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Review of the fossil record of early dinosaurs from South America, and its phylogenetic implications

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ABSTRACT

Triassic beds from Argentina and Brazil provide the most relevant fossil record of early dinosauriforms in terms of numerical abundance and taxonomic diversity. This record currently represents the best source to understand the origin and early evolutionary radiation of dinosaurs. In the present paper we offer an updated review focused on the available evidence of Carnian dinosaurs from this continent, but we also discuss the record of Triassic dinosaur precursors and the evolution of Triassic dinosaurs in other continents. It is clear that, aside the agreed taxonomic composition of some particular dinosaurian subclades (e.g., Herrerasauridae, Neotheropoda), there is no consensus about early dinosaur phylogeny, and our paper is not the exception. Recent years witnessed the discovery of several new early dinosaurian taxa, as well as reviews of the taxonomic allocation of several renowned forms such as *Lagerpeton*, *Lewisuchus*, *Pisanosaurus*, and *Eorpator*. New analyses demonstrate that evidence supporting the taxonomic referrals of pre-Norian dinosaurs to Theropoda, Sauropodomorpha and Ornithischia are tenuous, at best. Here we present new anatomical observations and comparisons for each of these South American early dinosauriforms with the aim to test previous phylogenetic interpretations. Evidence from South America allows reviewing the phylogenetic relationships of taxa from other continents, including *Tawa, Chindesaurus,* and *Daemonosaurus,* which are here suggested to nest within Herrerasauria. Evidence at hand indicates that herrerasaurs were a successful clade of archaic predatory saurischians that inhabited both South and North America, and probably also India and Europe.

1. Introduction

South America plays a key role in the understanding of the origin and early diversification of Dinosauria. The discovery of early dinosauromorphs in the Upper Triassic rocks of this continent dates back to 1958, the early 1960s, and 1970s, with the description of *Herrerasaurus* by Reig (1963) and *Lagosuchus* and *Lewisuchus* by Romer (1971, 1972), based on discoveries made in northwestern Argentina. Later, with the recognition of *Lagosuchus* as a "proto-dinosaur" by Bonaparte (1975), fossil findings from the Upper Triassic beds of South America gained worldwide attention. Further, by the 1990s, fossils of *Herrerasaurus* and the coeval *Eoraptor* were not only probably the oldest known dinosaurs, but also the most anatomically informative early dinosaurs known at that time (Sereno and Novas, 1992, 1994; Sereno et al., 1993; Novas, 1994). In Brazil, the fossil record of Triassic dinosaurs has consistently increased since the description of *Staurikosaurus* by Colbert in 1970 and, decades later, *Saturnalia* and *Guaibasaurus* in 1999 (Langer et al., 1999; Bonaparte et al., 1999). In the last 20 years, the available fossil record of Brazil has greatly expanded and now includes not only a wide array of early

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sauropodomorphs, but also herrerasaurians, silesaurids, and possible theropods (e.g., Ferigolo and Langer, 2006; Langer and Ferigolo, 2013; Cabreira et al., 2016; Marsola et al., 2019a; Müller et al., 2018a,c; Pacheco et al., 2019).

In addition, South America has an almost complete stratigraphical succession that covers most of the Late Triassic (Carnian and Norian) including a large succession of vertebrate faunas (Bonaparte, 1982). This allows comparing different stages of early dinosaur evolution in a way that is not possible in any other part of the world. In addition, recent radiometric dates of several classic fossil-bearing outcrops from Brazil (i.e., Santa Maria, Caturrita) and Argentina (Ischigualasto-Villa Unión Basin) allow a more reliable chronological framework for understanding the first steps of dinosaur evolution (Martínez et al., 2013b; Marsicano et al., 2016; Ezcurra et al., 2017; Langer et al., 2018; Desojo et al., 2020a).

With the recognition of a monophyletic Dinosauria by the early 1970s, the interpretations and hypotheses about the origin and early radiation of the group have greatly augmented. Traditional works (Bakker and Galton, 1974; Bonaparte, 1975) indicate that the ancestral dinosaur morphotype was a small-sized animal of gracile proportions and bipedal posture that ran behind the insects that formed part of its diet. However, recent discoveries changed this traditional view and opened the window to a diverse array of hypotheses on dinosaurian early steps. In this sense, the finding of *Silesaurus opolensis* at the beginning of the 2000s (Dzik, 2003), together with a large number of early dinosauriforms and dinosaurs found at different sites worldwide (e.g., Ezcurra, 2006; Irmis et al., 2007a; Nesbitt et al., 2009, 2010; Irmis, 2011; Novas et al., 2011; Sues et al., 2011; Cabreira et al., 2016) demonstrated that the early history of dinosaurs was far more complex than thought.

Most of the recent contributions on dinosaur phylogeny warn interpretation conflicts at the base of Dinosauria (Langer and Ferigolo, 2013; Cabreira et al., 2016; Baron et al., 2017a, b; Müller et al., 2018b; Pacheco et al., 2019; Müller and Garcia, 2020). However, the hypotheses advocated by most of these analyses depict Carnian dinosaurs as members of one of the three main dinosaur groups: Ornithischia, Sauropodomorpha or Theropoda (Langer et al., 2017). However, this seems to be a rather simplistic view of the radiation pattern of early dinosauriform clades. Novas and Ezcurra (2011) preliminary proposed that the early diversification of Dinosauria was much more complex than previously thought. They proposed that most Carnian dinosaurs from South America were successive sister groups of the main dinosaur clades that diversified in post-Carnian times (hereafter we call these groups as core ornithischians, core sauropodomorphs, and Neotheropoda or core theropods). More recently, Nesbitt et al. (2020) analyzed early dinosaur phylogenetic relationships, based on the phylogenetic dataset of Baron et al. (2017) as modified by Langer et al. (2017), depicting a large polytomy formed by core sauropodomorphs, neotheropods, and core ornithischians, plus a series of taxa including *Buriolestes, Pampadromaeus, Tawa, Chindesaurus, Saturnalia, Panphagia, Eoraptor, Guaibasaurus*, and a subclade formed by *Eodromaeus* plus Herrerasauridae. We agree with Nesbitt et al. (2020) in the uncertainty regarding the phylogenetic relationships among early dinosauriforms, and we agree with their comments about the tidal wave of phylogenetic hypotheses for early dinosauriforms, as well as with the possible placement of most of the Carnian dinosaurs as sister groups of the main ("core") dinosaurian groups.

The aim of the present paper is to comment on character distribution among early dinosaurs, and discuss the phylogenetic relationships of Carnian and early Norian dinosauriform taxa from South America. Based on this information, we also analyze the phylogenetic relationships of bizarre taxa from Norian and Rhaetian beds of North America. These observations may help clarifying some aspects of dinosaur relationships and may serve as a source for future discussions on the origin of dinosaurs.

2. Materials and methods

Institutional abbreviations – CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; **CM**, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA; **CRILAR-Pv**, Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, Argentina; **GR**, Ruth Hall Museum of Paleontology at Ghost Ranch, Abiquiu, New Mexico, USA; **ISIR**, Indian Statistical Institute, Reptile, Kolkatta, India; **LPRP/USP**, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; **MACN-Pv**, Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'', Paleovertebrados, Buenos Aires, Argentina; **MCZ**, Museum of Comparative Zoology, Cambridge, USA; **MLP**, Museo de La Plata, La Plata, Argentina; **PEFO**, Petrified Forest National Park, Arizona; USA; **PULR-V**, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Paleontología de Vertebrados, Instituto "Miguel Lillo", San Miguel de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **UFRGS-PV**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **ULBRA**, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Brazil; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA.

Specimens studied – The following Carnian dinosauriform and Norian-Rhaetian herrerasaur specimens have been studied first hand for the purpose of this research: *Lagosuchus talampayensis* (MCZ 4137; PULR-V 09: holotype; PVL 3870, 3871, 3872, 4671, 4672), *Lewisushus admixtus* (CRILAR-Pv 552; PULR-V 01: holotype, 53, 111, 113), *Herrerasaurus ischigualastensis* (MACN-Pv, 18,060; MCZ 4381, 7064; MLP 61-VIII-2-2, 61-VIII-2-3; PVL 2566: holotype; PVSJ 104, 373, 380, 407)*, Frenguellisaurus sanjuanensis* (PVSJ 53: holotype) *Sanjuansaurus gordilloi* (PVSJ 605: holotype)*, Eoraptor lunensis* (PVSJ 512: holotype)*, Panphagia protos* (PVSJ 874: holotype)*, Chromogisaurus novasi* (PVSJ 845: holotype)*, Eodromaeus murphi* (PVSJ 534, 560: holotype, 561, 562)*,Staurikosaurus pricei* (MCZ 1669: holotype)*, Gnathovorax cabrerai* (CAPPA/UFSM 0009: holotype)*, Saturnalia tupiniquim* (MCP 3844-PV: holotype, 3845-PV, 3846-PV)*, Buriolestes schultzi* (CAPPA/UFSM 0035; ULBRA-PV-T280: holotype)*, Pampadromaeus barberenai* (ULBRA-PVT016: holotype)*, Bagualosaurus agudoensis* (UFRGS-PV-1099-T: holotype)*, Nhandumirim waldsangae* (LPRP/USP 0651: holotype), *Pisanosaurus mertii* (PVL 2577: holotype), Herrerasauria indet. from the upper Maleri Formation (ISIR 282), *Tawa hallae* (GR 241: holotype, 242), "*Caseosaurus crosbyensis*" (UMMP 8870: holotype), *Chindesaurus bryansmalli* (PEFO 10395: holotype), and *Daemonosaurus chauliodus* (CM 76821).

Phylogenetic definitions – We use the following definitions of the main early dinosauriform clades that are relevant for discussing the phylogenetic relationships of Carnian dinosaurs.

Dinosauromorpha Benton, 1985 – the most inclusive clade containing *Compsognathus longipes*, but not *Pterodactylus antiquus* or *Alligator mississippiensis* (Ezcurra et al., 2020a).

Dinosauriformes Novas, 1992 – the least inclusive clade containing *Compsognathus longipes* and *Lagosuchus talampayensis* (Ezcurra et al., 2020a).

Dracohors Cau, 2018 – the most inclusive clade containing *Megalosaurus bucklandii*, but excluding "*Marasuchus lilloensis*" (= *Lagosuchus talampayensis* sensu Agnolin and Ezcurra, 2019) (Cau, 2018).

Silesauridae Langer et al., 2010; Nesbitt et al. (2010) – all archosaurs closer to *Silesaurus opolensis* than to *Heterodontosaurus tucki* and "*Marasuchus lilloensis*" (= *Lagosuchus talampayensis* sensu Agnolin and Ezcurra, 2019) (Langer et al., 2010).

Dinosauria Owen, 1842 – the smallest clade containing *Iguanodon bernissartensis*, *Megalosaurus bucklandii* and *Cetiosaurus oxoniensis* (Langer et al., 2020).

Ornithischia Seeley, 1888 – the most inclusive clade containing *Triceratops horridus*, but not *Passer domesticus*, or *Saltasaurus loricatus* (Sereno, 2005).

Saurischia Seeley, 1888 – the largest clade containing *Allosaurus fragilis* and *Camarasaurus supremus*, but not *Stegosaurus stenops* (Gauthier et al., 2020).

Herrerasauria Galton, 1985 – all dinosaurs that share a more recent common ancestor with *Herrerasaurus* than with *Liliensternus* and *Plateosaurus* (Langer, 2004).

Herrerasauridae Benedetto, 1973 – *Herrerasaurus*, *Staurikosaurus*, their most recent common ancestor, plus all its descendants (Novas, 1992; Langer et al., 2010).

Theropoda Marsh (1881) – the largest clade containing *Allosaurus fragilis* but neither *Plateosaurus engelhardti* nor *Heterodontosaurus tucki* (Naish et al., 2020).

Neotheropoda Bakker (1986) – the least inclusive clade containing *Coelophysis bauri* and *Passer domesticus* (Sereno, 2005).

Sauropodomorpha von Huene (1932) – the largest clade containing *Saltasaurus loricatus* but not *Allosaurus fragilis* and *Iguanodon bernissartensis* (Fabbri et al., 2020).

Saturnaliidae Ezcurra, 2010 – the largest clade containing *Saturnalia tupiniquim* but not *Plateosaurus engelhardti* (Langer et al., 2019).

We follow Langer et al. (2017) in supporting the classical hypothesis that Ornithischia is sister group of Sauropodomorpha plus Theropoda (= Saurischia). No support for a monophyletic Ornithoscelida over a monophyletic Saurischia has been found in the present analysis (contra Baron et al., 2017a).

Phylogenetic analyses – We tested the phylogenetic relationships of early dinosaurs using the dataset originally published by Nesbitt et al. (2009) and iteratively modified by Ezcurra and Brusatte (2011), Sues et al. (2011), You et al. (2014), Nesbitt and Ezcurra (2015), Martill et al. (2016), Ezcurra (2017), Martínez and Apaldetti (2017), Marsola et al. (2019a), Marsh et al. (2019), Griffin (2019), and Ezcurra et al. (2021a) (see Supplementary Information). We chose this data matrix because it was used to test the phylogenetic position of *Tawa hallae* within Dinosauria (Nesbitt et al., 2009), a taxon of interest for this review. In addition, this data set has been revised and improved by numerous subsequent authors in the last decade. Here, the herrerasaurid *Gnathovorax cabrerai* and the sauropodomorph *Buriolestes schultzi* were added to the version of the data set published by Ezcurra et al. (2021a). These species were scored based on first-hand observations of specimens. Here, three of the four new characters added by Sues et al. (2011) were included (the fourth character was already included in the data set) and six other characters were added. Some character formulations, scorings, and orderings were modified (rationale for these changes is given in Supplementary Information). '*Powellvenator podocitus* holotype', '*Lepidus praecisio* combined' and *Velociraptor mongoliensis* were deactivated before the analyses following Ezcurra (2017). *Nhandumirim waldsangae* was also deactivated before the searches because this taxon has been recently suggested to represent a sauropodomorph (Pacheco et al., 2019), rather than a possible theropod (Marsola et al., 2019a), and the matrix employed here does not have a comprehensive sample of early sauropodomorphs, neither of phylogenetically informative characters for that part of the tree. The three specimens that form the hypodigm of *Sarcosaurus woodi* were deleted as independent terminals, leaving only a 'combined' *Sarcosaurus woodi* operational taxonomic unit, because we follow the hypothesis that they belong to the same species (Ezcurra et al., 2021a). Characters 252 and 352 were also deactivated because we consider that they were not independent from other characters. The resulting matrix consists of 386 active characters and 57 active terminals (Supplementary Information).

The outgroup choice follows Nesbitt et al. (2009), and the following multistate characters were ordered: 9, 18, 30, 67, 128, 129, 174, 184, 197, 213, 219, 231, 236, 248, 253, 254, 273, 329, 343, 345, 347, 349, 354, 366, 371, 374, 377–379, 383, and 384. The data matrix was analyzed under equally weighted parsimony using TNT 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016). A heuristic search of 1000 replications of Wagner trees (with random addition sequence) followed by TBR branch swapping (holding 10 trees per replicate) was performed. Branches with a maximum possible length of zero among any of the recovered most parsimonious trees (MPTs) were collapsed (rule 3 of Swofford and Begle, 1993; Coddington and Scharff, 1994). The resulting cladogram is depicted in Fig. 1.

As a measure of branch support, decay indices (= Bremer support) were calculated (Bremer, 1988, 1994), and as a measure of branch stability, a bootstrap resampling analysis (Felsenstein, 1985) was conducted, performing 10,000 pseudoreplications. Both absolute and GC (i.e., difference between the frequency whereby the original group and the most frequent contradictory group are recovered in the pseudoreplications; Goloboff et al., 2003) bootstrap frequencies were reported. In order to analyze the effect that a few topologically unstable terminals may have on Bremer supports, this index was recalculated after the a posteriori pruning of such terminals, which were previously detected in the subsample of suboptimal trees with the iterPCR protocol (Pol and Escapa, 2009). Finally, analyses forcing topological constraints were conducted to find the minimum number of steps necessary to force alternative suboptimal positions among early saurischian dinosaurs.

3. Biostratigraphic framework for basal dinosauriforms

Continental tetrapods of Triassic age have a marvelous fossil record and are both taxonomically diverse and numerically abundant, with discoveries in every continent (e.g., Bonaparte, 1973; Romer, 1973; Colbert, 1982; Sues and Fraser, 2010). This record has been used as the main tools for biostratigraphic correlations among different stratigraphic units in South America (e.g., Romer, 1962; Bonaparte, 1973; Schultz et al., 2000; Schultz, 2005; Langer et al., 2007; Abdala and Ribeiro, 2010; Martinelli et al., 2017, 2020; Schultz et al., 2020; Ezcurra et al., 2021b) and with other regions of Pangea (e.g., Lucas, 1998; Lucas and Hancox, 2001; Bandyopadhyay and Ray, 2020; Hancox et al., 2020). Important progress has been made in Brazil by clarifying aspects of regional geology in the last decades (e.g., Zerfass et al., 2003; Horn et al., 2014; Philipp et al., 2018), which lead to the recognition of different assemblage zones thanks to a considerably enlarged fossil record (Soares et al., 2011; Horn et al., 2014; Langer et al., 2018). Similarly, new assemblage zones have been identified for both the Chañares and Ischigualasto formations in Argentina (Martínez et al., 2011, 2013b, 2013b; Ezcurra et al., 2017; Desojo et al., 2020a). In the last decades, and particularly for South America, the fossil record was complemented with radiometric dates and magnetostratigraphic surveys for the main Triassic basins (e.g., Rogers et al., 1993; Martínez et al., 2011; Santi Malnis et al., 2011; Kent et al., 2014; Ottone et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017; Langer et al., 2018; Philipp et al., 2018; Desojo et al., 2020a), which largely supported previous relative age interpretations, as well as refined the temporal extension of some of these tetrapod-bearing beds.

