considered Late Triassic (Norian) based on faunal and stratigraphic relationships (Stipanovic and Bonaparte, 1972; Bonaparte, 1982), an idea also supported by recent magnetostratigraphic studies (Kent et al., 2015). However, unlike the underlying Ischigualasto Formation, no radiometric age is available for this formation.

The Los Colorados Formation has yielded one of the key faunal assemblages needed to evaluate the changes in the terrestrial tetrapod communities at the Triassic-Jurassic transition (Arcucci et al., 2004). This led to the recognition of a particular local faunal association that has been considered later as a proxy for faunal comparisons (Coloradian; Bonaparte, 1982), and is maintained even in modern studies (Ezcurra, 2010). The vertebrate record of Los Colorados Formation comes mostly from what has been known as the “Upper Levels” of the classical locality of La Esquina, although additional remains have been recovered elsewhere (Caselli et al., 2001). The faunal assemblage is heavily dominated by a diverse association of archosaurs, with records of both pseudosuchians (aetosaurs, non-crocodylomorph paracrocodylomorphs and crocodylomorphs) and dinosaurs, with less common remains of other tetrapods such as turtles and synapsids (Arcucci et al., 2004). The crocodylomorph record of the Los Colorados Formation is quite diverse and three valid taxa have been recognized to date: *Pseudhesperosuchus jachaleri* Bonaparte (1967), *Hemiprotosuchus leali* Bonaparte (1967), and *Coloradisuchus abelini* Martínez et al. (2018). It is unique because it represents the first unambiguous record of crocodyliforms (*Hemiprotosuchus* and *Coloradisuchus*) and the oldest association between a non-crocodyliform crocodylomorph and a crocodyliform (Irmis et al., 2013). Apart from the recent description of *Coloradisuchus*, the rest of the taxa recovered from the formation has not been restudied since Bonaparte (1967, 1972) seminal studies of the vertebrates from the Los Colorados Formation. Below we will summarize what is known up to the date for these taxa.

Pseudhesperosuchus jachaleri is a basal non-crocodyliform crocodylomorph that was formally named by Bonaparte (1967) and later was well described by the same author (1972). *Pseudhesperosuchus* is known from a single specimen (PVL 3830) that is represented by an almost complete skull (Fig. 5 A–B) and a rather well represented postcranial skeleton, which includes several vertebrae (most without remains of the neural arches) and appendicular elements from the fore- and hindlimbs (e.g., Fig. 5 E). Bonaparte (1972) included reconstructions of its skull in several views and a photo of the skull in lateral view. This has proven problematical in several reviews or scorings involving the taxon, as different authors (Parrish, 1993; Clark et al., 2000) had different interpretations of the anatomy when compared with Bonaparte (1972) reconstructions. Although a restudy of this specimen is needed, general comments about the specimen and its placement among basal crocodylomorphs will be made here. It is important to note that most of the phylogenetic information comes from the skull of *Pseudhesperosuchus* (Lecuona et al., 2016 and Leardi et al., 2017 are the only recent data sets where this specimen has been included). Considering this, it is also relevant to note that the skull of the only known specimen (PVL 3830) is heavily deformed and has suffered ventrolateral crushing towards its right side (Fig. 5 A–B).

One of the most controversial points regarding *Pseudhesperosuchus* anatomy concerns the presence of a preorbital opening. This feature has been considered and artifact (Clark et al., 2000), because it is asymmetrical on either side of the skull, an interpretation we agree with. On the occipital region of the skull, Bonaparte (1972) identified two or three large openings and interpreted the lateralmost as the post-temporal fenestra (Bonaparte, 1972: Fig. 25). However, in most crocodylomorphs the post-temporal fenestrae have some participation of both the squamosal and the otoccipital in their borders (Pol et al., 2013: char. 74), thus falsifying Bonaparte (1972) initial interpretation. Thus, we interpret the smaller opening at the triple contact between the squamosal, parietal and otoccipital as the post-temporal fenestrae and the remaining one as the result of preparational damage. The snout of

PVL 3830 is also damaged precluding the recognition of some sutures, but personal observations (JML pers. obs) revealed that, as in most crocodylomorphs (Clark, 1986), the jugal does not enter the antorbital fossa/fenestra.

