



A new stahleckeriid dicynodont record from the late Ladinian-?early Carnian levels of the Chañares Formation (Ischigualasto-Villa Unión Basin) of northwestern Argentina

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ARTICLE INFO

Keywords:

Dicynodontia
Kannemeyeriiformes
Stahleckeriidae
Triassic
Postcranium
South America

ABSTRACT

The kannemeyeriiforms of the latest Ladinian-?early Carnian Chañares Formation (Ischigualasto-Villa Unión Basin) exemplify the historical taxonomic controversies of several South American dicynodonts. Three taxa were originally recognized based on skull anatomy: “*Chanaria*” *platyceps* and two species of *Dinodontosaurus* (genus otherwise known in the Pinheiros-Chiniquá Sequence, Brazil), but in a recent taxonomic revision they were all synonymized in a single valid species (i.e., *Dinodontosaurus brevirostris*). The only postcranial record includes some undescribed specimens referred to *D. brevirostris*, an indeterminate shoulder girdle (MCZ 3459), and an ulna recently referred to *Stahleckeria* sp. Here we describe a new, large dicynodont specimen (CRILAR-Pv 82) from the *Tarjadia* Assemblage Zone (AZ) of the lowermost levels of the Chañares Formation, consisting of a right scapula, left ilium, sternum, and a few indeterminate fragments. The tall, dorsally expanded scapular blade with anteroventrally inclined dorsal margin and the anterolaterally directed acromion process broadly match the stahleckeriid morphotype. CRILAR-Pv 82 shares with *Stahleckeria potens* a sharp, vertical scapular spine on the anteroventral margin of the scapular blade, markedly convex in anterior view. The “hook-shaped” curvature of the preacetabular iliac process also resembles *Stahleckeria potens* and *Eubrachiosaurus browni*. These features differ at least with the Brazilian specimens of *Dinodontosaurus* (*D. tener*). The available data shows that MCZ 3459 also fits the stahleckeriid morphology, becoming the first historical record of the clade for the unit. A rigorous comparison with *D. brevirostris* will await the examination of more complete specimens. The dicynodont postcrania described so far from the Chañares Formation represent the oldest record of Stahleckeriinae in the Ischigualasto-Villa Unión Basin, expanding back its Argentinian record very likely beyond the Ladinian-Carnian boundary.

1. Introduction

Dicynodontia, the most taxonomically diverse subclade of anomodont therapsids, was one of the most successful non-mammaliaform synapsid clades during the late Paleozoic and early Mesozoic. Its evolutionary history encompasses approximately 60 million years, from the earliest representatives in the Wordian (middle Permian) *Eodicynodon* Assemblage Zone of South Africa (Rubidge et al., 1994; Brocklehurst et

al., 2013; Olroyd and Sidor, 2017) to the latest confirmed records in the Late Triassic (Norian and possible Rhaetian; e.g., Kent et al., 2014; Viglietti et al., 2020) of USA, Poland, Morocco, Argentina, Brazil, and South Africa (Camp and Welles, 1956; Bonaparte, 1970; Dutuit, 1988; Vega-Dias and Schultz, 2004; Kammerer, 2018; Sulej and Niedźwiedzki, 2019). During this lengthy interval, the clade Dicynodontia achieved more than 90 species, following the most recent taxonomic and phylogenetic studies (e.g., Kammerer, 2019; Liu, 2020;

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<https://doi.org/10.1016/j.jsames.2021.103275>

Received 4 January 2021; Received in revised form 10 March 2021; Accepted 12 March 2021

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Kammerer and Ordoñez, 2021), and a Pangaeian distribution (Fröbisch, 2009), reaching its peak of taxonomic diversity in the Lopingian (late Permian) (Fröbisch, 2008; Ruta et al., 2013). After the Permo-Triassic mass extinction, at least four dicynodont lineages survived (e.g., Hammer and Cosbriff, 1981; Botha and Smith, 2007; Fröbisch, 2007; Fröbisch et al., 2010; Maisch and Matzke, 2014; Olivier et al., 2019; Liu, 2020), but only the kannemeyeriiform dicynodontoids gave rise to the second major dicynodont radiation during the Middle-Late Triassic (Fröbisch, 2009).

In South America, kannemeyeriiforms are known in western Argentina and southern Brazil. The Brazilian record is circumscribed to the Middle to Late Triassic Santa Maria Supersequence (Pinheiros-Chiniquá and Candelária sequences; von Huene, 1935; Tupí-Caldas, 1936; Romer, 1943; Romer and Price, 1944; Cox, 1965; Araújo and Gonzaga, 1980; Vega-Dias and Schultz, 2004; Martinelli et al., 2020; Kammerer and Ordoñez, 2021). In Argentina, kannemeyeriiforms also occur in the Middle to Late Triassic of the San Rafael Block (Quebrada de los Fósiles and Río Seco de la Quebrada formations; Bonaparte, 1965, 1966, 1981; DeFauw, 1993; Renault and Hancox, 2001; Domnanovich and Marsicano, 2012; Kammerer and Ordoñez, 2021) and the Cuyana (Cerro de las Cabras Formation; Bonaparte, 1969; Domnanovich and Marsicano, 2012; Kammerer and Ordoñez, 2021) and Ischigualasto-Villa Unión basins (Chañares, Ischigualasto, and Los Colorados formations; Cox, 1962, 1965, 1968; Bonaparte, 1970; Domnanovich, 2010; Mancuso and Irmis, 2020; Ordoñez et al., 2020; Kammerer and Ordoñez, 2021).

Although the validity of a few species has not been significantly objected (e.g., *Stahleckeria potens* von Huene, 1935 from the Pinheiros-Chiniquá Sequence, *Ischigualastia jenseni* Cox, 1962 from the Ischigualasto Formation, and *Jachaleria candelariensis* Araújo and Gonzaga, 1980 from the Candelária Sequence), the alpha taxonomy and phylogenetic relationships of South American kannemeyeriiforms have been object of several controversies during decades. Some taxa are still poorly studied, such as *Jachaleria colorata* Bonaparte (1970) (see also Keyser, 1974; Kammerer and Ordoñez, 2021). Others have an intricate taxonomic and nomenclatural history, as is the case of “*Kannemeyeria*” *argentinensis* Bonaparte (1965) (see discussions in Bonaparte, 1966, Renault and Hancox, 2001, and Maisch, 2020), *Stahleckeria* (or *Barysoma*) “*lenzii*” Romer and Price (1944) (see Cox, 1965; Lucas 1993; Maisch, 2020), and especially the potential wastebasket genus *Dinodontosaurus* Romer, 1943 (see Kammerer and Ordoñez, 2021 and references therein for a detailed summary of the fluctuating taxonomic status of the genus). Recently, this situation was dramatically changed by Kammerer and Ordoñez (2021), who presented a comprehensive revision of the entire South American dicynodont fauna, proposing resolutions for all of these taxonomic conflicts. For example, they transferred “*Kannemeyeria*” *argentinensis* to the new genus *Acratophorus*; synonymized *Barysoma*/*Stahleckeria* “*lenzii*” to *Stahleckeria potens*, and reduced the taxonomic diversity of *Dinodontosaurus* to only two species (see below).

During decades, the kannemeyeriiform assemblage of the Chañares Formation has been a paradigmatic case of several of these taxonomic controversies. The first specimens were discovered in 1964–1965, during a joint expedition of the La Plata Museum and the Museum of Comparative Zoology of the Harvard University to the Ischigualasto-Villa Unión Basin, led by paleontologist Alfred S. Romer. This team discovered one of the richest Triassic continental assemblages in the world and collected a huge amount of tetrapod specimens, including several dicynodont skeletons (Romer and Jensen, 1966; Cox, 1968). On the basis of this material, Cox (1968) named one new genus and three new species of dicynodont synapsids for the unit: the genus and species *Chanaria platyceps*, and the species *Dinodontosaurus brevirostris* and *D. platygnathus*, which were based exclusively on cranial material (holotypes PULR 14, PULR 03, and PULR 15, respectively). Among these three species, Cox (1968) only referred additional materials (skulls and

postcranial elements; MCZ 3452-3457 and MR-120) to *D. brevirostris*. However, he did not provide a formal description of the postcranium, and only mentioned that its morphology was congruent with that of Brazilian specimens of *Dinodontosaurus*. Until very recently, only a few studies had revisited in detail the taxonomy of the Chañares dicynodonts (e.g., Keyser and Cruickshank, 1979; Lucas and Harris, 1996; Domnanovich, 2010), without consensus among them. Keyser and Cruickshank (1979) reassigned *Chanaria platyceps* to *Dinodontosaurus platyceps*, and *D. platygnathus* to *Jachaleria platygnathus*. However, Lucas and Harris (1996) considered *Dinodontosaurus* as a monospecific genus composed only of *D. oliveirai* Romer (1943) (from the Pinheiros-Chiniquá Sequence). They considered *D. platyceps* and *D. brevirostris* as junior subjective synonyms of *D. oliveirai*, but omitted to mention the taxonomic status of *Jachaleria platygnathus*. Langer et al. (2007) agreed with this scheme, but proposed that *D. pedroanum* (Tupí-Caldas, 1936) was the type species because of temporal priority. Rogers et al. (2001) rejected the presence of *Jachaleria* in the Chañares Formation, considering *Dinodontosaurus platygnathus* as a valid combination (followed by Domnanovich, 2010; however, see comments of Maisch, 2020), but in an unpublished study, Morato (2006) considered this taxon as *nomen dubium*. In another unpublished review, Domnanovich (2010; followed by Mancuso et al., 2014; Ordoñez et al., 2020) accepted the validity of *D. platyceps*, *D. brevirostris* and *D. platygnathus*, in addition to the Brazilian type species *D. pedroanum*. Finally, Kammerer and Ordoñez (2021) synonymized most of the nominal species of *Dinodontosaurus* and circumscribed the genus only to *D. tener* in the Pinheiros-Chiniquá Sequence of Brazil (also applying temporal priority) and *D. brevirostris* in the Chañares Formation, establishing an important benchmark to stabilize the taxonomy of this taxon. Concerning non-*Dinodontosaurus* kannemeyeriiforms from the Chañares fauna, Mancuso and Irmis (2020) recently described an isolated right ulna (CRILAR-PV 602) as belonging to the stahleckeriid *Stahleckeria*, a genus previously known in the Pinheiros-Chiniquá Sequence (*Dinodontosaurus* AZ) of Brazil (von Huene, 1935; Romer and Price, 1944; Maisch, 2001; Martinelli et al., 2017; Kammerer and Ordoñez, 2021) and the upper Omingonde Formation of Namibia (Abdala et al., 2013).