The Ischigualasto-Villa Unión Basin has one of the most relevant tetrapod fossil records worldwide to understand Middle to the middle Late Triassic continental assemblages (see Fig. 2). In addition, the number of absolute dates obtained for different fossil-bearing levels has grown considerably in the last years, with data for the Chañares (Marsicano et al., 2016; Ezcurra et al., 2017) and Ischigualasto formations (e.g., Rogers et al., 1993; Martínez et al., 2011, 2013b; Desojo et al., 2020a), as well as magnetostratigraphic dating from the Los Colorados Formation (Kent et al., 2014).

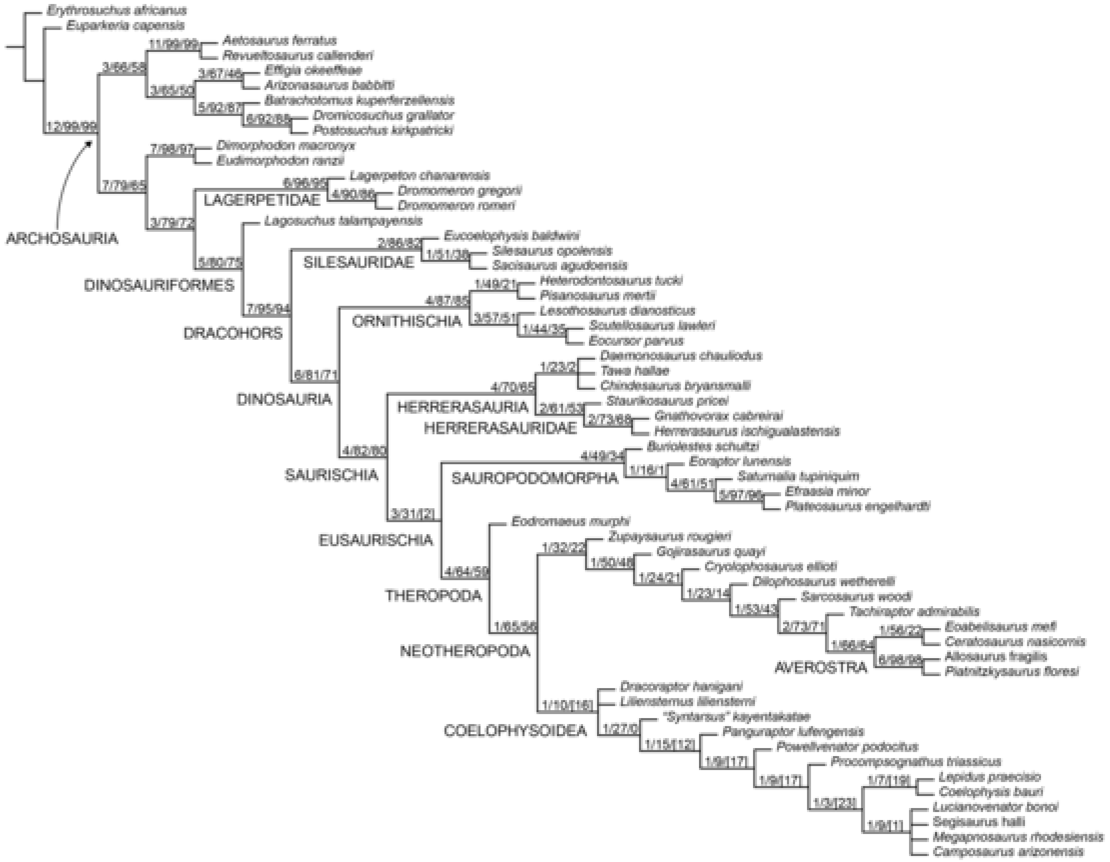

Fig. 1. Strict consensus of the most parsimonious trees found in the phylogenetic analisis. Values next to each branch represent absolute bootstrap frequency, and GC bootstrap frequency, respectively.

The Chañares Formation yielded an exquisite fossil record of non-dinosaurian dinosauromorphs, which places it as a key unit to understand the origin of dinosaurs (Romer, 1971, 1972; Bonaparte, 1975; Arcucci, 1986; Sereno and Arcucci, 1994a, b; Bittencourt et al., 2015; Ezcurra et al., 2020a, b). Until recently, only one faunal association was recognized in this unit, numerically dominated by the traversodontid *Massetognathus pascuali* and also including kannemeyeriiform dicynodonts, probainognathian cynodonts, proterochampsids, gracilisuchids, lagerpetids, and non-dinosaurian dinosauriforms. Intensive fieldwork resulted in the discovery of an older faunal assemblage at the base of the Chañares Formation, represented by dicynodonts, stenaulorhynchine rhynchosaurs, erpetosuchids, large and mid-sized suchians, and traversodontid and probainognathian cynodonts different from those recovered in the historical assemblage (Ezcurra et al., 2017, 2021b, 2021b). The younger unit was named the *Massetognathus-Chanaresuchus* Assemblage Zone (AZ) and the older the *Tarjadia* AZ (Ezcurra et al., 2017). Radioisotopic ages constrained the *Massetognathus-Chanaresuchus* AZ to 236.1 ± 0.6–233.7 ± 0.4 Ma (earliest Carnian; Marsicano et al., 2016; Ezcurra et al., 2017) and, as a consequence, the older *Tarjadia* AZ is inferred to extend into the Ladinian (Ezcurra et al., 2017, 2021b). Both AZs preceded the oldest AZ of the Ischigualasto Formation (see below) by ∼3.0–1.6 Ma (Fig. 2).

The traditional *Massetognathus-Chanaresuchus* AZ of the Chañares Formation was usually correlated with the *Dinodontosaurus* AZ of the Pinheiros-Chiniquá Sequence (Santa Maria Supersequence; Horn et al., 2014) of Brazil because they share abundant kannemeyeriform dicynodonts (*Dinodontosaurus*) and traversodontid (*Massetognathus*), chiniquodontid (*Chiniquodon*), and probainognathid cynodonts (Schultz et al., 2000, 2020; Langer et al., 2007; Martinelli et al., 2016, 2017). However, this Brazilian assemblage also includes species very closely related to those restricted to the *Tarjadia* AZ in the Chañares Formation, including the stenaulorhynchine rhynchosaur *Brasinorhynchus*, the chiniquodontid *Aleodon*, and the erpetosuchids *Archeopelta* and *Pagosvenator* (Schmitt et al., 2019). Recently, the poorly known taxon *Barberenasuchus* from the *Dinodontosaurus* AZ, historically thought to be related to sphenosuchians, was reinterpreted as possibly having dinosauromorph affinities (França et al., 2013). This new hypothesis is consistent with the record of this clade in the *Massetognathus-Chanaresuchus* AZ of Argentina. The taxonomic similarities of both AZs of the Chañares Formation with the whole *Dinodontosaurus* AZ of Brazil suggest that the latter may also include two different faunal associations, as already proposed by some authors (Abdala and Sá-Teixeira, 2004; Langer et al., 2007; Ezcurra et al., 2017; Martinelli et al., 2017; Schmitt et al., 2019), which could be correlated to the *Tarjadia* and *Massetognathus–Chanaresuchus* AZs of Argentina, respectively (Fig. 2).

The Brazilian *Dinodontosaurus* AZ is stratigraphically overlaid by the *Santacruzodon* AZ of the Santa Cruz Sequence (Horn et al., 2014). The *Santacruzodon* AZ represents the youngest faunal association in the Brazilian Triassic before the appearance of the typical Late Triassic tetrapod groups (for example, dinosaurs) of the *Hyperodapedon* AZ of the Candelária Sequence. The *Santacruzodon* AZ is still poorly sampled (Horn et al., 2014; Schmitt et al., 2019), but it is interesting in several aspects: (1) it contains the cynodont genera *Massetognathus* and *Chiniquodon*, which are both shared with the *Dinodontosaurus* AZ of Brazil and the *Massetognathus-Chanaresuchus* AZ of Argentina (Abdala et al., 2001; Schmitt et al., 2019); (2) it has an abundant record of the massetognathine cynodont *Santacruzodon* that is closely related to *Dadadon* from the Isalo II beds of Madagascar (Abdala and Ribeiro, 2003); (3) it has the gomphodontosuchine *Menadon*, which also occurs in the Isalo II (Flynn et al., 1999; Melo et al., 2015); (4) it includes a toothed dicynodont that suggests the presence of *Dinodontosaurus*

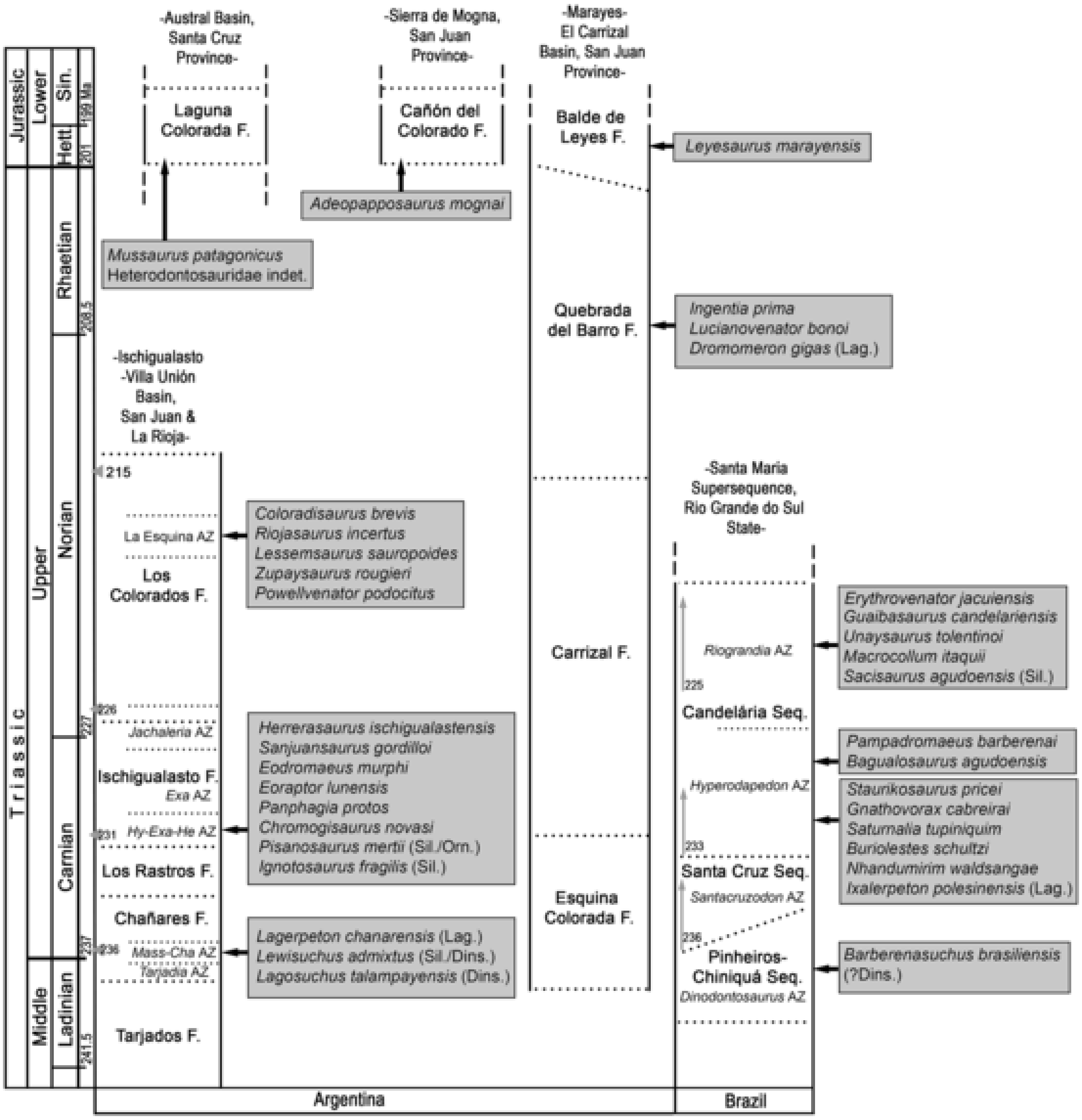

Fig. 2. Tetrapod-bearing sedimentary units from Argentina and Brazil indicating the taxonomic content of lagerpetids, silesaurids and dinosauriforms. Abbreviations: AZ, Assemblage Zone; Dins., Dinosauriformes; F., Formation; Lag, Lagerpetidae; Orn., Ornithischia; Seq., Sequence; Sil., Silesauridae.

(Martinelli et al., 2016); and (5) it was radioisotopically dated with a maximum deposition age of ~236 Ma, with an error of about 1.5 Ma (Phillips et al., 2018). This evidence suggests that the *Santacruzodon* AZ is temporally very close to the *Massetognathus-Chanaresuchus* AZ of the Chañares Formation, but with distinctive components (such as *Menadon*) related to those of the Isalo II unit of Madagascar. Thus, the *Santacruzodon* AZ possibly immediately follows the known AZs of the lower half of the Chañares Formation.

The South American sequences invite comment on the age of some African AZs. This is the case of the upper levels of the Lifua Member of the Manda beds in Tanzania, considered to be Anisian in age based on its faunal content (e.g., Nesbitt et al., 2010, 2017a). However, the faunal association documented in the upper level of Lifua Member closely resembles that of the *Tarjadia* AZ and *Dinodontosaurus* AZ of western Argentina and southern Brazil, respectively, due to the presence of the cynodonts *Aleodon* and *Scalenodon*, stenaulorhynchine rhynchosaurs, erpetosuchids, and the rauisuchian *Prestosuchus* (Schultz et al., 2016; Ezcurra et al., 2017, 2021b, 2021b; Martinelli et al., 2017; Melo et al., 2017; Desojo et al., 2020b). The same occurs with the upper part of the Ntawere Formation in Zambia and the upper part of the Upper Omingonde Formation of Namibia, which share dicynodont (*Stahleckeria*) and cynodont (*Luangwa*, *Aleodon, Chiniquodon*) synapsids with those of the *Dinodontosaurus* AZ and both Chañares Formation AZs (e.g., Abdala et al., 2013; Abdala and Smith, 2009; Ezcurra et al., 2017; Martinelli et al., 2017). Although absolute dates of these African units are yet unknown, the faunal similarities with the late Ladinian to early Carnian tetrapod faunas from Argentina and Brazil suggest a roughly similar age for all these units (e.g., Abdala et al., 2013; Ezcurra et al., 2017; Martinelli et al., 2017; Wynd et al., 2018). As a consequence, we support an interpretation in which these African assemblages should be temporally placed at around the middle-late Ladinian to early Carnian range (see Fig. 3).