From a phylogenetic point of view, *Pseudhesperosuchus* was included in several phylogenetic analyses (e.g., Benton and Clark, 1988; Parrish, 1991; Wu and Chatterjee, 1993; Clark et al., 2004). In these analyses *Pseudhesperosuchus* was recovered in a large polytomy involving several basal crocodylomorphs (Clark et al., 2004; Pol et al., 2013) or as a basal member of Sphenosuchia, when such a clade was recovered (e.g., Sues et al., 2003). In two most recent analyses, *Pseudhesperosuchus* was recovered near the base of Crocodylomorpha either closely related to the large bodied crocodylomorph *Carnufex* (Lecuona et al., 2016) or to *Trialestes* (Leardi et al., 2017). *Pseudhesperosuchus* bears some typical synapomorphies of Crocodylomorpha such as a lateral squamosal flange, a postglenoid process on the coracoid (Fig. 5 E) and elongated proximal carpals (Clark, 1986). The basal position recovered for this taxon in these modern analyses is usually due to the retention of plesiomorphies compared with other more nested crocodylomorphs, such as the presence of an elongated anterior part (anterior to the antorbital fenestra) of the facial lamina of the maxilla (Leardi et al., 2017).

The Los Colorados Formation has the oldest record of fossil crocodyliforms to date that has recently been augmented by the report of another taxon (Bonaparte, 1967; Martínez et al., 2018). This record contrasts with the presence of basal crocodyliforms in other parts of Pangea, which appear during the Early Jurassic age (e.g., Upper Elliot Formation; Lufeng Formation; Moenave Formation), with the possible exception of *Protosuchus micmac* from the McCoy Brook Formation that was recently assigned to the latest Triassic (Sues and Olsen, 2015). The first taxon reported was *Hemiprotosuchus leali* (Bonaparte, 1967). Bonaparte (1972) reported the presence of two specimens: the holotype (PVL 3829; not PVL 3833 as Bonaparte [1972] mentioned), which includes a badly preserved but complete skull (Fig. 5 C–D), osteoderms and partial remains of the hindlimb; and, an isolated left coracoid and humerus (PVL 3842, Fig. 5 F–G; not PVL 3843 as Bonaparte [1972]). Additional remains tentatively referred to *Hemiprotosuchus* can be found at the Instituto Miguel Lillo collections (PVL 4420), but these isolated cranial (anterior tip of the dentaries; partial maxilla) and hindlimb remains do not bear any shared autapomorphies that support this assignment.

Hemiprotosuchus was initially placed with *Protosuchus richardsoni* in the family Protosuchidae. These affinities were supported by the superficial resemblance of the skulls between both taxa, particularly between the elements of the temporal region and the suspensorium, although some differences were noted in the general shape of the snout (wider in *Hemiprotosuchus*) and the antorbital fenestra (which was thought to be absent in *Protosuchus*, based on Colbert and Mook's (1951) description) (Bonaparte, 1972). Subsequent studies using phylogenetic methods (Clark, 1986; Clark, 1994; Wu et al., 1997; Pol et al., 2004) have added support to this hypothesis, recovering a close relationship between *Hemiprotosuchus*, the genus *Protosuchus* (*P. richardsoni* and *P. haughtoni*; *P. micmac* has not been included in any phylogenetic analysis up to date), *Edentosuchus* and an undescribed “edentosuchid” from the Kayenta Formation (Clark, 1986; UCMP 97,638, 125,359, 125,871; see below). This clade has been equated to the Linnean family Protosuchidae Brown, 1934 (sensu Clark, 1986), which displays high support values in most analyses where these taxa are incorporated, and has been consistently recovered as the basalmost clade of Crocodyliformes (Clark, 1986; Pol and Norell, 2004; Martínez et al., 2018). Even though the preservation of the skull of the holotype (PVL 3829) is deficient and some features are difficult to observe (Fig. 5 C–D), the specimen displays typical synapomorphies of Protosuchidae (Pol et al., 2004; Pol and Norell, 2004; Martínez et al., 2018) such as: a long medial process of the articular that contacts the otoccipital and basisphenoid; a dorsally arched surangular posterior to the mandibular fenestra; at least a partially closed (completely closed in *Hemiprotosuchus*) notch for the

hypertrophied anterior mandibular tooth; and, a dorsoventrally high maxillary contribution to the antorbital fossa (Fig. 5 C–D).