Most of the taxonomic schemes of the Triassic dicynodonts of South America were focused on their cranial gross anatomy. Comparative studies focused on the postcranial anatomy of kannemeyeriiforms, especially those of the Chañares Formation, were mostly neglected. For more than five decades, the only informative postcranial specimen reported for the unit was one from the original Romer collection (MCZ 3459). This material, also briefly described and figured by Cox (1968), consists of a left scapulocoracoid and clavicle collected “two miles east of the Mogote del Gualo” (Cox, 1968: p. 17; see approximate location in Fig. 1). Cox (1968) suggested that MCZ 3459 may represent a potential fourth species of dicynodont in the Los Chañares assemblage, although without a formal assignment due to its fragmentary condition; since then, the taxonomic identity of this specimen was not further discussed. The partial ulna referred to *Stahleckeria* sp. by Mancuso and Irmis (2020) constitutes the second significative report of a kannemeyeriiform postcranium. Here, we improve the knowledge about the dicynodont assemblage of the Chañares Formation by describing a new specimen from the lowermost levels of the *Tarjadia* Assemblage Zone (sensu Ezcurra et al., 2017). This specimen (CRILAR-Pv 82) includes a right scapula, a partial left ilium, and a sternum that strongly resembles the classical specimens of *Stahleckeria* from the Middle-Late Triassic Pinheiros-Chiniquá Sequence of Brazil (i.e., von Huene, 1935; Romer and Price, 1944) and allows comparison with the historical specimen MCZ 3459.

1.1. Institutional abbreviations

CRILAR-Pv, Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, La Rio-

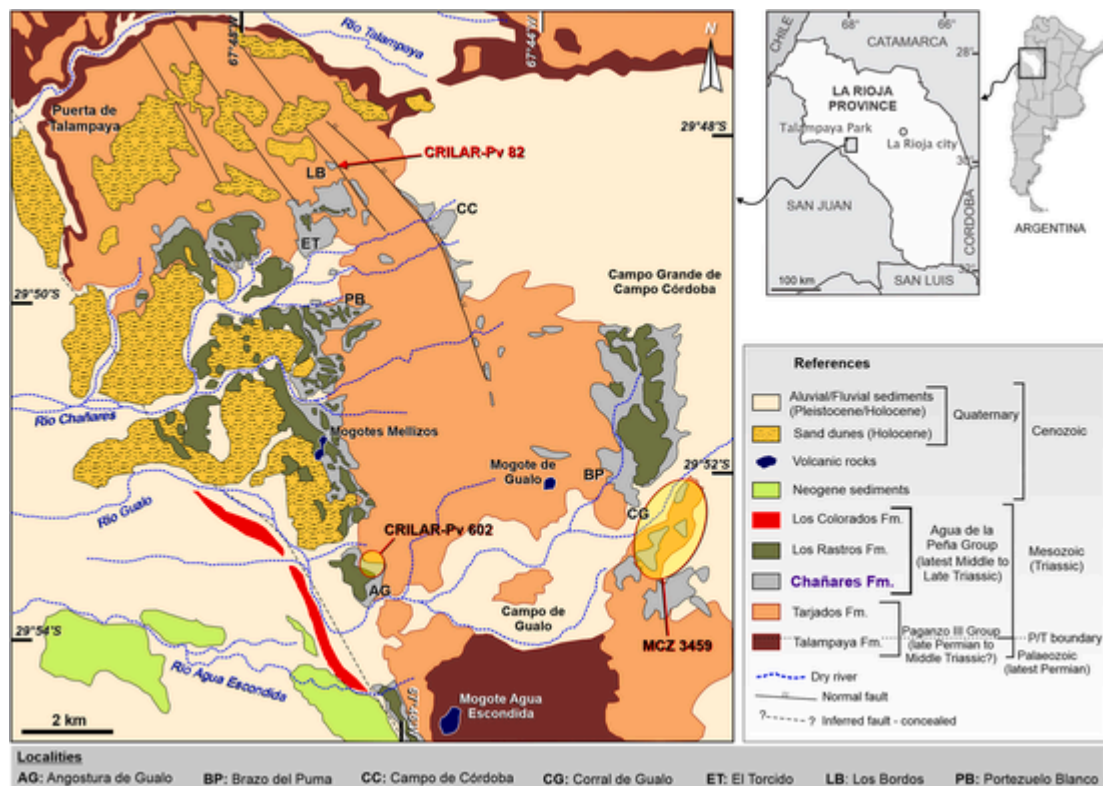


Fig. 1. Geological map of the Los Chañares region in the Talampaya National Park indicating the occurrence of the specimen CRILAR-Pv 82 at the Los Bordes locality and the other stahleckeriids from the unit (CRILAR-Pv 602 and MCZ 3459; see the text). Image taken and modified from Ezcurra et al. (2021).

oja, Argentina; GPIT, Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Tübingen, Germany; MACN-Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional de Paleovertebrados, Buenos Aires, Argentina; MCN-PV, Museu de Ciências Naturais (Paleovertebrate Collection), Fundação Zoobotânica do Rio Grande do Sul (FZBR), Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MPDC, Museu Padre Daniel Cargnin, Mata, Rio Grande do Sul, Brazil; MR, Earth Sciences Museum, Brigham Young University, Provo, Utah; NHMUK-PV, The Natural History Museum of the United Kingdom, Palaeontology Vertebrates, London, United Kingdom; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PULR, Museo de Antropología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Museo Miguel Lillo de Ciencias Naturales, San Miguel de Tucumán, Argentina; UFRGS-PV-T, Universidade Federal do Rio Grande do Sul (Paleovertebrate, Triassic Collection), Porto Alegre, Brazil.

2. Material and methods

We compared at first hand CRILAR-Pv 82 with the kannemeyeriiform specimens MACN-Pv 18055 (holotype of *Ischigualastia jenseni*), UFRGS-PV-0151-T, UFRGS-PV-0287-T (holotype and referred specimen, respectively, of *Jachaleria candelariensis*), and MPDC 232-48 and MPDC 504-120 (referred specimens of *Dinodontosaurus tener*). We also examined detailed photographs of MCZ 1688 (holotype of *Stahleckeria “lenzii”* Romer and Price, 1944). Comparisons with other postcrania of several other kannemeyeriiforms (e.g., *Angoniasaurus cruickshanki*, *Dinodontosaurus* spp., *Eubrachioceras browni*, *Acratophorus argentinensis*, *Kannemeyeria simocephalus*, *Lisowicia bojani*, *Placerias hesternus*, *Sangusaurus parringtonii*, *Shansiodon wangi*, *Sinokannemeyeria yingchiaoensis*, *Stahleckeria potens*, *Tetragonias njalilus*, *Wadiasaurus indicus*, *Zambiasaurus submersus*, and the indeterminate specimen MCZ

3459) were made on the basis of descriptions and figures in the literature (e.g., Angielczyk et al., 2018; Araújo and Gonzaga, 1980; Bandyopadhyay, 1988; Bonaparte, 1966; Camp and Welles, 1956; Cox, 1965; 1968; 1969; Cox and Li, 1983; Cruickshank, 1967; Govender et al., 2008; Kammerer et al., 2013; Pearson, 1924; Romer and Price, 1944; Sulej and Niedźwiedzki, 2019; Vega-Diaz and Schultz, 2004; von Huene, 1935; Yeh, 1959). Linear measurements were taken directly in CRILAR-Pv 82 and MACN-Pv 18055 with a digital caliper (maximum deviation of 0.2 mm) and a measuring tape (maximum deviation of 0.5 mm).

The description of the scapula follows the anatomical orientations of Romer (1956) and most descriptions of non-mammaliaform synapsids (e.g., Ray, 2006; Kammerer et al., 2013; Guignard et al., 2019; Gaetano et al., 2018), in which the terms “dorsal” and “ventral” refer to the regions located distally and proximally to the glenoid articulation, respectively.

3. Geological settings

The specimen CRILAR-Pv 82 was collected in the Los Bordes locality (Fig. 1) and comes from the first sandy levels of the *Tarjadia* Assemblage Zone (Ezcurra et al., 2017), 50 cm above the contact between the Tarjados and Chañares formations, lower member of the Chañares Formation, Ischigualasto-Villa Unión Basin, Talampaya National Park, La Rioja Province, NW Argentina. The Chañares Formation is part of a rift basin related to the pre-break-up of Pangea. This basin is represented by a continental succession of deposits of approximately 4000 m, from the upper Permian to the Upper Triassic (Kokogian et al., 1999; Gulbranson et al., 2015), bearing an extremely rich tetrapod record shedding important light on the origin and evolution of modern vertebrate faunas.

The Chañares Formation was classically worked by renowned colleagues (e.g., Romer 1966; Bonaparte, 1997; Rogers et al., 2001) who positioned its continental tetrapod assemblage as one of the most im-

portant worldwide for the Triassic. Subsequently, this assemblage has been intensively worked by several Argentinean research groups and, as a consequence, the geology and sedimentology of the Chañares Formation have been deeply studied and analyzed (Rogers et al., 2001; Fiorelli et al. 2013, 2018; Mancuso et al., 2014; Marsicano et al., 2016; Ezcurra et al. 2017, 2020, 2021; Perez Loinaze et al., 2018). Based on these and other works, the Chañares Formation has been characterized by volcanoclastic deposits reworked in alluvial and lacustrine settings as part of the syn-rift phase of sedimentation of the basin. In addition, the Chañares Formation has been recently radiometrically dated and bracketed between ~236 and ~233 Ma (early Carnian; Marsicano et al., 2016; Ezcurra et al., 2017) (Fig. 2), slightly before or encompassing the beginning of the Carnian Pluvial Episode (Simms and Ruffel, 1989, 1990; Benton et al., 2018; Bernardi et al., 2018). Here we follow the sedimentary geological framework of Fiorelli et al. (2013), where two members are described and the lower of them is divided into two beds. However, this model of two beds was subsequently improved into two tetrapod assemblage zones, namely the *Tarjadia* AZ (Assemblage Zone)

and the *Massetognathus-Chanaresuchus* AZ based on conspicuous differences in their faunal compositions and indicating deep faunistic turnovers during the early-middle Carnian (Ezcurra et al., 2017).