As aforementioned, the Isalo II beds of Madagascar has a fauna that was correlated with the *Santacruzodon* AZ of Brazil due to the presence of *Menadon besaire*, *Chiniquodon*, and closely related massetognathine cynodonts (*Massetognathus* and *Santacruzodon* in South America and *Dadadon* in Madagascar) (Melo et al., 2015; Schmitt et al., 2019). Also, this Malagasy stratigraphic unit has hyperodapedontine rhynchosaurs that may represent one of the oldest records for the clade, considering that the group occurs in South America only in younger beds (the late Carnian Ischigualasto Formation and *Hyperodapedon* AZ of the Candelária Sequence) (Ezcurra et al., 2020c, 2021b,

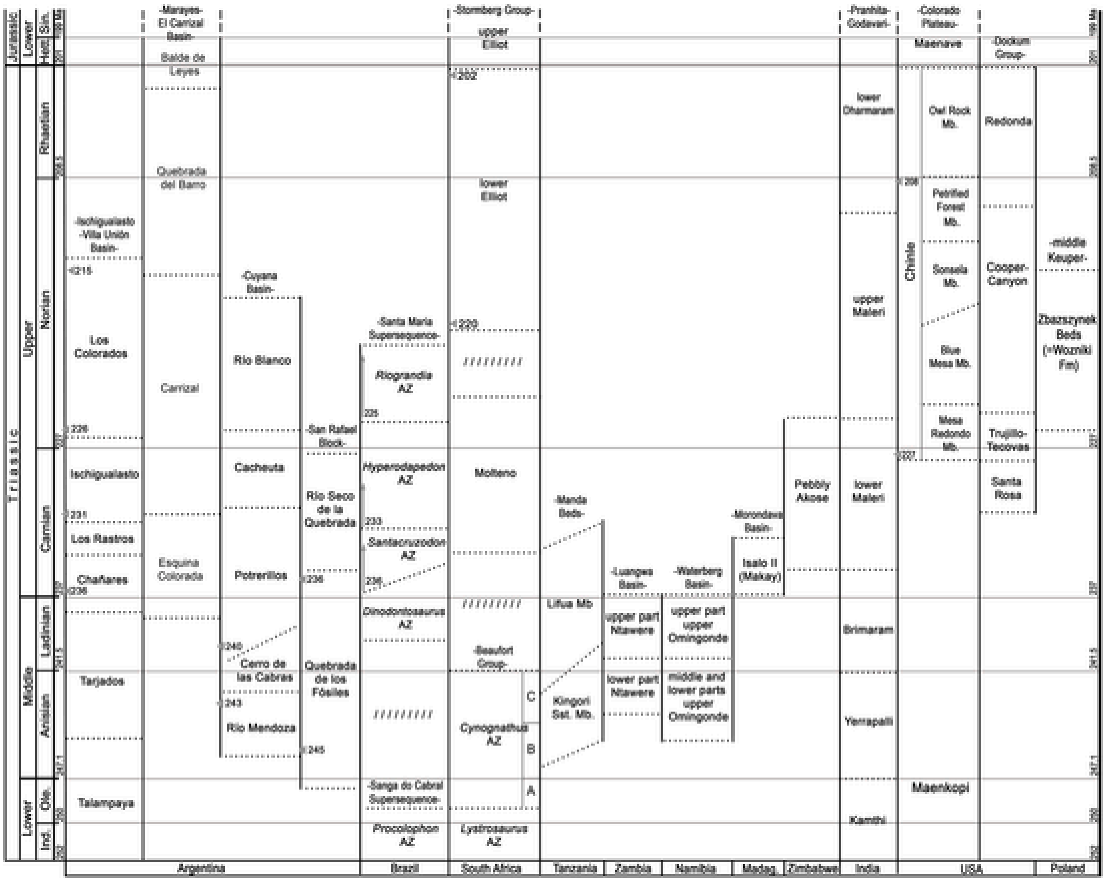

Fig. 3. Global correlations of main Triassic to Early Jurassic units bearing dinosaurs, from South America, Africa, India, North America and Europe.

2021b). The mixed nature of the Isalo II fauna is interesting, because it seems to be transitional between the *Massetognathus*-*Chanaresuchus* and *Dinodontosaurus* AZs and the Ischigualasto Formation and *Hyperodapedon* AZ (Ezcurra et al., 2021b).

Some comments are required here regarding the absolute dating of the Puesto Viejo Group, in southern Mendoza, western Argentina. The Río Seco de la Quebrada Formation, at the top of the Puesto Viejo Group, was traditionally considered of early Middle Triassic age, but recent radiometric dates supported a middle-late Carnian age (Ottone et al., 2014), thus implying an extensive revision of the therapsid biozonal models (Martinelli et al., 2017; Abdala et al., 2020). The Río Seco de la Quebrada Formation yielded early branching cynodonts, such as the cynognathians *Cynognathus* and *Diademodon* (Bonaparte, 1969a, b; Martinelli et al., 2009) and the traversodontid *Pascualgnathus* (Bonaparte, 1966; Martinelli, 2010). A middle-late Carnian age for this fossil-bearing unit does not fit with other South American beds dated as late Ladinian-early Carnian, because those two cynognathians are unknown from any similarly dated units from northern Mendoza (Cuyana Basin), San Juan, and La Rioja (Ischigualasto-Villa Unión Basin) provinces, in western Argentina, as well as from Rio Grande do Sul State (Santa Maria Supersequence) of southern Brazil. In contrast, these cynodonts are abundant in several localities of western Pangea (e.g., *Cynognathus* AZ of South Africa, lower part of the Ntawere Formation of Zambia, middle and lower parts of the Upper Omingonde Formation), which are usually considered late Olenekian to late Anisian (Kitching, 1995; Hancox, 2000; Abdala et al., 2005; Wynd et al., 2018; Hancox et al., 2020). Acceptance of a Carnian age for the Río Seco de la Quebrada Formation requires a complex paleobiogeographic explanation (Martinelli et al., 2017; Abdala et al., 2020; see also Wynd et al., 2018), supporting a high degree of endemism for the faunal association of this unit, with a conspicuous difference in relation to the geographically close Chañares Formation and *Dinodontosaurus* AZ. At the same time, these two latter units have faunal components shared between them and with other regions of Pangea, as explained before, which also weakens a similar age for the Río Seco de la Quebrada Formation (Fig. 3). We interpret such contradictions as indicative of problems with the solely radiometric date obtained and that the obtained age for the Puesto Viejo Group should be taken with caution until new studies come to light.

Recent radioisotopic age investigations of several Triassic rock units of NW Argentina confirmed an end-Carnian age for the oldest dinosaur records (Martínez et al., 2011, 2013a, b; Ottone et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017; Desojo et al., 2020a). Consequently, the time lapse between the AZs of the Chañares Formation-*Dinodontosaurus*/*Santacruzodon* AZs and the base of the Ischigualasto Formation-*Hyperodapedon* AZ was a phase of relatively rapid changing ecosystems and profound faunal replacements, which are still poorly documented. For example, there are no amniotan body fossils in the upper half of the Chañares Formation and in the entire Los Rastros Formation (Ezcurra et al., 2017).

The Late Triassic (late Carnian–earliest Norian) Ischigualasto Formation of Argentina and the *Hyperodapedon* AZ of Brazil have yielded a diverse vertebrate fauna that records the initial phase of dinosaur evolution. The Ischigualasto Formation includes volcanic ash layers that have yielded $^{40}Ar/^{39}Ar$ radioisotopic dates (Rogers et al., 1993; Martínez et al., 2011). The ages near the bottom and top of the formation – respectively 231.4 ± 0.3 and 225.9 ± 0.9 Ma in San Juan Province (Martínez et al., 2011b; Walker et al., 2013) and 230.2 ± 1.9 Ma and 221.4 ± 1.2 Ma in the neighbour La Rioja Province (Desojo et al., 2020a) – suggest that it was laid down over a period of less than 10 million years during the late Carnian to early Norian (Martínez et al., 2011). The vast majority of the fossil remains from the Ischigualasto Formation correspond to non-dinosaurian tetrapods, including temnospondyl amphibians, non-archosaurian archosauromorphs and archosauriforms, pseudosuchians, dicynodonts, and non-mammaliaform cynodonts. Early dinosauromorphs include an indeterminate lagerpetid, the silesaurid *Ignotosaurus fragilis* (Martínez et al., 2013b), the dinosauriform *Pisanosaurus mertii* (alternatively considered as an ornithischian or a silesaurid; e.g., Casamiquela, 1967; Agnolin and Rozadilla, 2017; Baron et al., 2017b; Desojo et al., 2020a) and the dinosaurs *Herrerasaurus ischigualastensis*, *Sanjuansaurus gordilloi*, *Eoraptor lunensis*, *Panphagia protos*, *Chromogisaurus novasi*, and *Eodromaeus murphi* (e.g., see Martínez et al., 2013a) (Fig. 2).

The Ischigualasto Formation has been divided into three abundance-based biozones: (1) the *Scaphonyx-Exaeretodon-Herrerasaurus* Biozone; (2) the *Exaeretodon* Biozone; and (3) the *Jachaleria* Biozone (Martínez et al., 2011, Fig. 2). The *Scaphonyx-Exaeretodon-Herrerasaurus* Biozone includes the highest diversity and abundance of fossils, being characterized by a predominance of the hyperodapedontine rhynchosaur *Hyperodapedon*, the traversodontid cynodont *Exaeretodon*, and the dinosaur *Herrerasaurus*. The *Exaeretodon* Biozone is characterized by a low diversity and high relative abundance of the cynodont *Exaeretodon*, lacking so far dinosaur remains. The *Jachaleria* Biozone, spanning the Quebrada de la Sal Member and continuing into the lower section of the overlying Los Colorados Formation, is almost devoid of vertebrate fossils (Martínez et al., 2013b). Recently, two different biozones were recognized at the Hoyada del Cerro Las Lajas locality of the Ischigualasto Formation in La Rioja Province, namely the *Hyperodapedon* (older) and *Teyumbaita* (younger) AZs, both of which are considered equivalent to the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone at the Valle de la Luna in San Juan Province (Desojo et al., 2020a).

For Brazil, the upper portion of the Santa Maria Formation includes one of the most comprehensive fossil records of early dinosaurs in the world. This part of the Santa Maria Formation and the lower part of the Caturrita Formation are enclosed in the Candelária Sequence (Horn et al., 2014), bearing two distinctive AZs: the older *Hyperodapedon* AZ and the younger *Riograndia* AZ. The *Hyperodapedon* AZ yields the dinosaurs *Staurikosaurus pricei*, *Gnathovorax cabrerai*, *Saturnalia tupiniquim*, *Buriolestes schultzi*, *Pampadromaeus barberenai*, *Bagualosaurus agudoensis,* and *Nhandumirim waldsangae* (e.g., Langer et al., 1999; Cabreira et al., 2016; Pacheco et al., 2019), whereas the *Riograndia* AZ has yielded *Macrocollum itaquii, Unaysaurus tolentinoi*, unnamed sauropodomorph specimens, and *Guaibasaurus candelariensis* (Bonaparte et al., 1999; Leal et al., 2004; Langer et al., 2010; Müller et al., 2017, 2018a) (Fig. 2). Radioisotopic age data was obtained for these two AZs (Langer et al., 2018): the maximum deposition ages obtained were ~233 Ma for the base of the *Hyperodapedon* AZ and ~225 Ma for the *Riograndia* AZ.

The two first biozones of the Ischigualasto Formation have been historically correlated with the *Hyperodapedon* AZ of Brazil (e.g., Langer, 2005; Langer et al., 2007, 2018), which is consistent with their fossil content and radiometric data. Both share the presence hyperodapedontine (*Hyperodapedon* and *Teyumbaita*) and lack of stenaulorhynchine rhynchosaurs (Martínez et al., 2013b; Langer et al., 2018; Desojo et al., 2020a; Ezcurra et al., 2020c), the presence of gomphodontosuchine traversodontid (*Exaeretodon* in Argentina and Brazil and other related forms in Brazil) and probainognathian (ecteniniids, basal prozostrodontians) cynodonts, proterochampsids (shared presence of genus *Proterochampsa*), aetosaurs (shared presence of *Aetosauroides scagliai*), and ornithosuchids (close affinities between *Venaticosuchus* and *Dynamosuchus*). The *Hyperodapedon* AZ may also include two subzones (Langer et al., 2007; Müller and Garcia, 2019), a lower one with abundant record of hyperodapedontinae rhynchosaurs, and an upper one where *Exaeretodon* is more common. In such a scheme, the *Hyperodapedon* Acme-Zone (i.e., the lower subzone of the *Hyperodadpedon* AZ; Langer et al., 2007) includes the dinosaurs *Staurikosaurus pricei, Gnathovorax cabrerai, Saturnalia tupiniquim, Buriolestes schultzi,* and *Nhandumirim waldsangae*, whereas *Pampadromaeus barberenai* and *Bagualosaurus agudoensis* come from *Exaeretodon* dominated beds (i.e., upper portion of the *Hyperodapedon* AZ).

Regarding dinosaurs, the herrerasaurid *Herrerasaurus* from the Ischigualasto Formation is a close relative of *Staurikosaurus* and *Gnathovorax* from the *Hyperodapedon* AZ (Benedetto, 1973; Novas, 1992; Pacheco et al., 2019), whereas the sauropodomorph *Chromogisaurus* from Ischigualasto show very close affinities with *Saturnalia* (Ezcurra, 2010). These close phylogenetic relationships bolster the strong faunal resemblance between both assemblages. Indeed, there is also a general similarity among the various early sauropodomorphs of both stratigraphic units, including *Eoraptor lunensis*, *Panphagia protos*, *Chromogisaurus novasi*, *Saturnalia tupiniquim*, *Buriolestes schultzi*, and *Pampadromaeus barberenai*. Both the Ischigualasto Formation and the *Hyperodapedon* AZ have fragmentary records of Lagerpetidae and Silesauridae (Martínez et al., 2013b; Garcia et al., 2019a), which is consistent with the range of such taxa from the Ladinian-early Carnian to the Rhaetian (Nesbitt et al., 2010; Müller et al., 2018a; Kammerer et al., 2020; Ezcurra et al., 2020a).

Hyperodapedontine rhynchosaurs (the genus *Hyperodapedon*) and gomphodontosuchine traversodontids (the genus *Exaeretodon*) highlight also a close resemblance of the Ischigualasto Formation and the *Hyperodapedon* AZ with the Lower Maleri Formation in India (e.g., Langer, 2005; Bandyopadhyay and Ray, 2020) (Fig. 3). Regarding African basins, most of them lack information about Carnian tetrapod assemblages. However, it should be noted that the Pebbly Arkose Formation of Zimbabwe seems coeval to the Ischigualasto Formation and *Hyperodapedon* AZ because of the presence of hyperodapedontine rhynchosaurs (*Hyperodapedon*; Langer et al., 2018), and a dinosaur specimen that closely resembles *Saturnalia* (Raath, 1996; Langer, 2004; Langer et al., 2010; Griffin et al., 2018) (Fig. 2).

The Los Colorados Formation is the uppermost unit of the Ischigualasto-Villa Unión Basin and includes two different faunal associations: the *Jachaleria* Biozone and the La Esquina Fauna. The *Jachaleria* Biozone (Quebrada de la Sal Member), which starts at the top of the Ischigualasto Formation and extends into the lower section of the Los Colorados Formation, includes only records of the dicynodont *Jachaleria colorata* (Martínez et al., 2011, 2013b, 2013b). The La Esquina Fauna is a much more diverse fossil assemblage, documented from the upper third of the formation (e.g., Bonaparte, 1972; Martinelli and Rougier, 2007; Ezcurra, 2017) (Fig. 2).

The *Jachaleria* Biozone was correlated with the *Riograndia* AZ of Brazil, due to the shared presence of the genus *Jachaleria*. This Brazilian AZ is quite diverse (Bonaparte et al., 2010; Soares et al., 2011; Langer et al., 2018; Romo de Vivar et al., 2020; Martinelli et al., 2020) and its cynodonts (the ictidosaurs *Riograndia* and *Irajatherium*) and dinosaurs (e.g., *Guaibasaurus, Macrocollum*) are different from those present in the younger La Esquina Fauna of the Los Colorados Formation (Martinelli et al., 2005; Martinelli and Rougier, 2007). On the other hand, the sauropodomorphs from the Brazilian AZ seem similar to those from the Upper Maleri Formation, India (Müller et al., 2018c; but see Pol et al., 2021). However, these Brazilian sauropodomorphs were recovered from outcrops lacking the typical fauna of the *Riograndia* AZ (see Soares et al., 2011; Martinelli et al., 2020) and may represent a younger age. It is expected that taxa similar to those of the *Riograndia* AZ may occur at the top of the Ischigualasto Formation and the base of the Los Colorados Formation, as is already the case for the dicynodont *Jachaleria*, but these two levels are still poorly sampled.

The La Esquina Fauna is related to the Lower Elliot Formation of South Africa (Sciscio et al., 2017) (Fig. 3). The tritheledontid *Chaliminia* from the Los Colorados Formation is closely related to *Elliotherium* from the Lower Elliot Formation, which differs considerably from *Pachygenelus* (Martinelli and Rougier, 2007) from the younger Upper

Elliot Formation of Early Jurassic age (Bordy et al., 2020). These affinities are mainly supported by the sauropodomorph content of both units, in which the Lower Elliot Formation includes *Eucnemesaurus fortis* (similar to *Riojasaurus* from Los Colorados), *Antetonitrus ingenipes* (similar to *Lessemsaurus* from Los Colorados), *Blikanasaurus cromptoni, Melanorosaurus readi,* and *Plateosauravus cullingworthi* (Yates, 2007a, b, 2008; Yates and Kitching, 2003; Yates et al., 2010; McPhee et al., 2018b; Pol et al., 2021).

The tetrapod fauna of the Quebrada del Barro Formation was considered as younger than the La Esquina Fauna of the Los Colorados Formation (Martínez et al., 2015) (Fig. 2). The dinosauromorph assemblage of this unit includes the coelophysoid *Lucianovenator*, the early sauropod *Ingentia*, and the lagerpetid *Dromomeron*. The former two genera are closely related to *Powellvenator* and *Lessemsaurus*, respectively, from the Los Colorados Formation. As for the occurrence of *Dromomeron*, this taxon is also present in the middle Norian to Rhaetian of the Chinle Formation and Dockum Group of the USA (Sarıgül, 2016; Marsh, 2018; Marsh and Parker, 2020, Fig. 3). The absence of lagerpetids in the La Esquina Fauna of the Los Colorados Formation is probably the result of preservational/collection biases, as fossils of medium to large-sized individuals are more abundant in that fauna (Bonaparte, 1972). Therefore, we consider that more studies are required to refine the correlation between the Quebrada del Barro Formation, the Los Colorados Formation, and other units, including those outside of Gondwana.