Besides the holotype, Bonaparte (1972) assigned an isolated coracoid and proximal part of a left humerus (PVL 3842, Fig. 5 F–G; as an hypodigm) based on a similar size and that they were recovered in close association with the holotype (“... en estrecha asociación con el resto de los materiales de *Hemiprotosuchus* ...” [sic Bonaparte, 1972: p. 118]). Although we agree with Bonaparte (1972) comment about the similar size, the traits in some of these remains preclude its referral to any known crocodyliform. The proximal part of the left humerus bears a hooked posteroproximal process that has been regarded as a synapomorphy of Rauisuchidae (e.g., *Rauisuchus triradentes*, *Postosuchus kirkpatricki*) plus Crocodylomorpha (Nesbitt, 2011) (Fig. 5 G). Furthermore, this trait is present in basal crocodyliforms such as the protosuchids *P. haughtoni* (SAM-PK-K 8026; Leardi et al., 2017) and the basal crocodyliform *Orthosuchus* (SAM-PK-K 409; Nesbitt, 2011). However, the morphology of the coracoid differs from the one observed in crocodyliforms, which have a wide, posteroventrally projected and distally expanded postglenoid process (Clark et al., 2000). PVL 3842 resembles the condition of non-crocodyliform crocodylomorphs (Fig. 5 F), which unlike other archosauriforms, bear a long and posteriorly projecting postglenoid process (e.g., *Pseudhesperosuchus*, Fig. 5 E; Wu and Chatterjee, 1993; Clark et al., 2000). This morphology is known exclusively in non-crocodyliform crocodylomorphs to date (JML, pers. obs), casting doubts on the assignment of PVL 3842 to Crocodyliformes (i.e., *Hemiprotosuchus leali*). On the other hand, PVL 3842 could represent an additional specimen of *Pseudhesperosuchus*, the only known non-crocodyliform crocodylomorph in the unit. Yet the coracoid of PVL 3842 is markedly smaller than the one of *Pseudhesperosuchus* (PVL 3830) and differs from it in several features: a) the postglenoid process of PVL 3842 is separated by a distinct step from the body of the coracoid, whereas it is not in *Pseudhesperosuchus*; b) the postglenoid process is curved and slightly dorsally directed in PVL 3842, unlike the straight process of *Pseudhesperosuchus*; and, c) both postglenoid processes have a crest in a region that is topographically consistent with the origins of the coracoid head of the *M. biceps brachii* (Meers, 2003), but in *Pseudhesperosuchus* the crest is located on the lateral surface and in PVL 3842 it is located on the ventral edge. Thus PVL 3842 represents the postcranial remains of a new, yet unknown smaller crocodylomorph taxon of the Los Colorados Formation. Given the few remains known, we leave this specimen as unnamed taxonomical unit and advise other researchers to do so until more material is recovered.

Finally, the latest addition to the Los Colorados crocodylomorphs has been *Coloradisuchus abelini* (Martínez et al., 2018). This taxon is known from a single specimen represented by a well preserved but flattened skull that lacks the skull roof, and some anterior axial elements (which remain unpublished). Martínez et al. (2018) describe this specimen, identifying on it typical protosuchid characters, such as the medial process of the articular that forms an additional articulation with the braincase, a dorsally projecting surangular and a partially closed notch for the hypertrophied mandibular tooth (Martínez et al., 2018, Fig. 5 H–G). *Coloradisuchus* is clearly differentiable from *Hemiprotosuchus* and represents a second crocodyliform (Protosuchidae) known for the formation, which in turn is the oldest Formation yielding remains of the clade globally. Furthermore, this increase of taxa known for the Los Colorados Formation documents the early diversification of crocodyliforms, suggesting that it was restricted to southwestern Pangea in the late Norian (Kent et al., 2015; Martínez et al., 2018), and that the clade diversified after that (e.g., Sues and Olsen, 2015).