In recent years, the holistic approach on the study of the Chañares Formation generated a broader understanding of its geology, sedimentology, paleobiology, and paleoenvironments, mainly related to the *Massetognathus-Chanaresuchus* AZ (e.g., Ezcurra et al., 2017, 2020; Fiorelli et al., 2013, 2018; Pérez Loinaze et al., 2018). However, the recent determination of the *Tarjadia* AZ (Fig. 2) has impacted on this understanding and opened new questions that need to be addressed, in particular regarding the sedimentology and paleoenvironment of the first meters (Ezcurra et al., 2017). The *Tarjadia* AZ shows a strong horizontal sedimentary variation because it was deposited on the markedly irregular paleorelief of the reddish Tarjados Formation through a noteworthy regional unconformity (Fiorelli et al., 2018). In the Los Bordes locality (Fig. 2), as in other localities that preserve the contact between the Tarjados and Chañares formations (e.g., Brazo del Puma, El Torcido), an uneven and thin mineralized surface of chert and carbonate

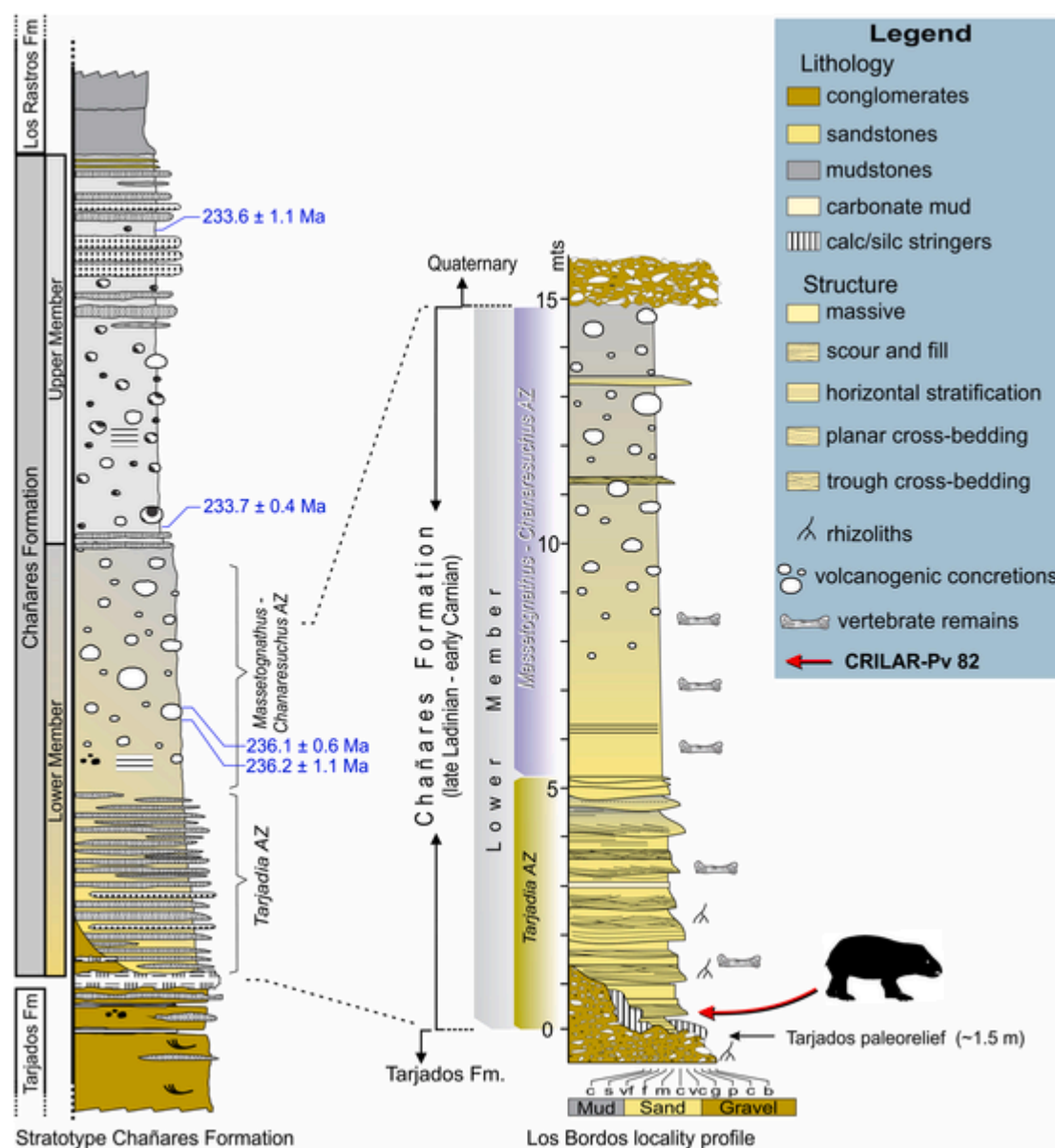


Fig. 2. Generalized stratotype of the Chañares Formation (left) and detailed stratigraphic profile at Los Bordes locality (right). The red arrow in the Los Bordes profile indicates the occurrence of the stahleckeriid CRILAR-Pv 82 approximately 50 cm above the boundary with the Tarjados Formation (modified from Ezcurra et al., 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

stringers characterize the boundary between these units (Ezcurra et al., 2017; Fiorelli et al., 2018). In the small outcrop of the Los Bordos locality, the Tarjados palaeorelief is up to 1.5 m (Figs. 2 and 3A), whereas in other localities it reaches several meters (Fiorelli et al., 2018). Thus, the low-lying areas between topographic highs were filled by the first sandy sediments of the *Tarjadia* AZ (Fig. 3A and B). This succession is characterized by massive or stratified bodies of grey-olive to yellow-green sandstones and conglomeratic sandstones mixed with tuffs (Fig. 3B). The sandy bodies possess clear sedimentary structures, such as rip-

ples and horizontal, planar, and trough cross-stratification. In Los Bordos locality, some thin calcrete levels with small horizontal root traces and bioturbations suggest the development of incipient paleosols near fluvial channels; these paleosol levels are more conspicuous in other localities (e.g., Campo de Córdoba; Fiorelli et al., 2018). The sandy channelized first meters, in particular the stahleckeriid-bearing level in Los Bordos locality, correspond to some isolated sheetflood cycles of distally braided rivers with high stream power of low sinuosity and stability, and moderate discharge of sediment. These facies show some vol-



Fig. 3. Overview of the Chañares Formation in the Los Bordos locality. A, first meter —*Tarjadia* AZ— of the Chañares Formation covering a clear paleorelief of the Tarjados Formation. B, facies of the lowermost levels of the Chañares Formation at El Torcido locality with large scale through and planar cross-bedded tuffaceous sandstones. C, panorama of the Los Bordos outcrops and the fossil site of CRILAR-Pv 82. Hammer length = 28 cm.

canic material mixed with sandstone, but the volcanic contribution is not as high as in the upper levels of *Massetognathus-Chanaresuchus* AZ, which were strongly influenced by volcanism when the syn-eruptive pulses were probably constant or less sporadic (Ezcurra et al., 2021). Instead, the *Tarjadia* AZ shows large inter-eruptive periods, a stasis evidenced by the development of paleosols with extensive horizontal root systems—abundant rhyzoliths—and large, complex tetrapod branched burrows (Fiorelli et al., 2018). However, the facies variations in the first few meters of the *Tarjadia* AZ probably occurred more chaotically, controlled by several factors that randomly filled the low-lying areas between topographic highs. Therefore, each filled micro valley developed particular sedimentological and taphonomic characteristics (e.g., a combination of the braided rivers, variation in topography, sedimentation rates, semiarid paleoenvironmental conditions, isolation and weathering of remains). Subsequently, the system was stabilized and leveled from local changes, such as fill up of the lowlands and increase of volcanic sediment, which indicates the beginning of the *Massetognathus-Chanaresuchus* AZ (Ezcurra et al., 2017; Fiorelli et al., 2018).

The *in situ* bones of the stahleckeriid specimen CRILAR-Pv 82 were found at the Los Bordos locality, a small outcrop of about 8000 square meters, during a field trip in September 2018 (Figs. 1 and 3). CRILAR-Pv 82 was found 55 m in straight line from a rhynchosaurid specimen in approximately the same stratigraphic level (CRILAR-Pv 112; see Ezcurra et al., 2021; Fig. 2). This tiny outcrop preserves the first sandy centimeters of deposition of the *Tarjadia* AZ and the stahleckeriid and rhynchosaur material collected bolster the hypothesis of a distinctive faunal association in the *Tarjadia* AZ from that of the *Massetognathus-Chanaresuchus* AZ, showing the same pattern as in other localities of the unit (e.g., Brazo del Puma, El Torcido, Campo de Córdoba Norte localities; Ezcurra et al., 2017, contra Ordoñez et al., 2020) (Fig. 2). The *Tarjadia* AZ includes the stahleckeriid reported here and the stenaulorhynchine rhynchosaur *Elorhynchus carrolli*, the medium-sized erpetosuchid pseudosuchian *Tarjadia ruthae*, other medium to large-sized suchians (e.g., *Luperosuchus fractus*), and small to medium-sized traversodontid and probainognathian cynodonts (Ezcurra et al. 2017, 2021). Although the Chañares Formation has been recently dated as early Carnian (236.1 ± 0.6 Ma and 233 ± 0.4 Ma; Marsicano et al., 2016), the entire *Tarjadia* AZ—up to 20 m—as well as the first 10 m of the *Massetognathus-Chanaresuchus* AZ lack absolute dates (Ezcurra et al., 2017). In line with recent suggestions, the first meters of the Chañares Formation (*Tarjadia* AZ) were probably deposited during the Ladinian and the Ladinian-Carnian boundary may occur in either the uppermost levels of the *Tarjadia* AZ or the lowermost levels of the *Massetognathus-Chanaresuchus* AZ (Ezcurra et al., 2017, 2021; Fiorelli et al., 2018).

4. Systematic paleontology

THERAPSIDA Broom (1905)

ANOMODONTIA Owen (1860).

DICYNODONTIA Owen (1860).

KANNEMEYERIFORMES Maisch (2001).

STAHLECKERIIDAE (Lehman, 1961).

STAHLECKERIINAE (Lehman, 1961).

Genus and species indet.

Material - CRILAR-Pv 82, a right scapula, a partial left ilium, sternum, and indeterminate bone fragments.

Locality and horizon - Los Bordos locality (29°48'23"S/67°46'40"W), almost 7 km east of the mouth of the Talampaya canyon and 2 km north of the El Torcido river. CRILAR-Pv 82 proceeds from 50 cm above the contact between the Tarjados and Chañares formations, lower levels of the *Tarjadia* AZ, lower member of the Chañares Formation, Ischigualasto-Villa Unión Basin, Talampaya National Park, La Rioja Province, NW Argentina.

Remarks - Two tiny, fragmentary cranial elements (a partial left squamosal and a dubious supraoccipital fragment) were found in association with the postcranium CRILAR-Pv 82. However, they were excluded from this study owing to their poor preservation and absence of informative features (a dicynodont generalized morphology could only be recognized in the squamosal fragment).

5. Anatomical description

5.1. Scapula

The right scapula of CRILAR-Pv 82 (Fig. 4A–C) is generally well preserved, with little sign of distortion, beside a slight mediolateral compression of the scapular blade. Only one important fracture extends anteroposteriorly (just below the acromion process: ac) and there is some damage in some regions of the anterior and posterior margins of the blade and in the scapular spine. The scapula has a maximum length of 51.5 cm, representing one of the largest South American dicynodont specimens reported so far (see Table 1 for additional measurements). It exceeds the measurements reported in MCZ 3459 from the Chañares Formation (Cox, 1968), *Ischigualastia jenseni* (holotype MACN-Pv 18055), *Jachaleria candelariensis* (Vega-Dias and Schultz, 2004), and *Dinodontosaurus tener* from the Pinheiros-Chiniquá Sequence (Cox, 1965). Only some specimens of *Stahleckeria potens* from the latter unit are slightly larger, with scapulae approximately 5% longer than that of CRILAR-Pv 82 (von Huene, 1935; Romer and Price, 1944).

The scapular blade is robustly built and relatively tall, with its dorsal end gradually expanded anteroposteriorly. In anterior view (Fig. 4 C), the scapular blade is gently bowed laterally (although this was probably attenuated by distortion). The anterior and posterior margins are gently concave in lateral view, with the curvature slightly more pronounced in the latter. As a result, the middle region of the scapula (immediately dorsal to the level of the acromion process) is anteroposteriorly constricted and the expansion is more pronounced on the dorsal third of the blade. The dorsal border of the scapula is gently curved, with a moderate posterodorsal-to-anteroventral orientation in lateral view. The posterodorsal and anterodorsal corners of the blade have an acute and an obtuse angle, respectively. Unfortunately, the ventral half of the posterior margin is considerably damaged, especially the area immediately dorsal to the glenoid articulation (gl). Thus, it is not possible to determine if an area for insertion of the triceps muscles was differentiated, as occurs frequently in other Kannemeyeriiformes (e.g., von Huene, 1935; Govender et al., 2008; Kammerer et al., 2013). Excluding the scapular spine and acromion process, the lateral and medial surfaces of the scapular blade lack any crest or tubercle.