The oldest dinosaurs from western USA and the so far oldest known neotheropods are *Camposaurus arizonensis* and *Lepidus praecisio* (Hunt et al., 1998; Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015). *Camposaurus* is a deeply nested coelophysid collected in the *Placerias* Quarry (ca. 219 Ma, Sonsela Member of the Chinle Formation), northern Arizona (Hunt et al., 1998). *Lepidus* has been collected from probably coeval beds in the Otis Chalck locality of the Dockum Group, Texas (Nesbitt and Ezcurra, 2015). Both *Camposaurus* and *Lepidus* are closely related to the Triassic coelophysids *Coelophysis* (Rhaetian of the USA) and *Lucianovenator*, as well as with the Early Jurassic *Megapnosaurus* (Hettangian-Sinemurian of Zimbabwe) and *Segisaurus* (Pliensbachian-Toarcian of the USA) (Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015; Martínez and Apaldetti, 2017; Ezcurra, 2017; Ezcurra et al., 2021a). As a result, these deeply nested coelophysids do not seem to be useful for biostratigraphic correlations because closely related forms have disparate ages. This may be a result of problems in the current phylogenetic hypotheses for the earliest neotheropods (Ezcurra et al., 2021a) and/or a rapid, cosmopolitan diversification of coelophysoids during the Late Triassic and Early Jurassic that it is still poorly sampled.

Chindesaurus and *Tawa* came from different localities of the Petrified Forest Member of the Chinle Formation dated in ca. 211–212 Ma (Long and Murry, 1995; Nesbitt et al., 2007, 2009); a previous record of *Chindesaurus* from Hayden Quarry, the type locality of *Tawa*, has not been recently included in the hypodigm of the species (Marsh et al., 2019). The temporal occurrence of these taxa in the Chinle Formation may suggest that the probable herrerasaurians from the Tecovas Formation/lower Cooper Canyon Formation of the Dockum Group (Sarıgü;l, 2017; but see Nesbitt and Chatterjee, 2008) may be approximately coeval because they came from levels that are stratigraphically higher than those of *Lepidus praecisio* (probably ca. 219 Ma) (Fig. 3). However, the occurrence of the possible herrerasaurian (see below) *Daemonosaurus* in the Rhaetian Owl Rock Member of the Chinle Formation would extend the range of herrerasaurs in North America until the end of the Triassic. In addition, because we do not have information about the postcranium of *Daemonosaurus* (with the exception of the anterior cervical vertebrae), that taxon cannot be compared with the herrerasaur remains of the Petrified Forest Member of the Chinle Formation and the Tecovas Formation/lower Cooper Canyon Formation of the Dockum Group. This hampers a more robust temporal correlation between the herrerasaurian assemblages of the North and South American units. In this context, previous interpretations of a middle-late Norian age for the herrerasaur-bearing levels of the Upper Maleri Formation of India and the Zbaszynek beds of Poland (Novas et al., 2011; Niedźwiedzki et al., 2014; Bandyopadhyay and Ray, 2020) are congruent with the American fossil record (Fig. 3).

4. Silesauridae: unexpected radiation of dinosaur forerunners

Until recently, non-dinosaurian dinosauriforms were mostly known from specimens recovered in early Carnian outcrops of the Chañares Formation, La Rioja Province, which include the small-sized *Lagosuchus talampayensis* and *Lewisuchus admixtus* (Romer, 1971, 1972, 1972; Bonaparte, 1975; Arcucci, 1997; Bittencourt et al., 2015; Langer et al., 2013; Agnolin and Ezcurra, 2019; Ezcurra et al., 2020b). Nevertheless, discoveries during the last twenty years in Europe, Africa, and the Americas have deeply changed our view about dinosaur precursors (e.g., Dzik, 2003; Irmis, 2005; Irmis et al., 2007a; Ezcurra, 2006; Langer et al., 2010; Nesbitt et al., 2009, 2010; 2020; Ezcurra et al., 2020b).

Silesaurus opolensis was the first described member of Silesauridae. This clade is currently recognized as the immediate sister group to Dinosauria (Irmis et al., 2007a; Brusatte et al., 2010; Langer et al., 2010; Nesbitt et al., 2010, 2017a, 2017a; Nesbitt, 2011; Ezcurra et al., 2020b), but some authors sustain that they may represent early dinosaurs themselves, forming part of the lineage leading to taxa historically considered as ornithischians (Ferigolo and Langer, 2006; Langer and Ferigolo, 2013; Cabreira et al., 2016; Pacheco et al., 2019; Müller and Garcia, 2020). Silesaurids are currently represented by nearly a dozen nominal species described from Poland (Dzik, 2003), North America (Ezcurra, 2006; Martz and Small, 2019), Brazil (Ferigolo and Langer, 2006), Africa (Nesbitt et al., 2010; Kammerer et al., 2012; Peecook et al., 2013), and Argentina (Martínez et al., 2013b; Agnolin and Rozadilla, 2017; but see Desojo et al., 2020a). The putative oldest records of unambiguous silesaurids (Fig. 3) are *Asilisaurus kongwe* from the Manda beds of Tanzania (Nesbitt et al., 2010, 2020) and *Lutungutali sitwensis* from the upper Ntawere Formation of Zambia (Peecook et al., 2013), both coming from units here interpreted as possibly middle-late Ladinian to early Carnian in age. Interestingly, silesaurids provided the first evidence for the survivorship of non-dinosaurian dinosauriforms in the Late Triassic, demonstrating that they co-existed with dinosaurs until the close of that period (Ezcurra, 2006; Irmis et al., 2007, Fig. 4).

Silesaurids depart from the hypothetical bipedal and faunivorous dinosaur precursor that was preconceived by researchers based on evidence from the Chañares Formation dinosauriforms (Bakker and Galton, 1974; Bonaparte, 1975; Sereno and Arcucci, 1994a). This hypothetical ancestor was a small and lightly-constructed bipedal reptile of faunivorous habits, probably similar to *Lagosuchus* and *Lewisuchus*. On the other hand, although also gracile and with a parasagittal posture, silesaurids were somewhat larger, with a body length of up to 2.5 m (Barrett et al., 2015), a specialized skull (Dzik and Sulej, 2007), and likely quadrupedal (Kubo and Kubo, 2012). Also, its members (with the exception of *Lewisuchus,* if it is actually a silesaurid) are characterized by a skull with a beaked snout and dentition apparently indicating an herbivorous diet (but see Qvarnström et al., 2019 for an insectivorous hypothesis).

Similarities in the silesaurid dentition with those of ornithischian dinosaurs, together with the finding of herbivorous pseudosuchian archosaurs, lead several authors to review the record of Triassic ornithischians, which was based mostly on isolated teeth. This resulted in the absence of positive evidence for that dinosaur group in North America (Parker et al., 2005; Irmis et al., 2007; Nesbitt et al., 2007). Regarding Carnian ornithischians from South America, recent authors have expressed some doubts about the ornithischian and even dinosaurian affinities of *Pisanosaurus* (Novas, 2009, Fig. 5), and it has been proposed that it probably belong to Silesauridae (Agnolin and Rozadilla,

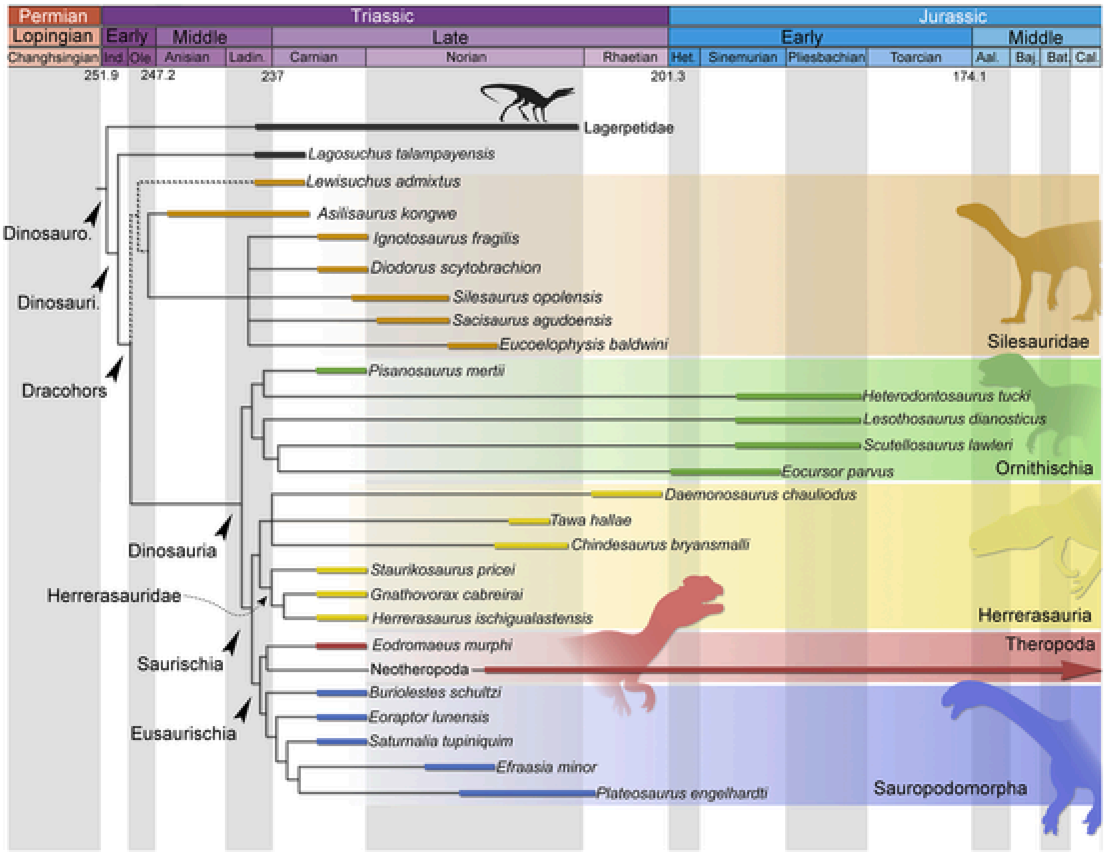

Fig. 4. Time-calibrated cladograms of dinosauromorphs (silesaurids based on Ezcurra et al., 2020c). Silhouettes based on the artwork by Márcio L. Castro, Gabriel Lio, and Tyler Keillor. Abbreviations: Dinosauro.: Dinosauromorpha; Dinosauri.: Dinosauriformes.

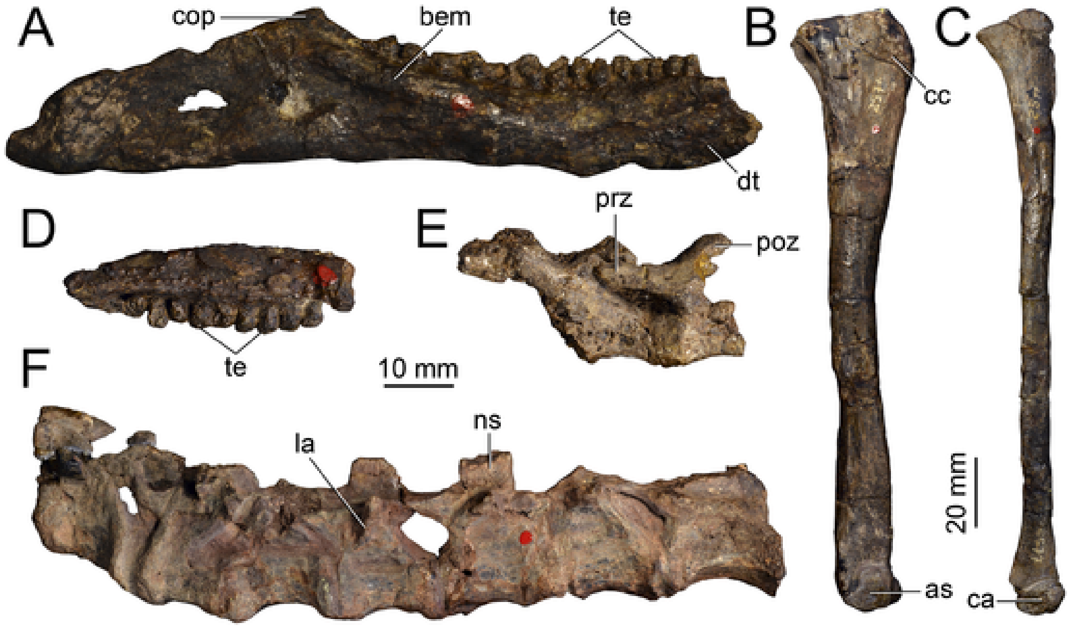

Fig. 5. ***Pisanosaurus mertii.*** Selected elements of specimen PVL 2577 (holotype). (A) right hemimandible lacking anterior end in lateral view. (B) right tibia and astragalus in lateral view. (C) right fibula and calcaneum in lateral view. (D) partial right maxilla in lateral view; (E) cervical vertebrae in left lateral view; (F) dorsal vertebrae in left lateral view. Abbreviations: as, astragalus; bem, buccal emargination; ca, calcaneum; cc, cnemial crest; cop, coronoid process; dt, dentary; la, lamina; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; rap, retroarticular process; te, teeth.

2017; Baron, 2019). However, a recent revision of the phylogentically informative character states of *Pisanosaurus* concluded that current evidence favors an ornithischian affinity (Desojo et al., 2020a). Yet, an alternative hypothesis considers *Pisanosaurus* as a transitional taxon between traditional silesaurids and traditional ornithischians (Müller and Garcia, 2020).

The vast majority of authors have agreed that Silesauridae represent the sister taxon to Dinosauria since the first quantitative analyses that tested their relationships (e.g., Ezcurra, 2006; Langer and Benton, 2006; Irmis et al., 2007; Nesbitt et al., 2010, 2013a, 2017a, 2020; Kammerer et., 2012, 2020; Ezcurra, 2016; Baron et al., 2017a; Langer et al., 2017; Cau, 2018; Ezcurra et al., 2020a, b). The Silesauridae + Dinosauria clade was named Dracohors by Cau (2018; Fig. 4) and its members share the presence of a well-developed anterior tympanic recess, axial epipophyses, centrodiapophyseal laminae on presacral vertebrae, enlargement of the postacetabular process of ilium, elongated pubis, and reduction of pedal digit IV compared to pedal digit III, among other character states. However, Ferigolo and Langer (2006) sustained that silesaurids may be included within Ornithischia, a proposal reinforced by Langer and Ferigolo (2013) on the basis of a numerical analysis (see also Cabreira et al., 2016; Pacheco et al., 2019; Müller and Garcia, 2020). These authors emphasized that uncertainties pervade the phylogeny of early dinosauriforms and nodes are supported by characters with high degree of homoplasy, making that part of the dinosauriform phylogeny prone to reinterpretations. In particular, attention has been drawn to the edentulous anterior end of the lower jaw of most silesaurids (with the exception of *Lewisuchus*). It has been hypothesized that the presence of a groove on the anterior end of the lower jaw may indicate the presence of an anterior tip homologous to the neomorphic predentary bone of ornithischians, representing an intermediate stage in which the bone is paired and still co-ossified to the respective dentary (Ferigolo and Langer, 2003). Other traits (several ambiguously) supporting the nesting of core-silesauridae within Ornithischia include: teeth with enlarged denticles, more than two sacral vertebrae, scapular blade longer than 3 times its dorsal width, anterior trochanter separated from the femoral shaft by a cleft, femur lacking a ‘trochanteric shelf’, femur with facies articularis antitrochanterica level with the ‘greater trochanter’, fibular condyle at the posterior margin of the proximal tibia, outer malleolus extending well lateral to the anterolateral corner of the distal tibia, and no astragalar posterior groove (Langer and Ferigolo, 2013). A more recent hypothesis recovers silesaurids as a paraphyletic array of low-diversity clades representing a stem group leading to traditional ornithischians (Müller and Garcia, 2020, Fig. 6).

Silesaurids share several apomorphic features (Nesbitt et al., 2010; but see Langer and Ferigolo, 2013), including not curved, blade-like tooth crowns (except for *Lewisuchus*), edentulous anterior end of dentary that tapers to a sharp point (except for *Lewisuchus*), exits of the hypoglossal carnial nerve (CN XII) aligned subvertically, rugose ridge on the anterolateral edges of the supraoccipital, ventral recess on the ectopterygoid, and distal condyles of the femur in posterior view proximally extending more than 1/4 the length of the femoral shaft (with the exception of *Lewisuchus*).

Below, we discuss the affinity of two South American dinosauriforms that have been more ambiguously referred to Silesauridae, *Lewisuchus admixtus* and *Pisanosaurus mertii*. For the less controversial *Ignotosaurus fragilis* and *Sacisaurus agudoensis* see Martínez et al. (2013b) and Langer and Ferigolo (2017), respectively.