4. Discussion

4.1. South American Crocodylomorph record

The detailed review of the units bearing crocodylomorph remains in South America allowed us to evaluate the distribution of the taxa in this

region of Pangea. In particular the presence of any crocodylomorph taxa previous to the Carnian has now been invalidated as the only putative taxa previous to this age (*Barberenasuchus brasiliensis*) does not preserve any synapomorphies of the clade (in accordance with previous studies, e.g., Irmis et al., 2013). Furthermore, the only specimen known of *Barberenasuchus* displays traits that are not present in any member of the clade known up to date. As such, the crocodylomorph bearing formations of South America are restricted to the two Argentinian units from the upper section of the Ischigualasto-Villa Unión basin: Ischigualasto and Los Colorados formations. Additionally, the review and data presented in this contribution has updated the knowledge on these two crocodylomorph assemblages.

The Ischigualasto crocodylomorph assemblage has the oldest “small-bodied” crocodylomorph remains worldwide. Other crocodylomorph-bearing units of Carnian age (Pekin Formation, North Carolina, USA) have remains of “large-bodied” crocodylomorphs (i.e., *Carnufex*), whereas smaller crocodylomorphs appear globally in units of Norian or younger ages (Irmis et al., 2013; Leardi et al., 2017). *Trialestes* is not the only crocodylomorph represented in the Ischigualasto Formation, as in previous sections we have reported at least one additional new taxon (depending on the final taxonomic status of PVSJ 890). This putative new taxon displays particular anatomical features unique among the crocodylomorphs known up to date, being its large size one of the most notable differences with other early crocodylomorphs (i.e., “small-bodied” crocodylomorphs sensu Zanno et al., 2015). However, the Ischigualasto new taxon bears characters that have only been reported in “small-bodied” taxa, such as a closed ectepicondylar groove and the presence of elongated proximal carpals (Fig. 3 H–I) and an elongated and posteroventrally directed postglenoid process of the coracoid (Fig. 3A).

The new Ischigualasto taxon is also relevant in both the global and local aspects of the Ischigualasto vertebrate association. The new taxon (PVSJ 846, PVSJ 1078, PVSJ 1088, PVSJ 1089, PVSJ 1090) represents the first record of a “large-bodied” crocodylomorph taxon on the southwestern region of Pangea, a record only restricted up to this contribution to the northwestern part of the supercontinent (Nesbitt et al., 2005; Nesbitt, 2011; Zanno et al., 2015). Additionally, considering the morphology of the new taxon, the assignment of the referred specimen PVL 3889 to *Trialestes* needs to be reviewed. The assignment was based on the presence of a laterally projected acromial crest on the scapula of both specimens (the holotype 2561, and PVL 3889; Lecuona et al., 2016). Our preliminary description of the new Ischigualasto materials show that this feature was more widely distributed among basal crocodylomorphs of the Ischigualasto crocodylomorph assemblage. Moreover, the assignment of PVL 3889 should be considered in the context of the entire crocodylomorph diversity of Ischigualasto.

The Los Colorados crocodylomorph assemblage is the unit that has the oldest crocodyliform record and the oldest coexistence of a non-crocodyliform crocodylomorph and two crocodyliforms (Irmis et al., 2013; see 3.3. Los Colorados crocodylomorph assemblage). The two best known taxa from this assemblage (*Pseudhesperosuchus* and *Hemiprotosuchus*) are well-represented but their detailed anatomy still needs to be reviewed (JML, in prep). However, both these taxa are recovered as basal members of their respective clades in recent analyses. Recently reported taxa (*Coloradisuchus*) also are recovered as basal among their clades (i.e., protosuchid crocodyliform). Finally, the Los Colorados Formation has a diverse vertebrate association (e.g., Arcucci et al., 2004), and during recent field seasons new specimens are being recovered (Apaldetti et al., 2018). This scenario does not seem any different among pseudosuchians, as in this contribution at least a putative new non-crocodyliform crocodylomorph has been identified from the formation.