The scapular spine (sp), slightly fragmented but generally well preserved, is well-developed dorsoventrally and laterally, starting approximately 13 cm from the dorsal border of the scapula and extending vertically adjacent to the anteroventral margin of the blade. The anterior surface of the spine has some cracks (cr) and it is relatively flat, lacking a groove or prespinous fossa (e.g., Govender et al., 2008) between the edge of the spine and the anterior margin of the blade. The dorsal portion of the spine is thick, rounded, and low. It progressively sharpens and rises from the lateral surface of the blade towards its ventral end, where it is slightly demarcated from the acromion process (ac). Thus, the edge of the spine is markedly convex in anterior view (see Fig. 4 C). In lateral view, the ventral third of the spine curves anterolaterally, giving the scapular spine an undulating profile in this region. The scapular spine is connected to an acromion process that projects anteroventrally and slightly laterally from the ventralmost end of the former structure. The acromion process is moderately developed, not reaching the great extension of some Brazilian specimens of *Dinodontosaurus* (Cox, 1965; Fig. 15A; Kammerer et al., 2013; see also Fig. 5G). It has a gently convex dorsal edge and a straight ventral margin. This

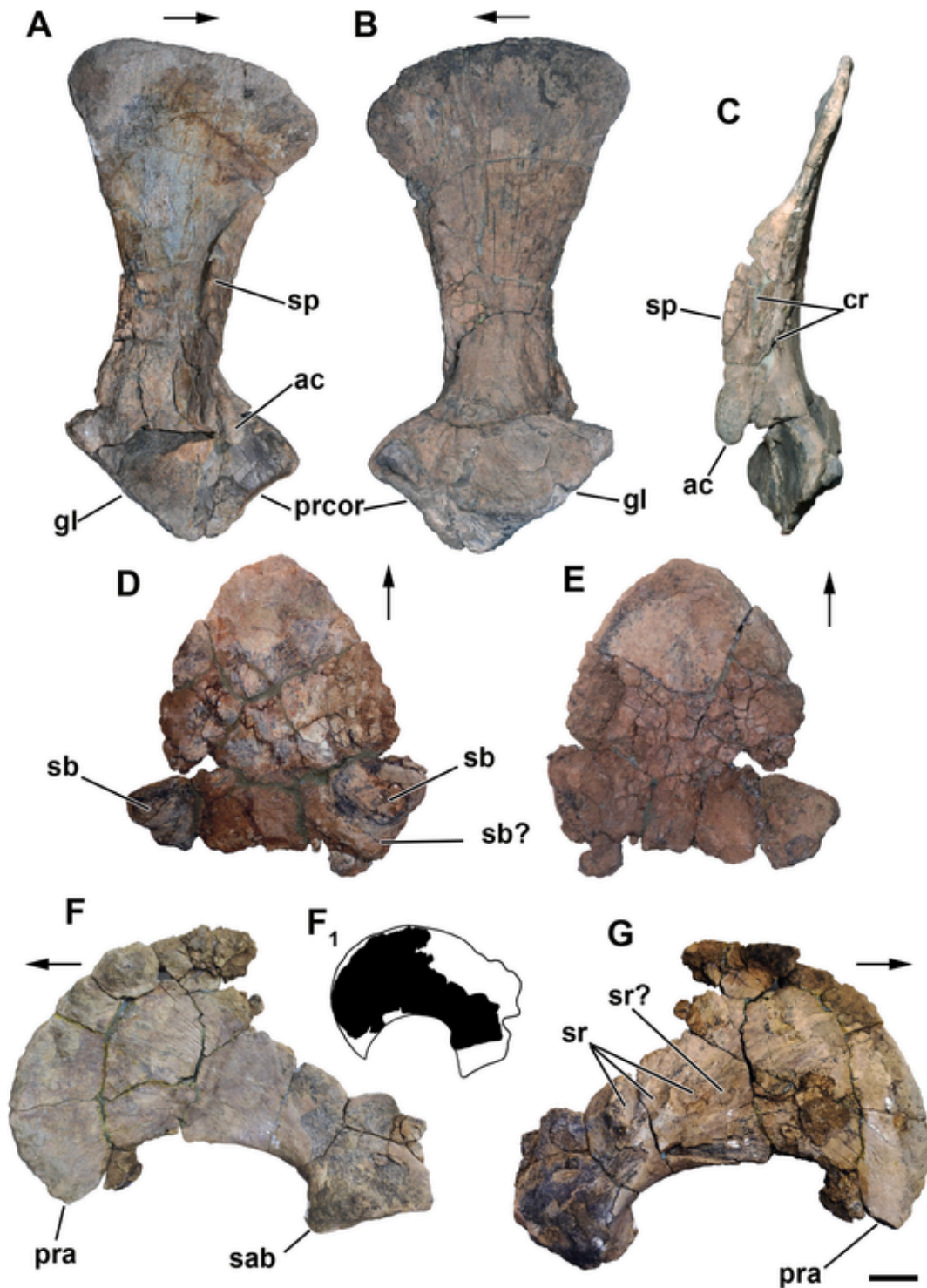


Fig. 4. CRILAR-Pv 82, Stahleckeriidae indet. Right scapula in (A) lateral, (B) medial, and (C) anterior views. Sternum in (D) dorsal and (E) ventral views. Partial left ilium in (F) lateral and (G) medial views. F₁, hypothesised restoration of the ilium of CRILAR-Pv 82 on the basis of *Stahleckeria potens* (von Huene, 1935). Abbreviations: ac, acromion process; cr, cracks; gl, glenoid articular surface; pra, preacetabular process; prcor, articular surface for precoracoid; sab, supraacetabular buttress; sb, sternal boss; sp, scapular spine; sr, sacral rib scar. Arrows point anteriorly. Scale bar equals 5 cm.

morphology of the scapular spine and acromion process is remarkably similar to specimens of *Stahleckeria potens* from Brazil (see Discussion).

Ventrally to the acromion process, the ventral part of the scapula is also broadly expanded, until reaching a similar anteroposterior extension to that of the dorsal margin of the blade. This region of the scapula is delimited anteroventrally by the articular surface for the precoracoid (prcor), and posteroventrally by the scapular contribution to the glenoid cavity (gl). These surfaces form an angle slightly higher than 90°

between each other. The glenoid fossa has a straight profile and its surface is longer than the articulation with the precoracoid, which is slightly concave in an anteroposterior direction. No evidence of a coracoid foramen is present; thus, it was probably entirely surrounded by the missing precoracoid.

Table 1

Linear measurements (in cm) of the postcranial elements of CRILAR-Pv 82.

Measurements	CRILAR-Pv 82
Right scapula	
Maximum length	51.50
Maximum width (at dorsal margin of the blade)	26.82
Minimum width (at the level of the acromion process)	10.93
Sternum	
Maximum preserved length	33.00
Maximum width	30.00
Left ilium	
Maximum preserved length	41.70
Preaceabular length	31.00

5.2. Sternum

The sternum of CRILAR-Pv 82 (Fig. 4 D, E) is severely cracked and worn out, several edges are damaged (especially the left one), and the entire posterior region of the bone is missing. Thus, the information that can be obtained from this element is limited. However, a roughly triangular outline is apparent, with the convex lateral margins converging into a blunt anterior end. The linear measurements of the sternum (see Table 1) also exceed those reported in most other South American dicynodonts (e.g., von Huene, 1935; Cox, 1965; Vega-Dias and Schultz, 2004).

As is typical in dicynodonts, the ventral and dorsal surfaces of the sternum are well differentiated. At least a pair of round bosses (sb), one on each left and right side, occurs on the posterolateral margins of the dorsal surface (see Fig. 4 D), which are differentiated from the posteriormost region of the sternum by a shallow groove. A convexity on the dorsal surface of the bone, immediately posterior to each groove (espe-