Lewisuchus admixtus is a dinosauriform described by Romer (1972) from the early Carnian beds of the Chañares Formation, Argentina. A more recently described dinosauriform from the same levels, *Pseudolagosuchus major* Arcucci (1997), has been recently interpreted as a subjective junior synonym of *Lewisuchs admixtus* (Ezcurra et al., 2020b). The holotype of *Lewisuchus* was redescribed by Bittencourt et al. (2015) and a new specimen has been recently described by Ezcurra et al. (2020b). *Lewisuchus* has been recovered as the sister taxon to all other silesaurids (Nesbitt et al., 2010; Sarıgü;l et al., 2018; Ezcurra et al., 2020a, b). The silesaurid clade excluding both *Lewisuchus* and the also early form *Asilisaurus* was named as Sulcimentisauria (sensu Martz and Small, 2019). The referral of *Lewisuchus* to Silesauridae is supported on the basis of several apomorphies, namely presence of a notch distal to the femoral head, sub-

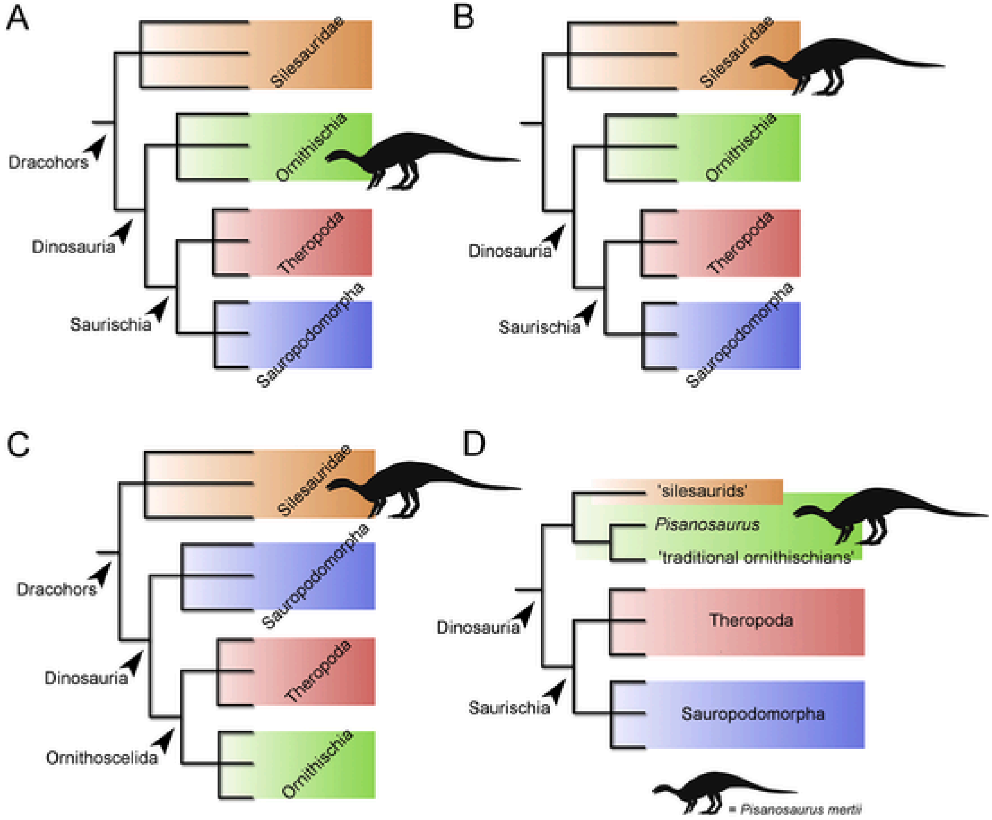

Fig. 6. Phylogenetic position of *Pisanosaurus mertii* according distinct hypotheses: (A) traditional arrangement (Langer et al., 2017); (B) within Silesauridae (Agnolin and Rozadilla, 2017); (C) within Silesauridae in the Ornithoscelida topology (Baron et al., 2017b); (D) within a paraphyletic ‘Silesauridae’ topology (Müller and Garcia, 2020).

vertically aligned openings of the hypoglossal nerves, rugose crest on the anterolateral margin of the supraoccipital, and centra of cervical vertebrae more elongate than mid-dorsal centra (Nesbitt, 2011). These character states were analyzed in detail by Bittencourt et al. (2015), who indicated that they are widespread among early dinosauriforms and dinosaurs, and should not be considered as prima facie silesaurid synapomorphies. In fact, at first glance, the skull of *Lewisuchus* is very different in shape and proportions to those of other silesaurids. Indeed, it lacks most silesaurid synapomorphies, including a dentary anterior end tapering to a sharp point, non-recurved tooth crowns, femoral proximal end with a transverse groove, and femoral popliteal fossa not proximally extended.

More recently, the silesaurid affinity of *Lewisuchus* was sustained on the basis of ilium with extensive, highly rugose areas on the dorsal and lateral surfaces of the preacetabular and postacetabular processes, notch distal to the femoral head, and ankylothecodont marginal tooth implantation (Ezcurra et al., 2020b). Yet, presence of extensive rugosities on the ilium as in *Lewisuchus* is a feature shared with several early dinosaurs, such as *Herrerasaurus, Chromogisaurus,* and *Saturnalia* (Novas, 1994; Ezcurra, 2010; Garcia et al., 2019b); thus, its condition as an apomorphy of Silesauridae strongly depends on the interrelationships among early dinosaurs. As a result, the notch between the femoral head and shaft and the tooth implantation of *Lewisuchus* stand as the only reliable synapomorphies among those listed above linking this genus with silesaurids. However, although the teeth seem to be fused to the bone in both core-silesaurids and *Lewisuchus*, the teeth of the latter differ from the 'typical' silesaurid condition in the absence of a mineralized tissue that attach the teeth to the bone forming a well-developed bone collar with distinct apicobasally extended ridges (Nesbitt, 2011; Langer and Ferigolo, 2013; Ezcurra et al., 2020b), and in lacking resorption pits at their bases. Because currently based on two features linking taxa with strong morphological differences, we consider the inclusion of *Lewisuchus* among silesaurids as weak, at least, and should be tested in the future after the expansion of character lists (the data matrix used by Ezcurra et al., 2020b is a slightly modified version of the controversial dataset of Baron et al., 2017a; see e.g., Langer et al., 2017) and, ideally, the discovery of new specimens of this taxon.

The discovery of silesaurids and other archosauriforms with teeth apparently adapted to herbivory have changed our picture about Triassic ornithischians (Irmis et al., 2007), and only one putative Triassic specimen may be assigned to the clade: *Pisanosaurus mertii* from the Ischigualasto Formation. This taxon was originally described by Casamiquela (1967) on the basis of a single and fragmentarily preserved skeleton (Bonaparte, 1976), and since then it has been considered the oldest representative of this dinosaurian clade (Bonaparte, 1976, 1996, Novas, 1989, 1996, 2009; Norman and Weishampel, 1990; Sereno, 1991, 2012, 2012; Norman et al., 2004; Brusatte et al., 2010; Langer et al., 2010; Butler, 2010; Desojo et al., 2020a). The phylogenetic position of *Pisanosaurus* among ornithischians is problematic, not only due to its preservational state, but also because the presence of a highly derived tooth morphology combined with several plesiomorphic postcranial traits. Although some authors suggested *Pisanosaurus* may be a chimaera (Sereno, 1991, 2012, 2012; Norman et al., 2004), this proposal is dismissed on evidence provided by researchers who originally prepared and studied the specimen (i.e., Casamiquela, 1967; Bonaparte, 1975), unambiguously demonstrating the original articulated nature of the partial skeleton (Bonaparte pers. comm., in Agnolin and Rozadilla, 2017).

Recently, Agnolin and Rozadilla (2017) reassessed the material of *Pisanosurus* through anatomical comparisons and phylogenetic analyses, suggesting its position outside Dinosauria, but forming part of Silesauridae, a hypothesis also followed by some other authors (e.g., Baron et al., 2017b; Baron, 2019; Coria, 2017; Cau, 2018; Raven et al., 2019; Norman, 2019; Bordy et al., 2020). It has been stated that the combination of character states usually regarded as uniquely shared between *Pisanosaurus* and ornithischians (e.g., relatively short jaw with a very tall coronoid process, reduced external mandibular fenestra —absent in *Pisanosaurus*—, ventrally positioned mandibular glenoid fossa, largest teeth on the distocentral portion of the series, non-recurved and low-crowned teeth with basal cingulum lingually expanded, well developed constriction between root and crown, and tooth crowns asymmetric in mesial and distal views) are also present in silesaurids (Agnolin and Rozadilla, 2017). It is worth mentioning that one of the most outstanding features classically recognized in support of the ornithischian affiliation of *Pisanosaurus* is the apparent palisade-like dentition (Bonaparte, 1976; Norman et al., 2004). However, teeth of *Pisanosaurus* do not form a palisade or continuous masticatory surface (*contra* Bonaparte, 1976; Norman et al., 2004). That means that *Pisanosaurus* lacks the contiguous facet described for some heterodontosaurid ornithischians (Sereno, 1991; Agnolin and Rozadilla, 2017).

As noted by previous authors, *Pisanosaurus* shows some features that strongly differ from those of ornithischians, including elongate dorsal vertebral centra that are transversely compressed and neural arches laterally excavated and bearing laminae. The pubis does not seem to be posteroventrally oriented and the hindlimb elements appear plesiomorphic for Dinosauriformes. The proximal end of the metatarsals are strongly transversely compressed (specially metatarsal II) and are appressed against one another along almost all their length, a condition absent in ornithischians, but present in most saurischians and silesaurids.

On the other hand, recent authors considered that *Pisanosaurus* share several apomorphies with Silesauridae (Agnolin and Rozadilla, 2017; Baron, 2019), including: reduced denticles on teeth (absence in *Asilisaurus* and shared with some heterodontosaurids), sacral ribs shared between two adjacent vertebrae (shared with ornithischians but absent in *Asilisaurus* and *Lewisuchus*), presence of fibular flange (present in heterodontosaurids), flattened ungual phalanges (but more similar to those of ornithischians), and ankylothecodont tooth implantation (but its presence has been criticized based on more recent repreparation of the specimen; Desojo et al., 2020a).

The inclusion of *Pisanosaurus* within Silesauridae implies that this taxon does not constitute the oldest known ornithischian, as advocated by most authors. Presently, *Pisanosaurus* would be the only putative Triassic ornithischian and this defines a significant gap, of more than 30 million years, between *Pisanosaurus* and the oldest unambiguous ornithischians, such as the Early Jurassic (Hettangian) *Eocursor*, *Laquintasaura*, and *Lesothosaurus* (Barrett et al., 2014; see Irmis et al., 2007b; Baron, 2019; Baron et al., 2017c).

However, Marsola et al. (2019a), Martz and Small (2019), Marsh et al. (2019), and (Desojo et al., 2020a) do not agree with the silesaurid affinities of *Pisanosaurus*, but sustain its historical ornithischian affinity. These authors supported the ornithischian affinity of *Pisanosaurus* based on a series of both cranial and postcranial traits shared between that taxon and core-ornithischians (or only heterodontosaurids), and absent in silesaurids. These include: reduced (or absent) external mandibular fenestra, external mandibular fossa (seen only in heterodontosaurids), medially expanded mandibular symphysis, torsion of the anterior portion of dentary, no dentary replacement foramina (seen only in heterodontosaurids), strongly concave dorsal margin of the dentary (seen only in heterodontosaurids), labiolingualy broad tooth crowns (seen only in heterodontosaurids), lingually inclined maxillary tooth crowns (seen only in heterodontosaurids), tooth crowns with primary ridge, anteroposteriorly short cervical vertebrae, broad and deep posterior notch on proximal tibia, lateromedially narrow astragalus, proximodistally deep ascending process of astragalus, and lateromedially compressed calcaneum. Nevertheless, the analysis by Desojo et al. (2020a) is not based on a numerical phylogeny, and should be also noted that other cladistic analysis found *Pisanosaurus* as an ornithischian, but including some silesaurids within that clade (Langer and Ferigolo, 2013). In this line of thought, it has been recently proposed

(Müller and Garcia, 2020) an alternative evolutionary hypothesis depicting traditional 'silesaurids' as a stem group leading to core ornithischians (Fig. 6). Within this context, the peculiar mosaic anatomy of *Pisanosaurus*, which combines traits present in traditional silesaurids and ornithischians, lies along a branch that connects the traditional silesaurids to core Ornithischia.

In conclusion, we consider that there are currently major uncertainties concerning the phylogenetic relationships of *Pisanosaurus*. Aside from the necessity to carry on detailed character sampling and careful scoring of character states (which may lead towards a general consensus on the affinities of these taxa), we urge for the recovery of new and more complete discoveries of this enigmatic archosaur, because available specimen shows features that may be interpreted in different ways. Even if *Pisanosaurus* is interpreted as an ornithischian, its morphology clearly departs from that of other members of the clade, and does not comfortably fits to any known clade of core-ornithischians known from the Early Jurassic onwards (Novas, 2009).

In sum, South American silesaurids (e.g., *Ignotosaurus, Sacisaurus*) include taxa that are very similar to previously known silesaurids, whereas other forms are morphologically disparate, and may belong to other dinosauriform groups (e.g., *Lewisuchus, Pisanosaurus*). In any case, the fossil record of South American silesaurids constitutes an important addition to the knowledge of the morphological and ecological disparity of silesaurids and dinosaur precursors.

5. Comments on the affinities of *Nyasasaurus parringtoni*

Nyasasaurus parringtoni was described by Nesbitt et al. (2013a) based on a partial humerus and six associated vertebrae, as well as five referred presacral vertebrae. The specimens come from the Lifua Member of the Manda beds of Tanzania, originally supposedly to be Middle Triassic (Anisian) in age (Nesbitt et al., 2013a). *Nyasasaurus* was suggested to represent the oldest known dinosaur or its most immediate sister taxon, and one of the oldest dinosauriforms yet recorded. However, the age of the Lifua Member is far from certain, being based only on the "evolutionary stage" of its faunistic content (Rubidge, 2005). In this sense, Marsicano et al. (2016) questioned the age of the Manda beds and concluded that this stratigraphic complex lacks a precise temporal framework (see also Irmis et al., 2011). Ezcurra et al. (2017, 2021b) also presented evidence supporting a Ladinian to early Carnian age for the Manda beds (see above). Thus, *Nyasasaurus* may not be older than other archosauriform taxa documented, for example, in the Chañares Formation.

We treat with some caution the referral of *Nyasasaurus* to Dinosauria or its most immediate sister taxon. Nesbitt et al. (2013a) considered the presence of the apex of the deltopectoral crest deflected laterally as a synapomorphy shared by *Nyasasaurus* and Dinosauria. Nevertheless, the humerus of *Nyasasaurus* seems proximodistally short and transversely expanded (as indicated by the distal portion of humeral shaft, preserving the beginning of the distal expansion of the bone). Such proportions differ from those of non-dinosaurian dinosauriforms (e.g., *Lewisuchus*: Bittencourt et al., 2015; Ezcurra et al., 2020b; *Asilisaurus*: Nesbitt et al., 2020; *Silesaurus*: Dzik, 2003), but resemble more those of non-ornithodiran archosaurs, such as the aphanosaurian *Teleocrater* (Nesbitt et al., 2017a). Regarding cervical vertebrae, the elongate condition of the centra, with a strongly offset anterior half, and the development and position of laminae and fossae of the neural arch in *Nyasasaurus*, are also similar to those in *Teleocrater* (Nesbitt et al., 2017a, b).

In sum, the combination of character states with apparently conflictive phylogenetic signals plus the fragmentary nature of the hypodigm of *Nyasasaurus parringtoni* lead us to not discuss further the implications of this taxon on the origin of dinosaurs.

6. The herrerasaurian radiation

Herrerasaurs have been undoubtedly recorded from South America, but specimens from the lower-middle Norian Upper Maleri Formation of India (Novas et al., 2011) and the Norian of both the USA (Sarıgü;l, 2017) and Europe (Niedźwiedzki et al., 2014) have been referred to this clade. As we discuss below, the North American taxa *Tawa, Chindesaurus* and *Daemonosaurus* are here also referred to this clade (Figs. 4 and 6). Thus conceived, Herrerasauria gathers predatory dinosaurs ranging from (approximately) 1.20 m long (*Staurikosaurus pricei*) up to 6 m long (*Frenguellisaurus ischigualastensis*, a probable junior synonym of *Herrerasaurus*; see below), spanning from the middle-late Carnian (*Staurikosaurus*) up to the Rhaetian (*Daemonosaurus*).

Because of its unique combination of character states, including features that are nearly exclusive of theropod dinosaurs (e.g., intramandibular sliding articulation, serrated dentition, grasping hands, pubis with distal pubic boot, distal caudal prezygapophyses elongated), with striking plesiomorphic traits (e.g., primitive-looking pelvic girdle and tarsus), the phylogenetic relationships of herrerasaurs remained unstable since they original description (e.g., Reig, 1963; Rozhdestvensky and Tatarinov, 1964; Walker, 1964; Romer, 1966; Colbert, 1970; Bonaparte, 1969a, b; van Heerden, 1978; Cooper, 1980, 1981; Galton, 1985). Some authors suggested that *Herrerasaurus* and its kin may constitute the sister group to Dinosauria (i.e., Ornithischia + Saurischia = Eudinosauria, sensu Novas, 1992; Gauthier and Padian, 1985; Gauthier, 1986; Brinkman and Sues, 1987; Benton, 1990; Novas, 1991, 1992; Bonaparte, 1997; Fraser et al., 2002; Baron and Williams, 2017), whereas others proposed theropod affinities for the group (e.g., Sereno and Novas, 1992, 1994; Novas, 1994; Sereno, 1994; Sereno et al., 1993; Sereno, 1999, 2007a; Benton, 1999; Rauhut, 2003; Nesbitt et al., 2009, 2013a; Nesbitt, 2011; Martínez et al., 2011; Sues et al., 2011). Baron et al. (2017a) gathered herrerasaurids and sauropodomorphs within a redefined Saurischia. A third proposal indicates that herrerasaurids may constitute a non-Eusaurischia branch of Saurischia, as originally proposed by Langer (2004) and followed by several authors (e.g., Yates, 2005, 2007b; Langer and Benton, 2006: Ezcurra, 2006, 2010; Upchurch et al., 2007; Irmis et al., 2007a, b; Smith et al., 2007a, b; Martínez and Alcober, 2009; Alcober and Martínez, 2010; Baron et al., 2017a; Langer et al., 2019; Müller and Garcia, 2020; Nesbitt and Sues, 2021). In agreement with this view, Herrerasauria is recovered here as the sister taxon to Sauropodomorpha plus Theropoda (= Eusaurischia).