4.2. Comparisons with other Crocodylomorph assemblages of Pangea

To compare the composition of the crocodylomorph assemblages of

South America the only coeval faunal associations are those of north-western (southwestern USA) and northcentral Pangea (Eastern USA and Central Europe) (Fig. 1). The Karoo Basin in South Africa has usually been compared with the faunal assemblages in South America, however the crocodylomorph bearing units of South Africa have been now confidently dated using absolute methods as Early Jurassic (i.e., Upper Elliot Formation; Bordy et al., 2020). Similar comparisons have been made with the Lufeng Formation, so the crocodylomorphs from this stratigraphic unit and their comparisons with the South American ones will be discussed later. Finally, the Upper Jurassic records (Morrison, Cañadón Calcareo, and Shishugou formations) will not be discussed, as they belong to a deeply nested array of crocodylomorph taxa with very particular anatomy and close affinities with Crocodyliformes (see Clark et al., 2004; Pol et al., 2013; Leardi et al., 2017, 2020).

All Triassic localities in northern Pangea have a similar faunal composition, with regard to Crocodylomorpha, as they are dominated by basal non-crocodyliform crocodylomorphs. As it has been noted previously (Irmis et al., 2013) the northern crocodylomorph absolute diversity (i.e., total number of taxa) in the Late Triassic is higher (7 valid taxa; Fig. 1) when compared to the number of taxa in southern Pangea (i.e., 4 in northwestern Argentina), mostly due to the diversity recovered in USA (5 valid taxa). These crocodylomorph assemblages are dominated by non-crocodyliform crocodylomorphs that in most recent phylogenetic analyses have been recovered close to the root of the clade (Lecuona et al., 2016; Leardi et al., 2017). In particular, the North American assemblages differ from the European ones not only in their diversity but also in the records of “large-bodied” taxa and that the “small-bodied” taxa of North America have been recovered forming a rather well-supported monophyletic clade (Leardi et al., 2017). On the other hand, the European assemblages have a very low diversity (1 valid species in each locality), but with high abundance (at least 9–18 humeri-specimens of *Terrestriusuchus*, Crush, 1984; and 4 specimens of *Saltoposuchus*).

The other units with good record of Crocodylomorpha are of Early Jurassic age. Strong affinities have been recovered among the South African and South American faunas, mostly due to the presence of massopodan sauropodomorphs and tritheledontid cynodonts (Ezcurra, 2010). Among crocodylomorphs, these assemblages share the presence of protosuchid crocodyliforms (*P. haughtoni*) and other basal crocodyliforms (*Orthosuchus strombergi*; and *Notochampsia istediana* and *Erythrochampsia longipes*, which are currently regarded as nomen dubium) (Fig. 1). However, when non-crocodyliform crocodylomorphs are considered the situation is different, as the Upper Elliot taxa (*Sphenosuchus* and *Litargosuchus*) have been recovered well nested and more closely related to Crocodyliformes than the South American Triassic taxa (Pol et al., 2013; Leardi et al., 2017).

Lower Jurassic units from northwestern Pangea (USA and Canada; Fig. 1) also have the presence of protosuchid crocodyliforms (*P. richardsoni*, and the Kayenta edentosuchid), but neither of the northern protosuchids are more closely related to the South American ones (Martínez et al., 2018). A taxon that is relevant in this context is the putative protosuchid *Eopneumatosuchus* (Crompton and Smith, 1980), whose affinities have not been studied in detail. On the other hand, another diverse northern crocodylomorph assemblage is the one recorded in the Lower Lufeng Formation in northeastern Pangea (Luo and Wu, 1994). This assemblage shares the presence of non-crocodyliform crocodylomorphs (*Dibothrosuchus elaphros* and the dubious *Phylodontosuchus changchiwaensis*) and the basal crocodyliforms *Platyognathus* and *Dianosuchus* (Luo and Wu, 1994). In past contributions both crocodyliforms of the Lower Lufeng Formation have been considered as members of Protosuchia (Luo and Wu, 1994; Wu and Sues, 1994), a clade that has not been recovered as monophyletic in most recent analyses (Pol et al., 2004; Clark et al., 2004; Leardi et al., 2017). In this context, both Lufeng crocodyliforms have a notch that receives one or more enlarged anterior mandibular teeth (Wu and Sues, 1994), a feature now known not to be exclusive of these basal forms and is more widely distributed.