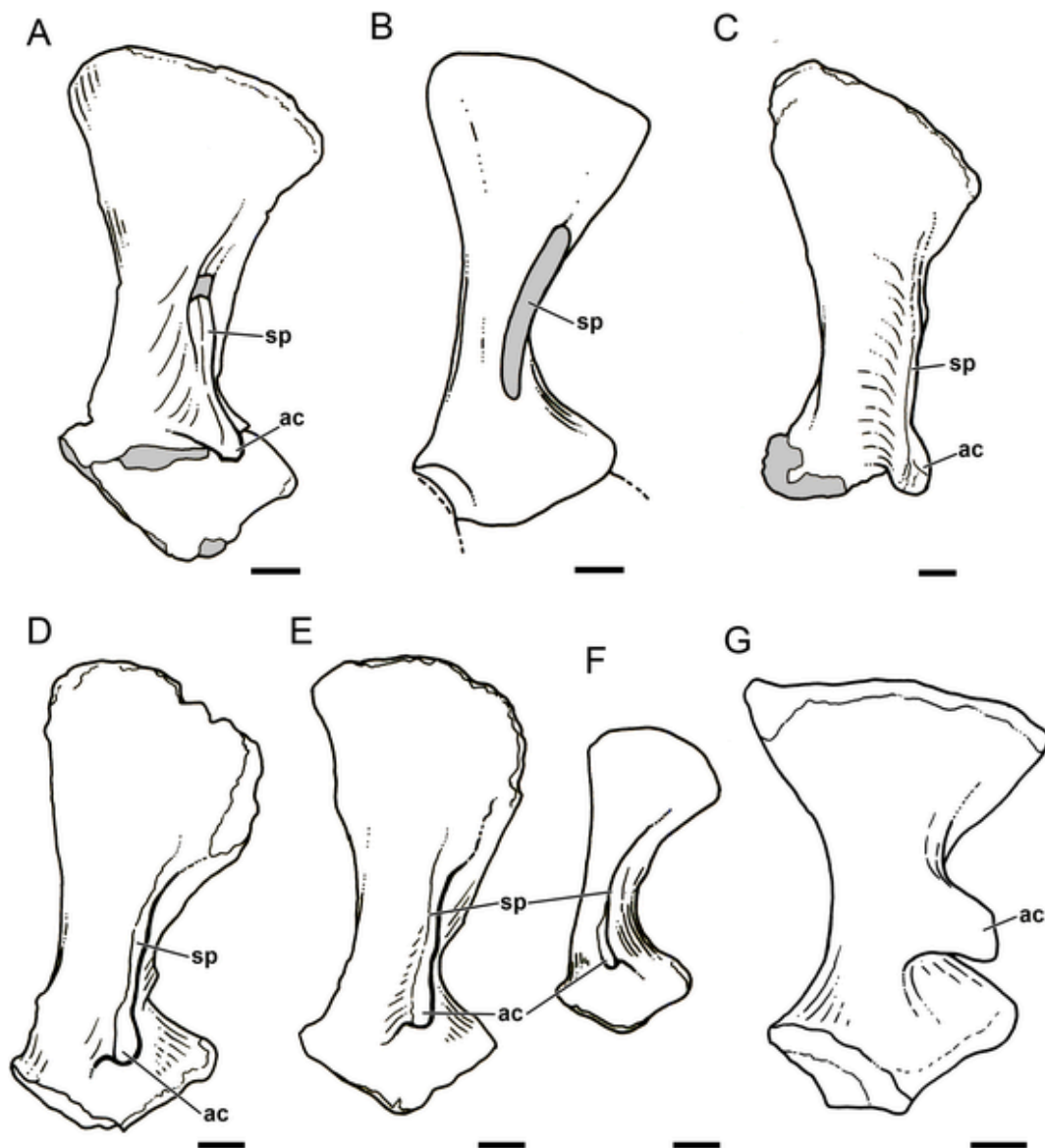


Fig. 5. Comparison of kannemeyeriiform scapulae from the Chañares Formation and the Pinheiros-Chiniqua Sequence in lateral view. A, CRILAR-Pv 82, *Stahleckeriidae* indet. B, MCZ 3459, *Stahleckeriidae* indet. C, MCZ 1688, *Stahleckeria potens* (holotype of *S. "lenzii"*). D, GPIT-PV-30792 (formerly GPIT/RE/8001), *Stahleckeria potens*. E, "scapula n°2" of von Huene, *Stahleckeria potens*. F, "scapula n°3" of von Huene, putative juvenile of *Stahleckeria potens*. G, MPDC 232-48, *Dinodontosaurus tener*. A correspond to a left scapula (reversed), A, C, D, E, F and G are right scapulae, B is a left scapula reversed for comparative purpose. B modified from Cox (1968); D, E and F modified from von Huene (1935). Abbreviations: ac, acromion process; sp, scapular spine. Scale bars equal 5 cm.

cially on the right side), suggests the possibility of a second pair of bosses (sb?). Unfortunately, the extremely poor preservation of this region prevents an unequivocal interpretation. A low, broad longitudinal crest extends anteromedially on the dorsal surface, from the right sternal boss until reaching a similar median crest a short distance posterior to the anterior end of the bone. Although not preserved, there was probably another crest extending from the left sternal boss. Beside its general concavity, no other features are recognized on the ventral surface.

5.3. Ilium

The ilium of CRILAR-Pv 82 (Fig. 4 F, G) preserves most of the preacetabular (or anterior) process (pra) (lacking its anteroventral end), and part of the neck or base of the iliac blade and supraacetabular region. A natural margin is undoubtedly present on the posteroventral region of the preacetabular process. The margin of the blade is dorsally obscured by matrix, and anteriorly bears signs of damage. However, it probably did not extend much further anteriorly. Besides its incompleteness, only the preserved length of the bone (see Table 1) largely exceeds the total iliac length reported in *Dinodontosaurus tener* by Cox (1965; also compare scales in Fig. 7A and D). Among the published South American dicynodonts, only some *Stahleckeria* specimens surpass this length (Fig. 7; von Huene, 1935; Kammerer et al., 2013; Fig. 7B).

The preacetabular process of CRILAR-Pv 82 is strongly anteriorly developed. In general, the lateral surface is slightly concave both dorsoventrally and anteroposteriorly, while the medial surface is convex in the same directions. The iliac blade gradually curves anterolaterally from approximately the mid-length of the anterior process. Besides the general damage of the iliac blade and loss of its anteriormost end, it is evident a strong anteroventral curvature of the preacetabular process, which is conspicuously represented by the deeply concave posteroventral margin of the process in lateral view (see Fig. 4F and G and 7A). As a result, the iliac blade acquires a 'hooked'-shaped profile in lateral view, similar to that of *Stahleckeria potens* and other stahleckeriine relatives (see Discussion). The posteroventral margin of the preacetabular process immediately leads to the transversely thickened anterior region of the iliac neck, which probably corresponds to the supraacetabular buttress. Neither the posterior margin of the neck nor the acetabular regions are preserved.

The medial surface of the iliac blade preserves scars for three (possibly four) sacral ribs (sr), positioned on the posterior half of the preacetabular process, immediately anterior to the iliac neck (Fig. 4 G). The ventral edges of the sacral rib scars are more conspicuous than dorsally, consisting of deep, dorsoventrally elongated depressions surrounded by strongly swollen margins that determine a rounded ventral outline for the scars. By contrast, the dorsal edges of these scars become gradually shallower dorsally until merging with the rest of the medial surface of the blade. The sacral rib scars are closely packed, being separated only by thin, thickened margins. A detailed characterization of the sacral rib scars of the ilium is generally overlooked in anatomical descriptions of kannemeyeriiforms, and comparisons of this region are mainly focused on sacral count (e.g., Griffin and Angielczyk, 2019). Taking this into account, it is worth noting that the overall morphology of the sacral rib scars of CRILAR-Pv 82 significantly matches those described for the ilium "n°1" of *Stahleckeria potens* (GPIT-PV-30792, formerly GPIT/RE/8001; von Huene, 1935). Although the scars in *Sangusaurus parringtonii* are in articulation with their corresponding sacral ribs, is interesting to note that the distal ends of the third-to-fourth ribs are expanded and rounded (see Angielczyk et al., 2018: Fig. 12B), a feature reminiscent of the morphology observed in the scars of CRILAR-Pv 82. Unfortunately, morphological variation in the ilio-sacral joint region is still poorly studied in other kannemeyeriiform taxa to address an adequate comparison.

6. Discussion

6.1. Comparisons and taxonomy of CRILAR-Pv 82

Although disarticulated, the elements of CRILAR-Pv 82 were found closely associated, lacking duplicated elements, and their sizes match those expected for the same single individual.

Comparative studies on the postcranial anatomy of the Chañares kannemeyeriiforms involve several challenges, not only due to the scarcity of detailed descriptions, but also to the higher historical relevance given to cranial morphology. In this regard, additional limitations arise owing to the confusing skull-based taxonomy of the taxa from this unit (see Introduction). Concerning Triassic dicynodonts, several studies involve descriptions of, at least, some postcranial elements (e.g., Pearson, 1924; von Huene, 1935; Romer and Price, 1944; Camp and Welles, 1956; Cox, 1965; 1969; Cox and Li, 1983; Bonaparte, 1966; Cruickshank, 1967; Vega-Dias and Schultz, 2004; Morato, 2006; Ray, 2006; Govender et al., 2008; Angielczyk et al., 2018; Kammerer, 2018; Kammerer et al., 2013; 2018; Sulej and Niedźwiedzki, 2019), but their level of detail varies from brief mentions to comprehensive descriptions of multiple elements. As discussed by Martinelli et al. (2020), this situation leads to an underestimation of informative postcranial characters in the most recent phylogenetic analyses.

Kannemeyeriiform dicynodonts have been more frequently divided into three main clades: Shansiodontidae, Kannemeyeriidae and Stahleckeriidae (e.g., Cox, 1965; Angielczyk et al., 2018; Angielczyk and Kammerer, 2018). However, their phylogenetic interrelationships are still controversial, and the monophyly of the first two groups has not been universally supported in quantitative analyses. Some analyses found a monophyletic Shansiodontidae and a "kannemeyeriid" grade at the base of Stahleckeriidae (e.g., Kammerer et al., 2011; 2013; Sulej and Niedźwiedzki, 2019); others, conversely, recovered a paraphyletic arrangement of "shansiodontids" at the base of Kannemeyeriiformes and a monophyletic Kannemeyeriidae (e.g., Angielczyk et al., 2018; Kammerer, 2018; 2019; Kammerer et al., 2019; Kammerer and Ordoñez, 2021). Only stahleckeriids have been consistently recovered as a natural group in most recent phylogenies, as the least inclusive clade including *Placerias hesternus* and *Stahleckeria potens* (Kammerer et al., 2013; Angielczyk et al., 2018). Additionally, the relationships of some taxa are particularly problematic, as is the case of the genus *Dinodontosaurus*, which has been recovered as closely related to Stahleckeriidae (e.g., Kammerer, 2019; Kammerer et al., 2019; Kammerer and Ordoñez, 2021), as the sister taxon of a clade containing "kannemeyeriids" plus stahleckeriids (Kammerer et al., 2011), or closely related to "shansiodontids" (Kammerer et al., 2013).

Regarding the kannemeyeriiform scapulae, Kammerer et al. (2013) recognized three basic morphologies that are broadly coincident with the tripartite systematic classification: shansiodontid, "kannemeyeriid" and stahleckeriid morphotypes. Differences between morphotypes are related to the relative size and orientation of the acromion process, relative extension and sloping of the dorsal margin of the scapular blade, and the morphology of the scapular spine if present. The combination of a moderately tall scapular blade with a marked anteroposterior expansion of its dorsal region, anteroventrally inclined dorsal margin, well developed scapular spine, and anterolaterally directed acromion process in CRILAR-Pv 82 better matches the stahleckeriid morphology. However, these scapular morphotypes are not as homogeneously distributed as expected when genera or even species are compared. Among stahleckeriids, for example, the acromion process is weakly developed in *Ischigualastia jenseni* (holotype MACN-Pv 18055), *Jachaleria candelariensis* (holotype UFRGS-PV-0151-T and UFRGS-PV-0287-T, Vega-Dias and Schultz, 2004), and *Lisowicia bojani* (Sulej and Niedźwiedzki, 2019). The scapular blade of *Lisowicia bojani*, in particular, has a symmetric and markedly rounded dorsal border (Sulej and Niedźwiedzki, 2019: supp. fig. 4). Von Huene (1935) and Romer and Price (1944) also

recognized individual variation in the scapular proportions of *Stahleckeria* (see below). *Ischigualastia jenseni* and *Jachaleria candelariensis* are also distinctive in the position of the coracoid foramen between the scapula and coracoid. As it was mentioned in the Description (Section 5.1), CRILAR-Pv 82 shows no signs of a scapular contribution to this foramen.