A recent study proposed that the small-sized dinosauriform *Saltopus elginensis* form the Upper Triassic of Scotland (Benton and Walker, 2011) belong to Herrerasauridae based on the presence of a scapular blade only weakly expanded at its distal end, and an ischial shaft anteriorly curved along its length (Baron and Williams, 2018). We agree that *Saltopus* share these character states with herrerasaurians, but both features are also present, for example, in lagerpetids (Cabreira et al., 2016; Ezcurra et al., 2020a). In contrast, *Saltopus* shows notably gracile and elongate hindlimbs and elongate dorsal vertebral centra that differ from those in Herrerasauria. As a result, here we follow the conclusion of Benton and Walker (2011) regarding *Saltopus* as a Dinosauriformes *incertae sedis* until updated phylogenetic analyses integrating recently published information comprehensively test this hypothesis.

6.1. *Herrerasauridae*

This dinosaur family includes *Staurikosaurus, Gnathovorax, Herrerasaurus*, *Sanjuansaurus* and possibly *Frenguellisaurus* —the vast majority of authors have considered this latter genus as a junior synonym of *Herrerasaurus* (Novas, 1994)— (Novas, 1986, 1997, 1997; Alcober and Martínez, 2010; Martínez et al., 2013b; Pacheco et al., 2019). *Staurikosaurus* and *Gnathovorax* were recovered from the *Hyperodapedon*

AZ of the Santa Maria Formation. On the other hand, *Herrerasaurus* and *Sanjuansaurus* were collected from the lower levels of the Ischigualasto Formation, and *Frenguellisaurus* probably from the upper levels of this unit (Martínez et al., 2013b). In a recent analysis, *Staurikosaurus* has been found as the sister group of an unresolved trichotomy including *Herrerasaurus*, *Sanjuansaurus,* and *Gnathovorax*, citing the following features in support of this last clade: tip of neural spine of trunk vertebrae lateromedially expanded, distal end of ischium subtriangular in cross-section, and femur longer than tibia (Pacheco et al., 2019). We lend support to this interpretation, also adding the following synapomorphies: pubis more retroverted, distal pubic boot anteriorly expanded, and proximal femur with an anterior keel. An apomorphic resemblance shared by *Herrerasaurus* and *Sanjuansaurus*, exclusive of *Staurikosaurus* and *Gnathovorax*, is the presence of an even more anteroposteriorly expanded pubic distal end. All seem to indicate that the slender, long-limbed *Staurikosaurus* falls outside a herrerasaurid subclade composed of heavier constructed, stout-limbed taxa. Although interrelationships among *Gnathovorax*, *Sanjuansaurus* and *Herrerasaurus* need to be further explored in the context of a phylogenetic analysis, we infer that the latter two taxa could be closer to one another. In the following sections we discuss problematic anatomical interpretations for each herrerasaur taxon and phylogenetically informative characters.

Staurikosaurus pricei – this taxon was named by Colbert (1970) based on a partial and poorly preserved skeleton (MCZ 1669) excavated in 1936 from the Sanga Grande/Sanga de Baixo outcrop, municipality of Santa Maria, Rio Grande do Sul, Brazil (Fig. 8). This outcrop belongs to the upper portion of Santa Maria Formation (lower portion of the Candelária Sequence). A high-precision U–Pb zircon geochronology study suggested a maximum age of 233.23 ± 0.73 Ma from a nearby locality (Langer et al., 2018). Therefore, the fossiliferous site that yielded *Staurikosaurus* is considered middle Carnian in age. In addition to the holotype, the strongly taphonomically altered specimens SNSB-BSPG AS XXV 53 and SNSB-BSPG AS XXV 54 (holotype of "*Teyuwasu barberenai*"), which respectively correspond to a right femur and tibia, were recently referred to *Staurikosaurus* (Garcia et al., 2019c). This assignment is based on the following combination of character states shared with *Staurikosaurus*: femur without trochanteric shelf, with symmetric fourth trochanter, and poorly separated tibiofibular crest from the lateral condyle at the distal end; and tibia with posterolateral flange of the distal end not exceeding the lateral margin of the bone, and with a rounded distal end (Garcia et al., 2019c). However, all these character states co-occur in some non-dinosaurian dinosauriform skeletally immature specimens of *Lewisuchus admixtus* (Ezcurra et al., 2020b) and *Asilisaurus kongwe* (Griffin and Nesbitt, 2016; Nesbitt et al., 2020), in which the trochanteric shelf is absent. In addition, the tibia of "*Teyuwasu*" possesses a straight cnemial crest that differs from the curved crest synapomorphic of dinosaurs (Irmis et al., 2007a; Nesbitt, 2011). As a result, we cast doubts on the referall of SNSB-BSPG AS XXV 53 and SNSB-BSPG AS XXV 54 to *Staurikosaurus*.

The only known cranial remains of *Staurikosaurus* is a strongly deformed lower jaw. The dentary bears ziphodont teeth and its anterior end is not downturned. Like in *Gnathovorax*, the dentary lacks a longitudinal ridge. The retroarticular process seems dorsally oriented, resembling that of *Gnathovorax* and *Herrerasaurus* (Pacheco et al., 2019; Sereno and Novas, 1994). The holotype preserves 21 presacral vertebrae (Bittencourt and Kellner, 2009). The number of cervical vertebrae is uncertain, but the preserved cervical vertebrae resemble those of other herrerasaurids, which are relatively short, and have epipophyses. The number of dorsal vertebrae is 15 according Bittencourt and Kellner (2009). However, the axial series is incomplete. Therefore, this number should be carefully considered. The elements are poorly preserved and still partially covered by matrix. The general morphology resembles that of other herrerasaurids, where the centrum is anteroposteriorly short and the neural spines are straight and short (Novas, 1992).

The sacrum of *Staurikosaurus* has been reconstructed as being formed by three vertebrae, with one of the vertebrae incorporated from the caudal series (Bittencourt and Kellner, 2009; Colbert, 1970). It is worth noting that Galton (1977) described the vertebra originally considered by Colbert (1970) as the "third sacral vertebra" as the first caudal. Moreover, in a more recent paper Galton (2000) clearly indicates that "much of the thickness of the left "third sacral rib" consists of smoothly ground matrix" and that the preserved bony part of this vertebra is similar to the first caudal vertebra of *Herrerasaurus*. It is important to note that primordial sacrals 1 and 2 of *Staurikosaurus* are laterally hidden by the ilia when the bones are rearticulated, but the purported sacral 3 is not. In brief, we concur with Galton (1977, 2000) regarding identification of sacral elements, suggesting that only two vertebrae composed the sacrum of *Staurikosaurus*, as also occurs in *Herrerasaurus* and *Gnathovorax* (see below). Similar to *Gnathovorax* and *Herrrerasaurus*, the distal caudal vertebrae of *Staurikosaurus* have elongated prezygapophyses.

The scapular girdle of *Staurikosaurus* is known by the left scapula and a co-ossified fragment of coracoid, preserving the blade, acromial process and glenoid cavity. This bone has been previously interpreted as a right ischium (Bittencourt and Kellner, 2009), but the latter bone is sharply different from its supposed counterpart. For reasons given by Novas (1992), and later endorsed by Galton (2000), the bone represents a scapula (instead of an ischium) with evidence supporting this conclusion including the strap-like and transversely compressed blade (contrasting with the distal shaft of the left ischium that is cylindrical and elliptical-shaped in cross-section), the smooth, saddle-shaped glenoid articular surface (different from the transversely narrow acetabular margin of ischium), and presence of a distinct glenoid lip, which is robust and pyramidal in lateral and posterior views (different from the iliac peduncle of ischium). In contrast, if interpreted as an ischium, the preserved portion of the purported pubo-ischiatic plate is transversely very thick and it is more reliably identified instead as the glenoid region of the coracoid. In sum, the scapular blade, glenoid cavity, scapular glenoid lip, and shape of acromial process preserved in *Staurikosaurus* matches the scapula of *Herrerasaurus*. From this it follows that the presence of anteroposteriorly narrow scapular blade alongside with a dorsoventrally deep acromion may represent a synapomorphy of Herrerasauridae, as it is also documented in *Herrerasaurus, Sanjuansaurus,* and *Gnathovorax*.

Similar to other herrerasaurids and "*Caseosaurus*", the ilium of *Staurikosaurus* is anteroposteriorly short. The preacetabular ala is rounded in lateral view, whereas in *Gnathovorax* it tapers to a point. The ilium lacks brevis shelf and fossa. Unlike *Herrerasaurus* and *Gnathovorax*, the preacetabular and postacebular alae are not covered by strong rugosities. The lateral margin of the pubis shaft folds posteriorly and at the distal portion of that bone there is a posterior expansion, which also occurs in other herrerasaurids. In anterior view, the straight lateral margin of the pubis of *Staurikosaurus* differs from that of other herrerasaurids, where the margin is sigmoid (Pacheco et al., 2019). The ischium (described as the left one by Bittencourt and Kellner, 2009, but corresponding in fact to the right one; Galton, 2000) lacks an obturator foramen on the obturator plate, which is present in *Gnathovorax* and *Herrerasaurus*. However, the bone is not completely preserved in the holotype of *Staurikosaurus*. The proximal articular surface of the femoral head has a transverse longitudinal groove and a posteromedial tuber, the latter of which is absent in *Gnathovorax*. The posterolateral flange of the distal end of the tibia does not exceed beyond the lateral margin of the bone, whereas in *Tawa* and *Chindesaurus* the inverse condition is the case (Marsh et al., 2019). As in *Gnathovorax*, *Sanjuansaurus*, and *Tawa*, the distal end of the tibia of *Staurikosaurus* is rounded.

Gnathovorax cabreirai – this taxon was described by Pacheco et al. (2019) based on an exceptionally preserved skeleton of a single individual (CAPPA/UFSM 0009; Fig. 9). The specimen was exhumed from the Marchezan site, municipality of São João do Polêsine, Rio Grande do Sul, Brazil. Strata in the site belong to the upper portion of Santa Maria Formation. The presence of *Hyperodapedon* remains associated with *Gnathovorax* place this site into the *Hyperodapedon* AZ (Martínez et al., 2011; Langer et al., 2018).

The holotype is mostly articulated and almost complete. The postnarial process of the premaxilla is anteroposteriorly wide and elongated, as in *Herrerasaurus* and *Daemonosaurus*. There are three premaxillary teeth, as in *Daemonosaurus*, *Tawa*, and *Heterodontosaurus* (Nesbitt and Sues, 2021), whereas *Herrerasaurus* bears four teeth (Sereno and Novas, 1994) as in *Buriolestes* and *Pampadromaeus*. Different from *Eodromaeus* (Martínez et al., 2011), the antorbital fossa of the maxilla is poorly developed and there is no promaxillary fenestra. The ventral ramus of the lacrimal is far more developed posteriorly than in *Herrerasaurus*. There is an anteriorly elongated supratemporal fossa on the anterior portion of the supratemporal fenestra. The quadratojugal is partially fused to the quadrate.

Gnathovorax bears nine cervical vertebrae and 16 articulated dorsal vertebrae. These elements are anteroposteriorly short, with ''H'' shaped neural spines in cross-section. This is the usual condition of herrerasaurids. In addition, the taxon shares with other herrerasaurids the presence of spine tables on the distal tip of the neural spines. The number of sacral elements among herrerasaurids has been matter of debate, mainly because the pelvis and sacrum are somewhat distorted in the holotype of *Herrerasaurus* and because in *Staurikosaurus* the sacral vertebrae are not in place with the ilia (see above). Most authors expressed that these herrerasaurids, as well as *Sanjuansaurus,* had three sacral elements (e.g., Galton, 1977; Alcober and Martínez, 2010). However, the discovery of *Gnathovorax* lends support to the interpretation that only two vertebrae from the sacrum of *Herrerasaurus*, as originally recognized by Novas (1994). Regardless of the sacrum being composed of two (*Herrerasaurus, Gnathovorax*) or three (*Sanjuansaurus*) vertebrae, the vertebrae anterior to the first primordial sacral exhibit slender transverse processes that project anterolaterally, almost reaching, but not contacting the ilia. This observation may affect the ancestral condition of sacral count for the common ancestor of Dinosauria. In fact, an increase in the number of sacral vertebrae is clear from the early stages of theropod and ornithischian evolution, whereas in sauropodomorphs this increase is not as abrupt, with several forms bearing a sacrum composed of two or three vertebrae.

The slender scapular blade of *Gnathovorax* resembles that of *Herrerasaurus*, *Sanjuansaurus*, and *Tawa*. However, in lateral view, the main shaft is straight in *Herrerasaurus* (PVSJ 380), but slightly bowed in *Gnathovorax*. Digits I, II, and III are elongated with sharp raptorial claws, whereas digit IV is reduced and digit V is not preserved. Unlike sauropodomorphs (e.g., *Eoraptor* and *Macrocollum*), the digit I is neither rotated nor hypertrophied.

Similar to other herrerasaurids, the ilium lacks brevis shelf and fossa. The pubis is co-ossified with the ilium. Similar to *Sanjuansaurus* (Alcober and Martínez, 2010), the pubis is relatively short if compared with other pelvic elements and also compared with the femur (64%). An interesting aspect that emerges here concerns the length of the pubis among herrerasaurids: in both *Sanjuansaurus* and *Gnathovorax*, the pubis is relatively short if compared with other pelvic elements and (in the case of *Sanjuansaurus*) also compared to the femur. In contrast, in *Herrerasaurus* and *Staurikosaurus* the pubis is proportionally longer (Novas, 1994; Bittencourt and Kellner, 2009). This variability is not easy to explain, but distribution of this character may affect one of the synapomorphies of Dracohors (Dinosauria + Silesauridae) depending on the phylogenetic topology, which is pubic length more than 70% of femur length (Novas, 1996). The ischium of *Gnathovorax* has an unusually wide obturator foramen on the obturator plate, which resembles that of the lagerpetid *Ixalerpeton*. The pubis is anteroposteriorly expanded at the distal end, as in *Herrerasaurus*, whereas in *Staurikosaurus* the pubis expands only posteriorly.

The femur is sigmoid in anterior and lateral views. The fourth trochanter is asymmetrical, resembling that of *Herrerasaurus* and sauropodomorphs. The tibia is shorter than the femur, whereas in *Staurikosaurus* it is longer. A marked tuberosity occurs on the anteromedial surface of the proximal portion of the fibular shaft, resembling that of *Buriolestes* (Müller et al., 2018b). The tarsal bones are not fused and the pes bears five digits. Digit I is slender and digit V is reduced to three, poorly developed phalanges.

Herrerasaurus ischigualastensis – this taxon represents the first dinosaur species named for the Ischigualasto Formation (Reig, 1963) (Fig. 10). The holotype was discovered in 1961 approximately 4 km from Aguada de la Peña in the lower levels of the Ischigualasto Formation. This specimen (PVL 2566) is represented by several vertebrae, a pelvic girdle, and numerous hindlimb bones. In addition, Reig (1963) referred other four specimens to *Herrerasaurus ischigualastensis*, adding information about the forelimbs and some cranial bones. All these specimens come from the Ischigulasto Formation, with the exception of an isolated femur collected in the overlying Los Colorados Formation (PVL 2264; Reig, 1963; but see below). In the same contribution, Reig (1963) erected a second dinosaur species for the Ischigualasto Formation, "*Ischisaurus cattoi*", based on a partial skeleton that includes both cranial and postcranial bones. This author also refers a second, more fragmentary partial skeleton to that species. Reig (1963) considered *Herrerasaurus ischigualastensis* as a carnosaur and "*Ischisaurus cattoi*" as a coelurosaur. Ten years later, Benedetto (1973) recognized the close affinities between *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei*, and erected the new family Herrerasauridae. This idea was followed by Novas (1986) in the description of another carnivorous dinosaur taxon from the Ischigualasto Formation, *Frenguellisaurus ischigualastensis*. However, Brinkman and Sues (1987) did not recognize the family Herrerasauridae when they described a new dinosaur specimen from the Ischigualasto Formation, which was regarded as a staurikosaurid cf. *Staurikosaurus* sp. These authors interpreted *Staurikosaurus pricei* and *Herrerasaurus ischigualastensis* as successive sister taxa to Dinosauria.