Furthermore, Luo and Wu (1994) suggested the presence of a dorsally projected surangular on both these taxa, a feature common among members of Protosuchidae (Martínez et al., 2018). However, this claim was not mentioned in later contributions dealing with *Platyognathus* anatomy (Wu and Sues, 1994) and the mandible of the only specimen of *Dianosuchus* (IVPP V4730) is crushed and precludes the observation of this feature (JML pers. obs.). Thus, the affinities of the crocodyliforms of the Lower Lufeng Formation are still in need of a review, but their membership to Protosuchidae (sensu Clark, 1986) can not be supported based on the features proposed by Luo and Wu (1994) and Wu and Sues (1994). The only taxon whose anatomy and affinities are well known is *Dibothrosuchus* (Wu and Chatterjee, 1993). This non-crocodyliform crocodylomorph has been recovered as closely related to other Jurassic forms (e.g., *Sphenosuchus*, *Junggarsuchus*, and hallopodids) that, in turn, are found more closely related to Crocodyliformes (Clark et al., 2004; Leardi et al., 2017).

South American crocodylomorph assemblages differ from other records of crocodylomorphs around Pangea. The Ischigualasto Formation has recorded basal members of the clade, both “small” (*Trialestes*) and “large-bodied forms” (Ichigualasto new taxon), a group of taxa also present in northwestern Pangea (North America). This contrasts with the general hypothesis, considering other members of the association, where the Ischigualastian association is found grouped with the Santa María association and distant from the North American ones (Ezcurra, 2010). On the other hand, the Los Colorados crocodylomorph assemblage has recorded basal non-crocodyliform crocodylomorphs and the first record of the initial diversification of crocodyliforms with the appearance of protosuchids (*Hemiprotosuchus* and *Coloradisuchus*). The composition of this assemblage is quite unique, as in most parts of Pangea the protosuchids appear in the Early Jurassic, and the non-crocodyliform crocodylomorphs of this age have different phylogenetic affinities (see above). The only exception is the Fundry Rift Basin in eastern Canada, where the protosuchid *P. micmac* has been recovered in the talus slope breccia deposits of the McCoy Brook Formation (Sues et al., 1996; Sues and Olsen, 2015). Thus, the Los Colorados Crocodylomorph Assemblage has a transitional nature between those of the Upper Triassic and the Lower Jurassic of most parts of Pangea.

5. Conclusions

In our review of the South American crocodylomorph assemblages we reduced the presence of the members of the clade solely to the two upper units of the Triassic sequence of the Ischigualasto-Villa Unión Basin in Argentina (Ischigualasto and Los Colorados formations) (Table 2). The other putative record was *Barberenasuchus barsiliensis* Mattar (1987) from the Santa María Supersequence in southern Brazil, but we found no evidence to support this assignment.

The Ischigualasto Formation from northwestern Argentina has the oldest “small-bodied” crocodylomorph (*Trialestes romerii*). Here we report for the first time a new, yet undescribed, taxon of a “large-bodied” crocodylomorph represented by four specimens (PVSJ 1078, PVSJ 1088, PVSJ 1089, and PVSJ 1090) (Table 2). This new taxon undoubtedly represents a large crocodylomorph, as its humeral length exceeds by far (i.e., more than 30 mm) the length of other taxa considered as such (i.e., *Carnufex carolinensis*). The new Ischigualasto taxon displays unique combination of characters when compared with other “large-bodied” crocodylomorphs, as it displays typical features that have been associated with classical crocodylomorphs (e.g. closed ectepicondylar groove, elongated proximal carpals). In addition, this new taxon has differences with *Trialestes* (e.g., less distally extended deltopectoral crest, lacks a crest on the anterior surface of the radiale, shallower depression on the distal surface of the calcaneum), justifying its separation as an independent taxonomical unit. Finally, this new taxon has a laterally projecting acromial crest, a feature that was previously cited as an autapomorphy of *Trialestes* (Lecuona et al., 2016). This raises the question about the assignment of the referred specimen (PVL 3889) of

Table 2

Taxa from the South American Crocodylomorphs Assemblages, before and after this review.