The most conspicuous feature of the scapula of CRILAR-Pv 82 is the vertical and sharp spine, laterally projected from the anterior margin of the blade. A crest or spine on the lateral surface of the blade is usually observed in some “kannemeyeriid”-grade taxa, such as *Kannemeyeria simocephalus*, *Wadiasaurus indicus* and *Sinokannemeyeria yingchiaoensis*. However, *K. simocephalus* and *S. yingchiaoensis* have a comparatively lower scapular spine, uniformly projected along its entire length (Pearson, 1924: Figs. 20-22; Govender et al., 2008: Fig. 3A and B; Kammerer et al., 2013: Fig. 3D and E). Referred specimens of *Wadiasaurus indicus*, on the other hand, have a more anterolaterally oriented crest (Bandyopadhyay, 1988: Fig. 15a-c, although in the figured scapula the spine is broken). Bonaparte (1966) also mentioned an “incipient” spine in *Acrotaphorus argentinensis*, which has been recovered as a “kannemeyeriid” dicynodont in the most recent phylogenetic analysis (Kammerer and Ordoñez, 2021). Available data on “shansiodontids” is scanty and ambiguous. According to Kammerer et al. (2013), *Tetragonias*, *Shansiodon* and *Rhinodicynodon* lack a scapular spine (Kammerer et al., 2013: Fig. 3A), but Cruickshank (1967) reported a distinct but weakly developed scapular spine in *Tetragonias*. A well-developed scapular spine is also present among most members of *Stahleckeriidae* for which scapular material is known, and its presence has been even recovered as a synapomorphy for the clade (i.e., “anterior edge of scapula extended laterally to form a strong crest”; character 145, state 1 of Angielczyk et al., 2018). However, the morphology of the spine is variable within both *Placeriinae* (i.e., *Placerias hesternus*, *Zambiasaurus submersus*, *Lisowicia bojani*) and *Stahleckeriinae* (i.e., *Stahleckeria potens*, *Eubrachioceras browni* and *Ischigualastia jenseni*), the two major groups in which stahleckeriids are usually divided (e.g., Kammerer et al., 2013). CRILAR-Pv 82 differs from the elongated and low spine observed in *Eubrachioceras browni* (Kammerer et al., 2013: Fig. 2), *Placerias hesternus* (Camp and Welles, 1956: Fig. 29A,B; Kammerer et al., 2013: Fig. 4A), and *Zambiasaurus submersus* (Cox, 1969: Fig. 3A,B and 16), with a more “kannemeyeriid”-like morphology. It also departs (as the rest of stahleckeriids) from the *placeriine Lisowicia bojani*, which has a broad, shallow, and weakly differentiated ridge that runs obliquely along the anterolateral surface of the scapular blade (Sulej and Niedzwiedzki, 2019). Although according to Kammerer et al. (2013) no scapular spine was present in *Ischigualastia* and *Jachaleria*, a similar low ridge as that of *L. bojani* occurs in the specimens MACN-Pv 18055 (holotype of *Ischigualastia jenseni*) and UFRGS-PV-0287-T (referred specimen of *Jachaleria candelariensis*).

Considering this variability within kannemeyeriiforms, the scapula of CRILAR-Pv 82 probably most closely resembles the stahleckeriine *Stahleckeria potens* (Fig. 5) than to other members of the clade, particularly the classic specimens from the Pinheiros-Chiniquá Sequence described by von Huene (1935; Chiniquá region) and Romer and Price (1944; Pinheiro region). Although the three scapulae referred to *Stahleckeria potens* by von Huene (1935; see also Fig. 5D–F) differ in some features, such as the size and proportions of the scapular blade (i.e., degree of convexity and inclination of the dorsal margin, and relative concavity between the anterior and posterior margins), their gross morphology is congruent with that of the stahleckeriid morphotype discussed by Kammerer et al. (2013). Von Huene’s scapula “n°1” (GPIT-PV-30792, formerly GPIT/RE/8001) differs from CRILAR-Pv 82 (and the rest of *Stahleckeria* scapulae) in possessing a unique rectangular cavity on the anterodorsal margin of its blade, originally interpreted as the articulation site for the cleithrum (von Huene, 1935; Vega and Maisch, 2014: Fig. 9.2; see also Fig. 5D). However, Vega and Maisch

(2014) described this structure as a pathological feature, and here we follow this interpretation.

The stahleckeriine specimen MCZ 1688 from the Pinheiro locality (Romer and Price, 1944; see also Fig. 5 C) also matches the stahleckeriid morphology, but its scapular blade differs from other taxa in the presence of a proportionally higher blade with a steeply sloping dorsal margin (unlike CRILAR-Pv 82 and von Huene’s specimens) and deeper concavity of its posterior margin (giving MCZ 1688 a more constricted appearance, as in CRILAR-Pv 82). As already mentioned (see Introduction), the taxonomic status of MCZ 1688 has been subject of debate over time. It was originally described by Romer and Price (1944) as the holotype and unique specimen of *Stahleckeria “lenzii”* (an additional member of the formerly monotypic genus *Stahleckeria* von Huene, 1935). Later on, Cox (1965) considered that this specimen represented a new genus more closely related to *Ischigualastia* than to *Stahleckeria*, creating the new combination “*Barysoma lenzii*” for MCZ 1688. Finally, Lucas (1993) concluded that MCZ 1688 was not significantly different than the stahleckeriines from Chiniquá locality, and “*Barysoma lenzii*” was considered a junior subjective synonym of *Stahleckeria potens*. Although recently Maisch (2020) questioned Lucas’ criterion and suggested the possible validity of the schemes of Romer and Price (1944) or Cox (1965), the synonymy of “*Barysoma lenzii*” with *Stahleckeria potens* has been widely accepted by most authors, including the most recent revision of Kammerer and Ordoñez (2021).

Beside the taxonomic conflicts and morphological variability, all the stahleckeriine scapulae from Pinheiros-Chiniquá and CRILAR-Pv 82 share a similar sharp and vertical scapular spine on the anteroventral margin of the scapular blade, strongly raising towards the acromion process and markedly convex in anterior view (see Figs. 5 and 6). Notably, although the small scapula “n°3” described by von Huene (1935)—and originally interpreted as a juvenile specimen of *Stahleckeria potens*—is the most disparate (markedly rounded dorsal margin and deeply concave anterior margin of the scapular blade, see Fig. 5F and Vega-Dias et al., 2005: Fig. 5B), its scapular spine also fits within this morphology (see Fig. 6E). Vega-Dias et al. (2005) also described a well-developed scapular spine in another specimen from the Pinheiros-Chiniquá levels near Cachoeira do Sul town, and interpreted it as a juvenile of *Stahleckeria* (MCP 272 PV; see also Lucas, 2002). Although ontogenetic changes in the scapular girdle of dicynodonts are still poorly understood, this evidence suggests that the morphology of the scapular spine is a taxonomically relevant feature, at least in the stahleckeriines from the Chañares Formation and Pinheiros-Chiniquá Sequence.

The ilium of CRILAR-Pv 82, although incomplete, is congruent with that of stahleckeriids. The evidently well-developed preacetabular process is typical of derived dicynodonts, especially Kannemeyeriiformes (Maisch, 2001). An elongated preacetabular process is present in stahleckeriids such as *Stahleckeria potens* (Fig. 7B and C; von Huene, 1935), *Eubrachioceras browni* (Kammerer et al., 2013), and *Sangasaurus parringtonii* (Angielczyk et al., 2018). *Angonisaurus cruickshanki*, frequently recovered as the sister taxon of *Stahleckeriidae* (e.g., Kammerer, 2019; Kammerer et al., 2019), also has an extremely elongated preacetabular process (Cox and Li, 1983; Kammerer et al., 2013: Fig. 8A). This condition differs from the relatively short preacetabular process present in the “shansiodontids” *Shansiodon wangi* (Yeh, 1959; Kammerer et al., 2013: Fig. 7D) and *Tetragonias njalilus* (Cruickshank, 1967: Fig. 18; Fröbisch 2006: Fig. 5), but also in the “kannemeyeriid” *Wadiasaurus indicus* (Bandyopadhyay, 1988: Fig. 18) and the stahleckeriine *Jachaleria candelariensis* (Vega-Dias and Schultz, 2004: Fig. 19A, B). Although Kammerer et al. (2013) considered *Kannemeyeria simocephalus* and *Placerias hesternus* as similar in morphology to *J. candelariensis*, limited information is available to evaluate these observations. Most descriptions of the iliac blade of *K. simocephalus* are based on specimen NHMUK-PV R3761, which has a broken anterior end (Govender et al., 2008: Fig. 9B; Kammerer et al., 2013: Fig. 8C; see

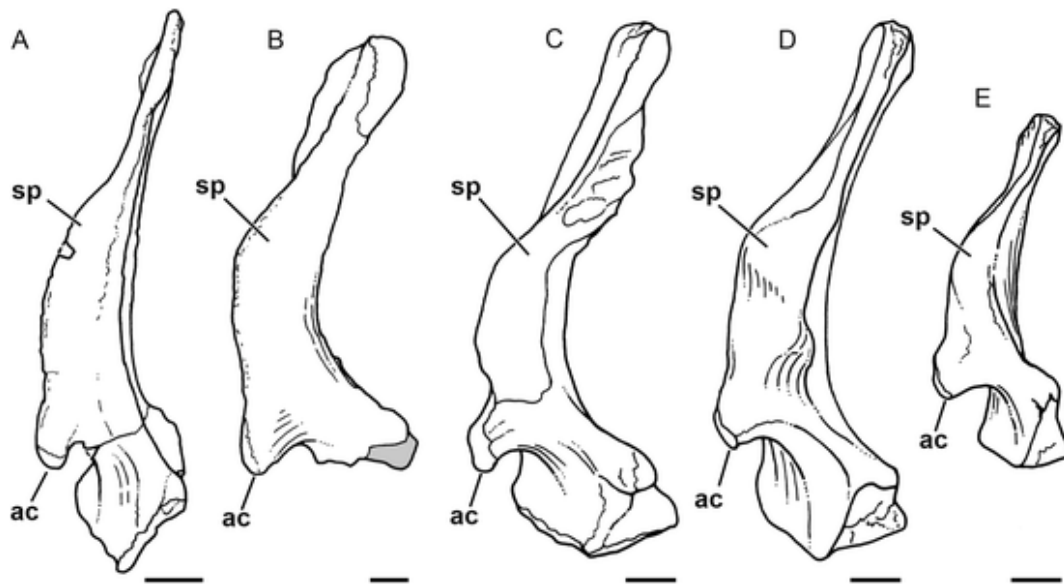


Fig. 6. Comparison of stahleckeriid scapulae from the Chañares Formation and the Pinheiros-Chiniqua Sequence in anterior view. A, CRILAR-Pv 82, *Stahleckeriidae* indet. B, MCZ 1688, *Stahleckeria potens* (holotype of *S. "lenzii"*). C, GPIT-PV-30792 (formerly GPIT/RE/8001), *Stahleckeria potens*. D, "scapula n°2" of von Huene, *Stahleckeria potens*. E, "scapula n°3" of von Huene, putative juvenile of *Stahleckeria potens*. Note the sharp, laterally convex spine shared by all specimens. All scapulae correspond to the right side. C, D and E modified from von Huene (1935). Abbreviations: ac, acromion process; sp, scapular spine. Scale bars equal 5 cm.