Fieldwork in the Ischigualasto Formation during the southern autumn of 1988 resulted in the recovery of highly informative herrerasaurid specimens. Sereno and Novas (1992) provided a preliminary description of some of these specimens and reported on a complete skull and the overall body plan of *Herrerasaurus ischigualastensis*. Novas (1992) revised the evidence for the monophyly of the family Herrerasauridae and considered it as a natural group sister to Dinosauria. Subsequently, the anatomy of *Herrerasaurus ischigualastensis* was described in detail in a series of papers that turn this species into the best known of the oldest dinosaurs (Sereno, 1994; Novas, 1994; Sereno and Novas, 1994). Novas (1994) revised the taxonomy of the herrerasaurid specimens from the Ischigualasto Formation and considered "*Ischisaurus cattoi*" and *Frenguellisaurus ischigualastensis* as junior synonyms of *Herrerasaurus ischigualastensis* (see below). In addition, Novas (1994) also assigned the specimen described by Brinkman and Sues (1987) to *Herrerasaurus ischigualastensis*. On the other hand, Novas (1994) reinterpreted the isolated femur from the Los Colorados Formation, which was referred to *Herrerasaurus ischigulastensis* by Reig (1963), as belonging to an indeterminate archosaur. More recently, Ezcurra (2017) agreed with the exclusion of this specimen from *Herrerasaurus ischigualastensis* and considered it as an indeterminate theropod. As a result, *Herrerasaurus ischigulastensis* is currently restricted to the lower levels of the Ischigualasto Formation (Sereno and Novas, 1992; Novas, 1994; Martínez et al., 2013b). Martínez et al. (2013b) reported that *Herrerasaurus ischigualastensis* is the most abundant dinosaur in this unit, being represented by at least 58 specimens.

Indeed, this species represents approximately 73% of the total dinosaur abundance of the unit in the census of Martínez et al. (2013b).

The skeleton of *Herrerasaurus ischigualastensis* is characterized by a relatively large skull that possesses a subrectangular profile as the result of a dorsoventrally tall rostrum. The premaxilla is anteroposteriorly short, dorsoventrally tall, and possesses a massive posterodorsal process. The antorbital fenestra is short and is bounded by a poorly developed antorbital fossa. The mandibular ramus has a tall dentary and a large, upturned retroarticular process. The premaxilla possesses four teeth and the maxilla 17–18 tooth positions, whereas the dentary has 16 teeth. The maxillary and dentary tooth crowns are large, distally curved and finely serrated on both mesial and distal margins. The overall dorsoventrally tall morphology of the skull of *Herrerasaurus ischigualastensis* resembles that of Middle and Late Jurassic theropods (e.g., *Ceratosaurus*, *Allosaurus*), contrasting with the lower skulls with tapering rostrum of non-averostran neotheropods (Sereno and Novas, 1994).

The cervical vertebrae of *Herrerasaurus ischigualastensis* are relatively short and lack pneumatic features (Sereno and Novas, 1994). The dorsal vertebrae are anteroposteriorly compressed and possess high neural spines with spine tables. The sacrum is composed of two vertebrae, contrasting with the presence of three or more sacral vertebrae in most dinosaurs (Novas, 1992, 1994). The shoulder girdle has a long and unexpanded scapular blade and the coracoid possesses a well-developed, tapering posterior process (Sereno, 1994). The forelimb is characterized by a proportionally long manus that bears trenchant unguals (Sereno, 1994), resembling the condition in some early ornithischians (e.g., *Heterodontosaurus tucki*; Santa Luca, 1980) and neotheropods (e.g., *Coelophysis bauri*; Barta et al., 2018).

The pelvic girdle of *Herrerasaurus ischigualastensis* is highly diagnostic as a result of the presence of a pubis with a shaft more posteriorly oriented and ending in a more strongly developed distal boot than in other herrerasaurids. The pelvic girdle of *Herrerasaurus ischigualastensis*, as well as that of other herrerasurids, combines a series of plesiomorphic and apomorphic features. The absence of a brevis fossa, a short postacetabular process, and a concave dorsal margin of the iliac blade resemble the condition in non-dinosaurian avemetatarsalians (Novas, 1992, 1994), whereas a similar orientation and distal expansion of the pubis have been independently acquired by Late Jurassic and Cretaceous neotheropods (Reig, 1963; Novas, 1994). The hindlimb bones are relatively robust, with a tibia slightly shorter than the femur. The tarsus possesses a very low ascending process of the astragalus and a calcaneum with a well-developed ventromedial projection and calcaneal tuber, resembling the condition in non-dinosaurian dinosauriforms and some other early saurischians (Novas, 1989, 1994; Langer, 2003; Nesbitt et al., 2020). The pes is quite symmetric lateromedially, with metatarsals I and V subequal in length (Novas, 1994). The fifth pedal digit retains a single, non-ungual pahalanx.

Sanjuansaurus gordilloi – this herrerasaurid taxon was erected by Alcober and Martínez (2010) based on a single specimen (PVSJ 605) collected from 40 m above the base of the Ischigualasto Formation (La Peña Member) in 1994. Martínez et al. (2013b) reported on a second, slightly stratigraphically higher specimen but did not provide further information about it. As a result, the stratigraphic range of *Herrerasaurus ischigualastensis* overlaps that of *Sanjuansaurus gordilloi* in the Ischigualasto Formation (Alcober and Martínez, 2010). The holotype of *Sanjuansaurus gordilloi* is represented by a partial skeleton that includes the left maxilla, most of the postcranial axial skeleton, both shoulder girdles, left ulna, manual ungual phalanx, partial pelvic girdle, and several hindlimb bones (Alcober and Martínez, 2010).

The overall morphology of *Sanjuansaurus gordilloi* resembles that of *Herrerasaurus ischigulastensis*, but Alcober and Martínez (2010) distinguish them (as well as from *Saturikosaurus pricei*) because of the presence of the following character states in the former species: shelf-like, posterolaterally directed transverse processes on the posterior cervical vertebrae; neural spines of the sixth to eighth dorsal vertebrae, at least, bearing acute anterior and posterior processes; everted lateral margins of the shoulder glenoid; short pubis (63% of the femoral length); and pronounced, rugose scar on the medial surface of the femur at the level of the fourth trochanter. The size of the holotype of *Sanjuansaurus gordilloi* is comparable to that of medium-sized specimens of *Herrerasaurus ischigualastensis* (Alcober and Martínez, 2010), and considerably larger than the holotypes of *Staurikosaurus pricei* and *Gnathovorax cabrerai*. The phylogenetic position of *Sanjuansaurus gordilloi* within Herrerasauridae has been stable since its original description, but the interrelationships of this taxon within the clade need to be explored in more detail.

Frenguellisaurus ischigualastensis – this taxon was named by Novas (1986) and the holotype was recovered from La Chilca Creek in northern outcrops of the Ischigualasto Formation, probably from the upper levels of the Ischigualasto Formation (Martínez et al., 2013a). *Frenguellisaurus* differs from *Herrerasaurus* and *Sanjuansaurus* in being twice their sizes, with proportionally higher and shorter maxilla and jugal bones, and strongly sinuous ventral margin of these bones. Nevertheless, Novas (1994) regarded *Frenguellisaurus ischigualastensis* a junior synonym of *Herrerasaurus ischigualastensis*, assuming it represented a large individual of the species. However, considering the probable higher stratigraphic provenance of the holotype, and the discovery of new materials from the Ischigualasto Formation (as reported by Martínez et al., 2013a), we consider that the taxonomic validity of *Frenguellisaurus* should be carefully reassessed on the light of new data.

6.2. *Tawa, Chindesaurus, "Caseosaurus"* and *Daemonosaurus* as North American herrerasaurs

The fossil record of herrerasaurids from Argentina and Brazil (including different species, some represented by several specimens and fairly complete skeletons) represents a useful source of information to better understand the less complete North American early dinosaurs *Chindesaurus, Caseosaurus, Tawa,* and *Daemonosaurus*. These taxa have been recorded from Norian to Rhaetian beds, cropping out in different fossil sites in southwestern USA. The phylogenetic interpretations of these four taxa have been tortuous, mainly due to their fragmentary nature (except for *Tawa*).

As follows, we offer a brief review of each of these taxa, compare them to one another with the aim to set down their close relationship, and then discuss the anatomical evidence originally listed in support of their theropod affinities. Finally, we describe the several apomorphic and plesiomorphic traits that these North American taxa share with herrerasaurids.

Chindesaurus bryansmalli – this taxon comes from the upper Norian (213–210 Ma) Petrified Forest Member of the Chinle Formation, Arizona (Long and Murry, 1995). *Chindesaurus* was originally described as a herrerasaurid (Long and Murry, 1995) and this hypothesis was followed by some authors (Novas, 1997). Langer (2004: p. 46) considered *Chindesaurus* as an indeterminate saurischian, but he also stated that this species 'might represent a later wanderer of the herrerasaur lineage, indicating a greater chronological and geographic distribution for the group'. More recent studies tested the phylogenetic relationships of *Chindesaurus* in a numerical analysis and found it as a herrerasaur outside of Eusaurischia (Irmis et al., 2007a). Subsequent analyses agreed in the placement of *Chindesaurus* as a herrerasaurid and recovering this clade within Theropoda (e.g., Nesbitt et al., 2009; Ezcurra and Brusatte, 2011; Sues et al., 2011; Niedźwiedzki et al., 2014). However, more recent analyses have recovered more disparate results, in which *Chindesaurus* was found as a non-neotheropod theropod (e.g., Nesbitt and Ezcurra, 2015; Langer et al., 2017; Marsh et al., 2019; Ezcurra et al., 2021a), non-eusaurischian saurischian (e.g., Cabreira et al., 2016; Marsola et al., 2019a; Müller et al., 2018a; Pacheco et al., 2019), one of the sister taxa to Sauropodomorpha (Baron et al., 2017a), one of the sister taxa to Ornithoscelida (Baron et al., 2017b), and even outside of Dinosauria (Baron and Williams, 2018). In all these analyses, with the exception of Baron et al. (2017a, b) and Baron and Williams (2018), *Chindesaurus* was found outside of Herrerasauria. In more recent years, the sister taxon relationship between *Tawa* and *Chindesaurus* was recovered in several studies (e.g., Cabreira et al., 2016; Baron et al., 2017b; Marsola et al., 2019a; Müller et al., 2018a; Pacheco et al., 2019) and stronger evidence for this hypothesis has been recently provided (Marsh et al., 2019).

Tawa hallae – *Tawa* is from the upper Norian (ca. 212 Ma) Petrified Forest Member of the Chinle Formation, Arizona (Nesbitt et al., 2009). The vast majority of previous phylogenetic analyses consistently found this species close to Neotheropoda (Nesbitt et al., 2009; Sues et al., 2011; You et al., 2014; Nesbitt and Ezcurra, 2015; Martill et al., 2016; Baron et al., 2017a; Cabreira et al., 2016; Ezcurra, 2017; Langer et al., 2017; Martínez and Apaldetti, 2017; Müller et al., 2018a; Marsola et al., 2019a; Marsh et al., 2019; Griffin, 2019; Pacheco et al., 2019; Ezcurra et al., 2021a). Yet, departing from this apparent consensus, *Tawa* has been also found as the earliest branching member of Coelophysoidea within Neotheropoda (Martínez et al., 2011). In contrast, Novas and Ezcurra (2011) reported a preliminary result in which *Tawa* was recovered as a herrerasaur and as the sister taxon to the South American herrerasaurids. More recently, *Tawa* was found as one of the sister taxa to Ornithoscelida (Baron et al., 2017b) or as the most immediate sister taxon to Eusaurischia (Pretto et al., 2019; using a modified version of the data matrix of Ezcurra, 2010). In these two latter analyses, herrerasaurids were either positioned as the sister taxon to Dinosauria (Baron et al., 2017b) or as the sister taxon to the *Tawa* + Eusaurischia clade (Pretto et al., 2019), respectively.

"*Caseosaurus crosbyensis*" - the single and incomplete right ilium that represents the holotype of "*Caseosaurus crosbyensis*" was found in the upper Carnian–lower Norian Tecovas Member (correlated with the Blue Mesa Member of the Chinle Formation, constrained to 225–218 Ma based on radioistotopic datings; Ramezani et al., 2014) of the Dockum Group, Texas (Hunt et al., 1998). This taxon was originally described as belonging to *Chindesaurus* (Long and Murry, 1995), but a more recent revision reinterpreted "*Caseosaurus*" not beyond the level of Dinosauriformes and considered it a nomen dubium (Nesbitt et al., 2007). However, a recent redescription of the holotype found "*Caseosaurus*" to be a diagnostic herrerasaur, being placed in a polytomy with all currently recognized members of Herrerasauridae (Baron and Williams, 2018). We follow Nesbitt et al. (2007) in interpreting "*Caseosaurus*" as a nomen dubium (owing its lack of diagnostic features), but the available materials match well the morphology of herrerasaurs, thus lending support to its interpretation as an herrerasaur (Baron and Williams, 2017). Probably the most relevant aspect of this fragmentary specimen is its late Carnian–early Norian age, indicating that herrerasaurs were present in slightly younger North American ecosystems than those in South America.

Daemonosaurus chauliodus – this bizarre North American dinosaur was discovered from the Rhaetian Rock Point Member of the Chinle Formation, *Coelophysis* Quarry at Ghost Ranch, New Mexico (Sues et al., 2011). *Daemonosaurus* was originally found within Theropoda, as the sister taxon to the clade composed of *Tawa* and Neotheropoda (Sues et al., 2011). Subsequent analyses recovered multiple, disparate phylogenetic positions for *Daemonosaurus*, namely as a non-eusaurischian saurischian (e.g., Cabreira et al., 2016; Müller et al., 2018a; Marsola et al., 2019a; Pretto et al., 2019; Pacheco et al., 2019), a non-neotheropod theropod (Baron and Williams, 2018), and the earliest branching ornithischian (Baron et al., 2017b). Recently, Nesbitt and Sues (2021) offered a detailed description of the available material of this taxon, tentatively concluding that "it is a saurischian at the base of the clade, possibly before the split of theropods and sauropodomorphs". Interestingly, these authors noted that its morphology appears to link the morphology of *Herrerasaurus* with that of later-diverging eusaurichians.

Recently published studies (e.g., Baron and Williams, 2018; Marsh et al., 2019; Nesbitt and Sues, 2021) consistently show that the Late Triassic North American taxa *Chindesaurus*, "*Caseosaurus*", and *Tawa* show striking anatomical similarities in their postcranium, and *Tawa* and *Daemonosaurus* in their skull morphology, supporting their close relation. We advocate for this view, which represents, no doubt, a step forward in the understanding of the diversity and relationships of North American Triassic dinosaurs. In particular, a recent study concluded that *Tawa* and *Chindesaurus* are sister taxa, both sharing derived features absent in other dinosaurs, including a distinctive transversely short astragalus with distal condyles separated by a "V" shaped groove (Marsh et al., 2019). Owing that *Chindesaurus* and *Tawa* come from the same stratigraphic unit (the Petrified Forest Member of the Chinle Formation) and because they exhibit notable apomorphic similarities, one might interpret *Tawa* as a junior synonym (possibly composed of more immature specimens) of *Chindesaurus*. However, we keep their validity based on the autapomorphies identified for these two taxa (Marsh et al., 2019).

Having demonstrated the close affinities among these North American taxa, the next point is to review the anatomical evidence supporting their purported theropodan affinities.

Review of the theropodan characteristics of *Tawa, Chindesaurus,* and *Daemonosaurus* - In the original description of *Tawa*, this genus was recovered within Theropoda based on several features considered synapomorphic for this clade (Nesbitt et al., 2009; see also Marsh et al., 2019). However, current knowledge of new early saurischians and dinosauriforms indicates that most of these features are more widespread than previously thought. As an example, the first description of *Tawa* emphasized on its similarities with coelophysoid theropods concentrated on the premaxilla (Nesbitt et al., 2009), including: relatively elongate and low premaxillary body, elongate nasal process, nasal process forming an angle of less than 20°, presence of an additional medial process on premaxilla, and presence of a diastema between premaxilla and maxilla. Although this set of features is positively present in *Tawa* and coelophysoid theropods, several of these are also shared by other early dinosaurs, such as *Eoraptor* and *Pampadromeus* (Cabreira et al., 2011; Sereno et al., 2013). The presence of elongate cervical vertebrae as well as of diverse fossae on the neural arch and centrum have been interpreted as synapomorphic of *Tawa* plus Neotheropoda (Nesbitt et al., 2009). However, some of these features have been reported for *Eoraptor* (Sereno et al., 2013) and *Silesaurus* (Piechowski and Dzik, 2010). Besides, a strap-like scapula, transversely compressed pubic boot, and elongate manus are features that *Tawa* shares with neotheropods but also with herrerasaurids, such as *Herrerasaurus* (Novas and Ezcurra, 2011).

One of the most recent phylogenies recovered the group formed by *Chindesaurus* plus *Tawa* as a member of Theropoda, depicting Herrerasauridae as sister of the clade formed by *Chindesaurus* + *Tawa* and the remaining theropods (Marsh et al., 2019). One feature in support of this view is the shared presence in *Chindesaurus* of the supraacetabular crest terminating before the distal end of the pubic peduncle, contrasting with herreasaurids, in which the crest extends to the distal extremity of the peduncle. Either this represents a synapomorphy of *Tawa* + *Chindesaurus* plus other Theropoda, or it represents a synapomorphy uniquely shared by *Tawa* and *Chindesaurus* among herrerasaurs, strongly depends on the interrelationships among early saurischians.