Crocodylomorph Assemblage	Before	After
Santa María	<i>Barberenasuchus brasiliensis</i> Mattar (1987) (MCP 3844 PV)	–
Ischigualasto	<i>Trialestes romeri</i> Reig (1963) (PVL 2561, 3889) Unpublished tax (PVSJ 846, 890)	<i>Trialestes romeri</i> Reig (1963) (PVL 2561) Unpublished tax (PVSJ 890)? PVL 3889? Ischigualasto n. tax (PVSJ 846, 1078, PVSJ 1088, PVSJ 1089, 1090)
Los Colorados	<i>Pseudhesperosuchus jachaleri</i> Bonaparte (1967) (PVL 3830) <i>Hemiprotosuchus leali</i> Bonaparte (1967) (PVL 3829, 3842) <i>Coloradisuchus abelini</i> (CRILARPV 301)	<i>Pseudhesperosuchus jachaleri</i> Bonaparte (1967) (PVL 3830) Non-crocodyliform Crocodylomorpha (PVL 3829) <i>Hemiprotosuchus leali</i> Bonaparte (1967) (PVL 3829) <i>Coloradisuchus abelini</i> (CRILARPV 301)

Trialestes to that taxon. When compared with other Triassic records of Pangea, the Ischigualasto crocodylomorph assemblage shares closer similarities with the assemblages of North America, as these share the presence of “large-bodied” taxa (*Carnufex*, *Redondavenator*, CM 73372, Ischigualasto new taxon) and other smaller early members of Crocodylomorpha (*Hesperosuchus*, *Dromicosuchus*, *Trialestes*). Analyzing only the crocodylomorph assemblages, this contrasts with the more general trend observed by [Ezcurra \(2010\)](#) who obtained a closer similarity of the Ischigualasto association with the one present in Santa María Supersequence.

Finally, in this contribution, we add a putative additional new taxon (PVL 3842) to the already diverse Los Colorados crocodylomorph assemblage. This new occurrence represents the second non-crocodyliform crocodylomorph from the formation (Table 2). The co-occurrence of both non-crocodyliform crocodylomorphs and crocodyliforms has been noted as unique among other associations in Pangea ([Irmis et al., 2013](#)), and this makes the Los Colorados crocodylomorph assemblage of transitional nature between the typical Norian assemblages in northern Pangea and the more widely distributed Early Jurassic assemblages (Upper Elliot, Kayenta, Moenave, Lower Lufeng formations).

CRediT authorship contribution statement

Juan Martín Leardi: Conceptualization, Investigation, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Imanol Yáñez:** Investigation, Writing - original draft, Writing - review & editing, Visualization. **Diego Pol:** Investigation, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank C. Marsicano, L. Gaetano and R. Irmis for the invitation to participate in this special volume. We would like to thank A. Ribeiro (MCP), Pablo Ortíz (PVL), R. Martínez (PVL) and L. Fiorelli (CRILAR) for access to material under their care. We also thank S. Nesbitt (VT) for sharing better photographic material of

Barberenasuchus. We are thankful for the input of the two anonymous reviewers whose comments greatly improved the final version of this paper. This research was made possible by the grants of the Agencia de Promoción Científico y Tecnológica PICT 2013–2725 (to JML), 2015–0504, and 2016–0267 (to JML), PIP 112201501 and by a CONICET doctoral fellowship (to IY). This is J.M.L.’s R-328 contribution to the Instituto de Estudios Andinos Don Pablo Groeber.

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