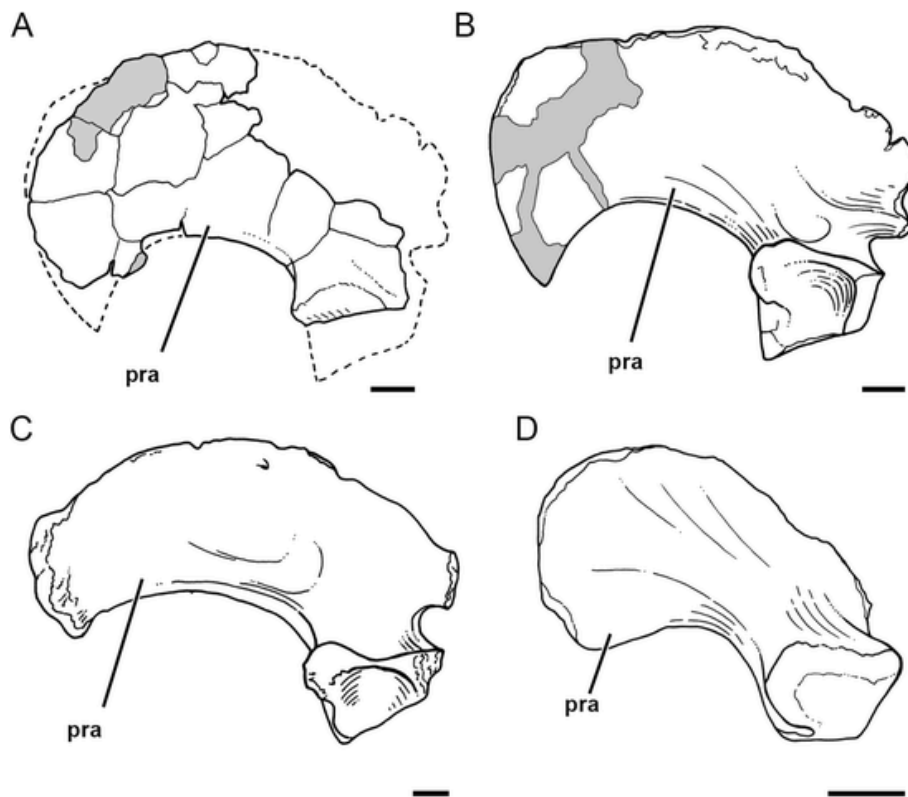


Fig. 7. Comparison of kannemeyeriiform ilia from the Chañares Formation and the Pinheiros-Chiniqua Sequence in lateral view. A, CRILAR-Pv 82, *Stahleckeriidae* indet. (dotted line indicates a hypothetical restoration based on *Stahleckeria potens*). B, GPIT-PV-30792 (formerly GPIT/RE/8001), *Stahleckeria potens*. C, "ilium n°2" of von Huene, *Stahleckeria potens*. D, MPDC 504-120, *Dinodontosaurus tener*. Note the anteroventrally curved, "hooked-shaped" preacetabular process of the three stahleckeriid specimens A, B and C. A, C and D represent left ilia, B is a right ilium reversed for comparative purpose. B and C modified from von Huene (1935). Abbreviation: pra, preacetabular process. Scale bars equal 5 cm.

a tentative reconstruction in Pearson, 1924: Fig. 19), and the iliac elements of *P. hesternus* are very fragmentary (Camp and Welles, 1956: Figs. 34C, 57 and 59; Kammerer et al., 2013: Fig. 13C). Comparison with *Ischigualastia jenseni* is also ambiguous because the specimen MCZ

3121 figured by Cox (1965: Fig. 9A, B) possesses an elongated preacetabular process, but that of a specimen referred to this species by Kammerer et al. (2013: Fig. 8D; PVL 3847) is similar to *J. candelariensis*. The most informative trait of the ilium of CRILAR-Pv 82 is the pro-

nounced anteroventral curvature (“hook-shaped”) of the preacetabular iliac process. This morphology is very similar to that of the classic material of *Stahleckeria potens* described by von Huene (1935; see also Fig. 7), e.g., GPIT-PV-30792, and *Eubrachiosaurus browni* from the probably late Carnian Popo Agie Formation of North America (Kammerer et al., 2013; Fig. 7A). At the same time, it constitutes a singular condition, at the moment not recognized among other kannemeyeriiform taxa.

The number of sacral vertebrae of CRILAR-Pv 82 inferred based on its ilium is relevant of discussion. Dicynodonts are characterized by a high variation in the number of sacral vertebrae, departing from the typically conservative plan of most synapsids (Griffin and Angielczyk, 2019). Sacral count is frequently used in most phylogenetic analyses focused on dicynodonts, being actually the only vertebral character included in recent data matrices (e.g., Angielczyk et al., 2018; Kammerer et al., 2019; Kammerer and Ordoñez, 2021). As described above, the medial surface of the ilium of CRILAR-Pv 82 preserves scars for three to four sacral ribs. However, the entire median and posterior regions of the iliac blade are missing. Considering that the preserved sacral rib scars are positioned mostly on the posterior region of the preacetabular process, it is expected that probably two or three additional scars would be present. A tendency to an increase in sacral count is observed in more derived taxa, especially in some Permian clades and all the Triassic forms (e.g., Griffin and Angielczyk, 2019). Within Kannemeyeriiformes, sacral count lacks a clear phylogenetic signal, ranging from a minimum of four in *Lisowicia bojani* (Sulej and Niedzwiedzki, 2019); five in *Shansiodon wangi* (Yeh 1959), *Kannemeyeria simocephalus* (Govender et al., 2008), *Dinodontosaurus tener*, *Ischigualastia jenseni* (Cox, 1965), and *Jachaleria candelariensis* (Vega-Dias and Schultz, 2004); five to six in *Acratophorus argentinensis* (Bonaparte, 1966), *Wadiazaurus indicus* (Bandyopadhyay, 1988), and *Tetragonas njalilus* (Cruikshank, 1967); and six in *Angonisauros cruickshanki* (Angielczyk et al., 2018). The highest sacral counts have been reported in the stahleckeriines *Sangusaurus parringtonii* (7 sacral vertebrae, Angielczyk et al., 2018) and *Stahleckeria potens* (6–7 sacral vertebrae according to Angielczyk et al., 2018, but even 8 according to von Huene, 1935). Another possible evidence to infer a high sacral count is the large size of CRILAR-Pv 82. However, although Griffin and Angielczyk (2019) recognized a significant positive correlation between body size and sacral count in dicynodonts, the most important evolutionary shift was identified at the origin of Bidentalina (one of the major dicynodont subclades, in which kannemeyeriiforms are nested; e.g., see phylogeny of Kammerer and Ordoñez, 2021), without a clear pattern inside this group. Besides that, these authors provided a general characterization of the first sacral ribs in dicynodonts with six or more sacral vertebrae, which is quite consistent with the preserved scars in CRILAR-Pv 82, at least in their relatively large size and homogeneous morphology. Considering this evidence, the medial surface of the iliac lamina suggests that CRILAR-Pv 82 probably exceeded by far the minimum sacral count of kannemeyeriiforms, possibly reaching a high number similar to that of the stahleckeriines *Sangusaurus* and *Stahleckeria*.

A rigorous comparison of CRILAR-Pv 82 with *Dinodontosaurus* is difficult because of the limited information available on its postcranial anatomy. Regarding Brazilian specimens, Kammerer et al. (2013; Fig. 3B) referred specimen MCN-Pv 3584 to *Dinodontosaurus pedroanum* (= *Dinodontosaurus tener* according to Kammerer and Ordoñez, 2021) and included this taxon in their “shansiodontid” morphotype. Although the morphology of this element agrees with this characterization (widely expanded, “fan”-shaped dorsal region of the scapular blade; large and anteriorly directed acromion process; scapular spine absent; specimen MPDC 232-48 shown in Fig. 5G also exemplifies this morphotype), the scapular anatomy of the classic *Dinodontosaurus* specimens is poorly known. A well-developed acromion process and absence of scapular spine were also noticed by Cox (1965) in the classic specimens from the Pinheiro region (Pinheiros-Chiniquá Sequence), but the scapula figured by this author (MCZ 1670, the holotype of *Dinodon-*

tosaurus “oliveirai” Romer, 1943) is not as dorsally flared as that of MCN-Pv 3584 and MPDC 232-48 (see Cox, 1965; Fig. 15A). In an unpublished morphofunctional study, Morato (2006) performed similar observations in additional specimens of *Dinodontosaurus tener* from Bom Retiro and Pinheiro regions (according to Martinelli et al., 2017), mostly attributed to juvenile individuals (e.g., UFRGS-PV0113T).

Concerning the iliac morphology, the lack of a clear taxonomic signal in *Dinodontosaurus tener* is even more evident. Cox (1965) described two morphologies in the Pinheiro assemblage, which were exemplified by specimens MCZ 1687 and MCZ 3108. The first one has a relatively short and tall preacetabular process (as in *Shansiodon* and *Tetragonias*), but has also a large and deep acetabulum, surrounded by a thickened margin; although Cox explains this acetabular morphology as the result of intraspecific or taphonomic variation, it is very similar to that of *Jachaleria candelariensis* (pers. obs, also compare Fig. 19A, B of Cox, 1965 with Fig. 19A, C of Vega-Dias and Schultz, 2004). By contrast, MCZ 3108 has a conspicuously elongated preacetabular process, like those of *Angonisauros*, *Stahleckeria*, *Sangusaurus*, and CRILAR-Pv 82 (Cox, 1965; Fig. 19D; see also specimen MPDC 504-120 in Fig. 7D). Regardless of this variation in the preacetabular morphology, all the ilia considered lack the anteroventrally curved preacetabular blade present in *Stahleckeria*, *Eubrachiosaurus*, and CRILAR-Pv 82. Unfortunately, CRILAR-Pv 82 cannot be confidently compared with *Dinodontosaurus brevisrostris* from the Chañares Formation because their referable postcrania (Cox, 1968; Mancuso et al., 2017; Ordoñez et al., 2020; Kammerer and Ordoñez, 2021) remain unstudied. In any case, and considering current evidence, the anterolaterally directed, moderately developed scapular acromion, strongly developed scapular spine, and “hook”-shaped iliac preacetabular process of CRILAR-Pv 82 seem to constitute significant differences with (at least) *Dinodontosaurus tener* from the Pinheiros-Chiniquá Sequence (Fig. 7). Taking into account the corroboration of *Dinodontosaurus brevisrostris* as the only valid species of this genus in the Chañares Formation (Kammerer and Ordoñez, 2021), its postcranial anatomy should not differ significantly from its Brazilian cogenetic forms; according to this proposal, two morphotypes linked to two kannemeyeriiform lineages would occur in the Chañares assemblages. In this sense, Ordoñez et al. (2020) recently assigned a new specimen from the Chañares Formation to *Dinodontosaurus* sp. on the basis of its cranial anatomy. Although its scapula appears to fit with that of the “shansiodontid”-like pattern (see Mancuso et al., 2017; Fig. 8C), the postcranium is still undescribed and, thus, no further observations will be made here. Thus, a rigorous comparison with *Dinodontosaurus brevisrostris* is hampered until more complete skeletons (including both cranial and postcranial regions) are studied.

As already mentioned (see Introduction) Cox (1968) also briefly described a scapulocoracoid and clavicle (MCZ 3459) of a possible fourth dicynodont taxon in the Chañares Formation, providing a schematic illustration of the pectoral girdle (Fig. 5B; see also Cox, 1968; Fig. 12). A reassessment of this data allows a comparison of MCZ 3459 with CRILAR-Pv 82 and the stahleckeriines from the Pinheiros-Chiniquá Sequence (see Fig. 5). As is typical in stahleckeriids, the dorsal part of the scapular blade of MCZ 3459 is anteroposteriorly expanded and its dorsal margin is anteroventrally inclined. In addition, Cox (1968) suggested that its scapular spine (although broken-off) was probably well-developed and positioned along the anterior border of the scapular blade, in a position very similar to that of CRILAR-Pv 82 and *Stahleckeria potens* (Fig. 5B; see also Cox, 1968; Fig. 12). MCZ 3459 has also the typical condition of Kannemeyeriiformes (including CRILAR-Pv 82 and *Stahleckeria potens*), in which the scapula is excluded from contribution to the coracoid foramen (Fig. 5B; see also Cox, 1968; Fig. 12). The combination of these features indicates that MCZ 3459 also matches the stahleckeriid morphology and thus would constitute the first historical record of this subclade in the Chañares Formation. Strictly speaking, the stahleckeriid affinities of MCZ 3459 were partially suggested by

Cox (1968). Although this author assigned MCZ 3459 to “Kannemeyeriidae”, he was employing a different, precladistic taxonomic scheme (see Cox, 1965), and he also included *Ischigualastia*, *Placeras* and “*Barysoma lenzii*” (i.e., the specimen MCZ 1688) within that group. In fact, Cox (1968) highlighted a close resemblance between MCZ 3459 and the specimen MCZ 1688. CRILAR-Pv 82 and MCZ 3459 differ from von Huene’s specimens (see Fig. 5A and B) in a more slender scapular blade, with a more abrupt dorsal expansion. As a result, the scapulae of both specimens from the Chañares Formation are markedly constricted at the level of the spine (although this condition is apparently more pronounced in MCZ 3459). However, a detailed first-hand comparison is essential to confirm these observations and to determine whether CRILAR-Pv 82 and MCZ 3459 represent a single morphotype.

6.2. Implications in the evolutionary history of *Stahleckeriidae*

The early evolutionary history of *Stahleckeriidae* is still under debate, especially owing to the scanty record of kannemeyeriiforms in the Early Triassic (Maisch and Matzke, 2014; Olivier et al., 2019, but see Liu, 2020). Maisch and Matzke (2014) described *Sungeodon kimkramererae* from the Lower Triassic Jiucayuan Formation in northwestern China as the oldest known stahleckeriid, hypothesizing an Asian origin for the clade. However, Kammerer et al. (2019) questioned this statement and suggested closer affinities to earlier branching kannemeyeriiforms or dicynodontoids. Besides this controversy, the two major stahleckeriid subgroups (*Stahleckeriinae* and *Placeriinae sensu Kammerer et al., 2013*) are already present in the possible Middle-early Late Triassic African record (e.g., Nesbitt et al., 2018; Ezcurra et al., 2017; Peacock et al., 2018; Hancox et al., 2020). *Stahleckeriinae* are represented by *Ufudocyclops mukanelai* (Kammerer et al., 2019) in the South African *Cricodon-Ufudocyclops* Subzone (= *Cynognathus* Subzone C), *Sangusaurus edentatus* in the Zambian upper Ntawere Formation (Cox, 1969; Angielczyk et al., 2018), *Sangusaurus parringtonii* and the indeterminate postcranium NMT RB463 (possibly a new species) in the Tanzanian middle-upper Lifua Member of the Manda Beds (Cruikshank, 1986; Angielczyk et al., 2018; Kammerer et al., 2018), and the typically South American taxon *Stahleckeria potens* (see below) in the upper Omingonde Formation (Abdala et al., 2013). From the Lifua Member also came the ‘stahleckeriid’-like *Angonisaurus cruickshanki* (Cox and Li, 1983; Hancox et al., 2013). *Placeriinae* are only represented by *Zambiasaurus submersus* in the upper Ntawere Formation (Cox, 1969; Angielczyk et al., 2014). By the late Carnian-Norian, the clade *Stahleckeriidae* became the latest surviving dicynodonts and achieved its maximum paleogeographic distribution, with stahleckeriines mostly represented in southern Pangea (Cox, 1965; Bonaparte, 1970; Vega-Díaz and Schultz, 2004; Martinelli et al., 2020; Kammerer and Ordoñez, 2021) and placeriines in northern Pangea (Camp and Welles, 1956; Dutuit, 1988; Sulej and Niedźwiedzki, 2019). Notable exceptions are the stahleckeriine *Eubrachioceras browni* in the Popo Agie Formation of North America (Kammerer et al., 2013) and the placeriine *Pentassaurus goggai* in the Lower Elliot formation of South Africa (Kammerer, 2018).

The South American stahleckeriid record is only represented by the subclade *Stahleckeriinae*. Until recently, it was restricted to the Ladinian-Carnian Pinheiros-Chiniquá Sequence (*Dinodontosaurus* AZ) and the Norian Candelaria Sequence (*Riograndia* AZ) in southern Brazil, and in the upper Carnian-Norian levels of the Agua de La Peña Group in northwestern Argentina. In the Pinheiros-Chiniquá Sequence they have been historically represented by *Stahleckeria potens* (von Huene, 1935; Maisch, 2001; Vega-Díaz et al., 2005; Martinelli et al., 2017; Schultz et al., 2020; Kammerer and Ordoñez, 2021). However, the exact number of stahleckeriine taxa is currently under discussion, considering the problematic referral of MCZ 1688 to *Stahleckeria potens* (Romer and Price, 1944; Lucas, 1993; Maisch, 2020; Kammerer and Ordoñez, 2021; see above); some cranial fragments (GPIT-PV-47003; formerly GPIT-

RE/9622) recently suggested as possibly a distinct taxon by Maisch (2020); and especially the recent first record in Brazil of the Tanzanian and Zambian genus *Sangusaurus* (Kammerer and Ordoñez, 2021). The record of the Candelaria Sequence is only represented by *Jachaleria candelariensis* (Araujo and Gonzaga, 1980; Vega-Díaz and Schultz, 2004; Martinelli et al., 2020; Kammerer and Ordoñez, 2021). Argentinian stahleckeriines, on the other hand, were historically restricted to the upper Carnian-Norian levels of the Ischigualasto Formation and the Norian Los Colorados Formation (*Ischigualastia jenseni* and *Jachaleria colorata*, e.g., Cox, 1962, 1965; Bonaparte, 1970; Martínez et al., 2013; Kammerer and Ordoñez, 2021), coincident with the last stage of stahleckeriid diversification (see above). Considering the historical biostratigraphic links between the Chañares Formation and the Brazilian *Dinodontosaurus* Assemblage Zone (e.g., Ezcurra et al., 2017; Langer et al., 2007; 2018; Martinelli et al., 2017; Schmitt et al., 2019; Schultz et al., 2020), occurrences of stahleckeriines were expected in the former unit but not confirmed until very recently (Mancuso and Irmis, 2020).

Mancuso and Irmis (2020) reported the partial right ulna CRILAR-PV 602, and assigned it to *Stahleckeria* sp. on the basis of its enlarged, dorsally rounded olecranon process. As a consequence, they proposed a new component for the correlations of the Chañares Formation with the *Dinodontosaurus* AZ of Brazil and the uppermost Omingonde Formation of Namibia. Certainly, the overall morphology of CRILAR-Pv 602 is very similar to the specimens of *Stahleckeria potens* from the Pinheiros-Chiniquá Sequence, e.g., the mounted specimen GPIT-PV-30792 (see von Huene, 1935: plate 7, Fig. 8 A,B) and especially the specimen MCZ 1688, and can be confidently referred at least to *Stahleckeriinae*. However, as discussed for CRILAR-Pv 82 and MCZ 3459, several factors make a taxonomic assignment at the genus or species level difficult. These include the isolated condition of CRILAR-Pv 602, an incomplete comparative framework about ulnar variation in *Stahleckeriinae* (the recent record of *Sangusaurus* in Brazil is particularly relevant, since the ulnar morphology of this genus is currently unknown), and the lack of overlapping with other kannemeyeriiform specimens from the Chañares Formation. More complete skeletons are needed to strengthen the taxonomic conclusions of Mancuso and Irmis (2020), as the authors themselves recognized. CRILAR-Pv 602 and CRILAR-Pv 82 came from the lowermost levels of the Chañares stratigraphic section in Angostura del Gualo and Los Bordes localities, respectively (Fig. 2; see also Mancuso and Irmis, 2020: Fig. 1.2). According to the biostratigraphic scheme proposed by Ezcurra et al. (2017), the fine-grained levels with abundant root traces of CRILAR-Pv 602 (Mancuso and Irmis, 2020: Fig. 1.2) possibly also correspond to the *Tarjadia* AZ. Unfortunately, no unequivocal data is available about the stratigraphic provenance of MCZ 3459. However, the outcropping levels at the east region of the Corral de Gualo locality—estimated geographic provenance for MCZ 3459—mostly are represented by the typical pedogenic fluvio-sandy sediments of the *Tarjadia* AZ (pers. obs.). Field works in this almost unexplored locality are required to address these indeterminate issues.

Aside from these uncertainties, all the dicynodont postcranial material described so far from the Chañares Formation (MCZ 3459, CRILAR-Pv 602 and CRILAR-Pv 82) represents the oldest record of *Stahleckeriinae* in the Ischigualasto-Villa Union Basin, expanding its record in Argentina back in time beyond the Ladinian-Carnian boundary. Despite the ambiguous provenance of MCZ 3459, future occurrences of stahleckeriines are expected also in the *Massetognathus-Chanaresuchus* AZ, considering that their presence is well known in the overlying Ischigualasto and Los Colorados formations of the same basin.

7. Conclusions

Here are described postcranial materials (CRILAR-Pv 82, scapula, sternum, and ilium) discovered at the lowermost levels of the *Tarjadia* AZ of the Chañares Formation and it is unambiguously referred to a stahleckeriid dicynodont. The scapular morphology of CRILAR-Pv 82 allows a linkage to the historical material MCZ 3459 described by Cox (1968). Considering this historical material and the ulna recently reported by Marsicano and Irmis (2020), the new specimen here described constitutes the third record of Stahleckeriidae for the Chañares Formation, probably a member of the major subclade Stahleckerinae. Aspects of the postcranial anatomy of South American dicynodonts remain poorly understood, suggesting that future contributions should be oriented not only to cranial studies, but also to an integrative approach of the complete skeletal morphology of the group.

Author statements

Conceptualization: all authors; Main investigation: JAE; Writing – original draft: all authors; Writing – review & editing: all authors; Figures: JAE, AGM, LEF.

Uncited references

Angielczyk and Kammerer, 2017; Boos et al., 2013; Boos et al., 2016; Ezcurra et al., 2015; Horn et al., 2014; Krapovickas et al., 2013; Peruzzo and Araújo-Barberena, 1995; Zerfass et al., 2003.

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.

Acknowledgements

We want to thank the Secretaría de Cultura de La Rioja, Subsecretaría de Patrimonio, and the Administración de Parques Nacionales of Argentina for granting permits to work in the Talampaya National Park. We are also indebted to the rangers of the Talampaya National Park, and special thanks to Neno, for their help in the field.

We thank the Chañares field crew of 2018, in which the specimen studied here was collected, and all the members of the “Archosauriform Research Group” (ARG) for the invaluable work of the last decade in the Chañares Formation. We thank Voltaire D. Paes Neto for providing photographs of MCZ collection, and Cesar L. Schultz for access to UFRGS collection. We are grateful to Jeferson Saurin and Claudio Bortolas for access to specimens housed at the Museu Padre Daniel Cargnin (Mata, RS, Brazil). Finally, the comments and suggestions of both anonymous reviewers greatly improved the original manuscript. This research was supported by Agencia Nacional de Promociones Científicas y Técnicas (PICT 2018-0717 to JBD).

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