Finally, the presence of a transversely reduced calcaneum has been interpreted as diagnostic of the *Tawa* + Neotheropoda clade (Nesbitt et al., 2009). However, the calcaneum of *Tawa* is much more reduced than in other early dinosaurs (including neotheropods such as *Dilophosaurus* and *Liliensternus*; Welles and Long, 1974; Novas, 1989;

Marsh and Rowe, 2020). Thus, this unique condition may be autapomorphic for *Tawa*, rather than a synapomorphy of *Tawa* + *Chindesaurus* plus Neotheropoda. Thus, the only previously cited condition that stands as a unique shared feature between *Tawa* and neotheropods is the jugal having the anterior extent of the slot for the quadratojugal at or anterior to the posterior edge of the dorsal process of jugal (Nesbitt et al., 2009; Marsh et al., 2019).

Regarding the manus of *Tawa*, it has been indicated that its elongate condition is particularly theropod-like, i.e., more than 50 percent of the length of the humerus plus radius (Nesbitt et al., 2009). This is in agreement with the current available information on manual morphology among dinosauriformes. Manual remains are elusive for *Lagosuchus*, but in the immediate sister group of Dinosauria (i.e., *Lewisuchus* and *Asilisaurus*; Ezcurra et al., 2020b; Nesbitt et al., 2020) the hands were small, e.g., the metacarpal II represents 10% of the combined length of humerus plus radius in *Asilisaurus* (Nesbitt et al., 2020). This indicates that Dinosauria differs from silesaurids in having longer metacarpals and hands. Assuming that proportionally short hands is a plesiomorphic condition for Dinosauria, being inherited by early sauropomorphs (e.g., *Eoraptor*) and ornithischians (e.g., *Lesothosaurus*), it must be concluded that *Herrerasaurus*, *Tawa,* and *Eodromaeus* share the derived condition of an elongate manus (also present in *Heterodontosaurus*), more than 50% the length of humerus plus radius (Sereno, 1994, 2012). Aside from general manual proportions, we concur with Sereno (1994), Nesbitt et al. (2009), Sereno et al. (2013), and Martínez et al. (2011) in considering the following features as derived traits shared by *Tawa, Herrerasaurus*, *Eodromaeus* and Neotheropoda, but also present in *Heterodontosaurus* (Sereno, 2012): penultimate phalanges longer than the preceding phalanx; manual unguals large and trenchant; extensor depressions on the distal ends of metacarpals I-III (although they are shallow in *Tawa*, and present in *Eoraptor*); extreme reduction of manual digits IV and V; and metacarpals abutting each other along their shafts (without overlapping margins).

In sum, most of the features supporting the theropod affinities for *Tawa* and *Chindesaurus* are widespread among early dinosauriforms and non-neotheropod dinosaurs. The exceptions are the articulation of quadratojugal with jugal and the several manual features enumerated above.

Regarding *Daemonosaurus*, this taxon was interpreted as a theropod on the basis of the following characters: anterior process of quadratojugal reaching posterior margin of dorsal process of jugal (also present in *Tawa* and *Pampadromeus*; Cabreira et al., 2011); cervical vertebrae with deep pneumatic fossae; and parapophysis and diapophysis close to each other in anterior postaxial cervical vertebrae (Sues et al., 2011).

Comparisons of *Tawa, Chindesaurus, Daemonosaurus* and "*Caseosaurus*" with neotheropods - *Tawa* and *Daemonosaurus* share with *Herrerasaurus* and *Gnathovorax* striking plesiomorphic features that are absent among neotheropods (e.g., *Coelophysis, Dilophosaurus*). These include a weakly excavated basisphenoid recess, premaxilla with relatively tall postnarial process that extends dorsally beyond the posterior border of the naris, premaxilla-nasal suture lacking a W-shaped morphology, lack of an extensive antorbital fossa on the lateral surface of the maxilla, jugal participating in the antorbital fenestra, maxilla lacking distinct lateral ridges, and an anterodorsally inclined lacrimal. As for the postcranial skeleton, *Tawa* exhibits only two sacral vertebrae, humeral shaft straight and lacking bowing of the proximomedial end (Baron et al., 2017a), metacarpal I slender and slightly asymmetrical distally, manual phalanx I-1 proximally rounded lacking the proximodorsal triangular process seen in other dinosaurs, brevis fossa absent (as also in *Chindesaurus* and "*Caseosaurus*"; Marsh et al., 2019), pubic peduncle enlarged and projected anteroventrally much more than the ischiadic peduncle (also in "*Caseosaurus*"), proximal end of tibia devoid of proximally expanded and prominent cnemial crest, tibia without fibular crest, distal tibia lacking an expanded medial edge, distal tibia lacking distinct proximodistally elongate posterior ridge, distal fibula as anteroposteriorly broad as distal tibia, fourth distal tarsal lacking a rounded posterior edge, metatarsal I with its proximal end anteroposteriorly expanded and contacting distal tarsals and medial surface of proximal metatarsal II, and proximal metatarsal IV with a trapezoidal proximal end. All these character states constitute a strong amount of evidence against the position of these taxa within the node-based Neotheropoda.

As already discussed above, the hand of *Tawa* shows several theropodan characteristics. Nevertheless, they occur together with a notable set of plesiomorphies, also documented in *Herrerasaurus*. They are: metacarpal III is the longest of the hand, unlike ornithischians, sauropodomorphs, and theropods, in which this metacarpal is equal to or shorter than metacarpal II; digit III in *Tawa* and *Herrerasaurus* is much longer than digit II, a condition present also in *Heterodontosaurus*; and ungual phalanx of digit III is as large as the unguals of inner digits. Such development of metacarpal III and its digit in *Tawa* and *Herrerasaurus* is in contrast with the condition present in core theropods (e.g., *Megapnosaurus*; Galton, 1971) and sauropodomorphs (e.g., *Efraasia*; Galton, 1973), in which digit III is not only shorter than digit II, but its constituent phalanges are shorter and narrower, including the ungual phalanx, which is smaller in size relative to those of the inner digits. The elongation of digit III in *Tawa* and *Herrerasaurus* apparently represents a plesiomorphic feature, being also documented among lagerpetids (Ezcurra et al., 2020a) and early pterosaurs (e.g., *Eudimorphodon*; Wild, 1978), but no information is yet available on this regard for closer sister groups of Dinosauria (such as *Lagosuchus* and silesaurids). In other early dinosaurs (e.g., *Heterodontosaurus, Eoraptor, Eodromaeus*; Martínez et al., 2011; Sereno, 2012) digit III is slightly longer than digit II, albeit not to the proportions described above for *Tawa* and *Herrerasaurus*. Available information suggests that the manual digit proportions of *Tawa* and *Herrerasaurus* may have been retained from ornithodiran ancestors. In *Tawa* and *Herrerasaurus*, the ungual of digit III is proportionally large, thus manual unguals are subequal in size, whereas in *Megapnosaurus* and *Efraasia* there seems to be a gradient in size, from the largest in digit I, to the smallest in digit III.

A radius longer than 80% the humerus length is present in *Dromomeron romeri*, *Eudimorphodon, Lagosuchus, Silesaurus, Herrerasaurus*, *Asilisaurus*, and *Eodromaeus*, thus suggesting that this condition was inherited by Dinosauria from ornithodiran ancestors (Ezcurra et al., 2020a). *Tawa* also exhibits this condition, which is different from sauropodomorphs (e.g., *Eoraptor*, 74%) and neotheropods (e.g., *Coelophysis*, intraspecific variation ranges between 54–69%), in which the radius is much shorter than the humerus. In other terms, *Tawa* does not exhibit neotheropodan features in the proportions of the antebrachium.

The metacarpal I of *Tawa* and *Herrerasaurus* is elongate, slender, slightly asymmetrical distally, contrasting with *Megapnosaurus*, *Eodromaeus*, and *Eoraptor*, in which this bone is more robust and markedly asymmetrical distally. In the latter taxa, the distal articular condyles are globose and separated by a deep groove, which fits a sharp proximodorsal process on phalanx 1-I. In *Heterodontosaurus,* metacarpal I resembles that of *Tawa* and *Herrerasaurus* in being slender, but the distal end is grooved, as also evidenced by the presence of a sharp proximodorsal process of phlanx 1-I. In other words, metacarpal I (and proximal end of phalanx 1.I) in *Tawa* and *Herrerasaurus* lacks features seen in other dinosaurs but resembles the condition in non-dinosaurian ornithodirans (e.g., *Dromomeron romeri*, *Raeticodactylus*; Ezcurra et al., 2020a).

Regarding the ilium, the brevis fossa of *Tawa* is exposed in lateral view, being different from the condition in theropods (e.g., *Liliensternus*), in which the brevis shelf is ventrally projected, hiding the fossa in lateral view. The condition described for *Tawa* matches well with that of *Silesaurus* (Dzik, 2003). Although a slight depression is present on the posteroventral region of the ilium in *Staurikosaurus*, *Chindesaurus*, "*Caseosaurus*", and *Herrerasaurus*, in all these taxa there is a pronounced subhorizontal ridge on the posterodorsal corner of the iliac blade, which coincides with the position of the more marked brevis shelf of *Tawa* and *Silesaurus*. Thus, the morphology of the posterior half of ilium of *Tawa* and herrerasaurids corresponds to a plesiomorphic condition, unlike that of neotheropods (e.g., *Liliensternus, Dilophosaurus, Coelophysis*), ornithischians (e.g., *Lesothosaurus*; Baron et al., 2017c), and sauropodomorphs (e.g., *Efraasia*; Galton, 1973).

Regarding the distal end of femur, *Chindesaurus, Tawa, Herrerasaurus*, and *Staurikosaurus* have a lateral condyle and tibiofibular crest that are not well differentiated from one another in distal view and combined form a larger structure that projects more posteriorly than the medial condyle (Marsh et al., 2019). In *Herrerasaurus, Staurikosaurus, Tawa, Lewisuchus* (PULR-V 111), and *Silesaurus*, and apparently also in *Eodromaeus*, the distal surface of femur is almost flat. In contrast, in *Eoraptor, Saturnalia*, *Heterodontosaurus*, and *Liliensternus* the distal end has more globose medial and lateral condyles and crista tibiofibularis, and a deeper sinuous groove.

The distal end of tibia in *Tawa* is circular in distal view (as in *Staurikosaurus* and *Silesaurus*), but it has a well-developed outer malleolus (i.e., distally and laterally projected). Although this condition resembles that of theropods and some sauropodomorphs (Novas, 1989), *Silesaurus* also exhibits these features (see Dzik, 2003).

In sum, *Tawa, Daemonosaurus, Chindesaurus*, and "*Caseosaurus*" exhibit several characteristics that can be interpreted as plesiomorphic not only with respect to theropods (e.g., *Coelophysis*), but also to sauropodomorphs and ornithischians, but resembling herrerasaurids. All these comparisons establish strong anatomical evidence for the non-neotheropod affinities of these species, as it has been previously concluded by most authors (e.g., Nesbitt et al., 2009; Marsh et al., 2019; Nesbitt and Sues, 2021; but see Martínez et al., 2011).

Herrerasaurian affinities of *Tawa, Daemonosaurus, Chindesaurus*, and "*Caseosaurus*" - Several features previously reported and described for *Chindesaurus* (Long and Murry, 1995; Marsh et al., 2019) are suggestive of herrerasaurian affinities for this taxon. These include: 1) short and deep dorsal centra; *Chindesaurus* has "centrum length less than 1.33 times the height of the anterior articular surface" (Marsh et al., 2019: p. 17), a proportion that also applies to *Staurikosaurus* and *Herrerasaurus*; 2) neural spines of dorsal vertebrae with spine tables dorsally (present in *Herrerasaurus and Gnathovorax*), and 3) proximal articular surface of the femur lacking a posteromedial tuber (present in *Gnathovorax*).

In addition to the above mentioned set of plesiomorphic features, *Tawa* shares with *Herrerasaurus, Sanjuansaurus* and *Gnathovorax* several derived features that are considered diagnostic for Herrerasauria (Novas, 1992, 1994; Alcober and Martinez, 2010; Pacheco et al., 2019): 1) dorsoventrally deep jugal, representing more than 30% of the orbital height, 2) retroarticular process block-like and dorsally raised, 3) cervical vertebrae with pronounced ventral keels, 4) scapular blade anteroposteriorly narrow, poorly expanded distally and with a straight anterior margin, 5) atrophied metacarpals IV and V even more than in *Heterodontosaurus, Eoraptor, Eodromaeus, Megapnosaurus,* and *Efraasia*, in which metacarpal IV and its phalanges are larger, 6) pubic shaft fan-shaped distally, resulting from the posterior flexion of the lateral margin of pubis (Langer and Benton, 2006) in contrast, the pubic shaft exhibits subparallel anterior and posterior margins in *Lewisuchus*, *Silesaurus*, *Eoraptor*, *Saturnalia*, and neotheropods, such as *Megapnosaurus* and *Dilophosaurus*, 7) anteroposteriorly expanded pubic boot (*Tawa, Herrerasaurus, Sanjuansaurus, Gnathovorax* and *Staurikosaurus* are unique among early dinosaurs in possessing an enlarged pubic boot, triangular-shaped in lateral aspect; whereas in early neotheropods such as *Megapnosaurus* and *Dilophosaurus* the distal expansion of pubis consists in a modest bump that is anteriorly projected, with the posterior projection more extensive but still notably dorsoventrally low, 8) anteroposteriorly wide pubic peduncle that is distinctly more ventrally projected than the ischial peduncle, a similar condition is present in *Chindesaurus*, "*Caseosaurus*", *Gnathovorax* and *Staurikosaurus*, but not in *Herrerasaurus*, and 9) supraacetabular crest horizontally projected outwards, shared by *Staurikosaurus, Gnathovorax* and *Tawa*, but not *Herrerasaurus*.

Daemonosaurus shares the following features with Herrerasauridae: 1) dorsoventrally deep premaxilla, 2) premaxilla having a strongly posterodorsally extended postnarial process that is anteroposteriorly expanded, 3) jugal dorsoventrally tall, 4) maxilla with a strongly convex ventral margin, 5) maxilla with small "U"-shaped antorbital fossa, 6) fang-shaped maxillary teeth, and 7) absence of longitudinal ridge on maxilla. Also, *Daemonosaurus* shares with *Gnathovorax*, *Tawa*, and heterodontosaurids (Sereno, 2012) the presence of three premaxillary teeth.

With the aim to test the phylogenetic position of *Tawa, Chindesaurus* and *Daemonosaurus*, we scored these taxa into the matrix employed by Nesbitt et al. (2009) in the original description of *Tawa*, but with modifications introduced by subsequent authors (see Materials and Methods). The tree searches found three most parsimonious trees (MPTs) of 1351 steps, with a consistency index of 0.34863 and a retention index of 0.67883. The best trees were found in 860 of the 1000 replications. The North American early dinosaurs *Tawa hallae*, *Chindesaurus bryansmalli*, and *Daemonosaurus chauliodus* were recovered outside Theropoda and within a clade that is the sister to Herrerasauridae (Figs. 1 and 7). As a result, Herrerasauria is composed of the Carnian South American Herrerasauridae (including *Staurikosaurus pricei, Herrerasaurus ischigualastensis*, and *Gnathovorax cabrerai* —also *Sanjuansaurus grodilloi* and *Frenguellisaurus ischigualastensis*, but they were not included in the analysis—, and the Norian-Rhaetian North American taxa *Tawa hallae*, *Chindesaurus bryansmalli* and *Daemonosaurus chauliodus*.

In the original analysis of Nesbitt et al. (2009), the phylogenetic position of *Tawa* as the sister taxon to Neotheropoda was supported by eleven unambiguous apomorphies. Although this evidence for the theropod affinities of *Tawa* is still present in our data set, it is less numerous than the evidence favouring a position outside the sauropodomorph-theropod split (= Eusaurischia).

The more taxonomically inclusive Herrerasauria found in our analysis is supported by the following synapomorphies:

1) Premaxilla, height: length ratio below external naris > 1.25 (ch 1 - 0 → 2). An anteroposteriorly short premaxillary body is present in the herrerasaurians *Herrerasaurus*, *Gnathovorax* and *Daemonosaurus*, and was convergently acquired in several early averostrans, such as *Ceratosaurus* and *Allosaurus*. In contrast, a proportionally low premaxillary body is optimized as independently developed in *Tawa* and non-averostran neotheropods (e.g., *Coelophysis*, '*Syntarsus*', *Megapnosaurus*, *Dilophosaurus*). As a result, the coelophysoid-like premaxilla of *Tawa* is interpreted in our analysis as an autapomorphy of this taxon.
2) Exoccipital, lateral surface without subvertical crest (ch 77 - 1 → 0). The absence of a subvertical ridge on the lateral surface of the exoccipital is a rare condition among early dinosauromorphs that occurs in *Gnathovorax*, *Herrerasaurus*, and *Daemonosaurus* (Sues et al., 2011; Nesbitt and Sues, 2021). This crest is present in *Tawa* (Nesbitt et al., 2009).
3) Rostrum, antorbital fossa restricted to the lacrimal and dorsal process of the maxilla, absent on the horizontal process (ch 87 - 1 → 0). *Tawa*, *Daemonosaurus*, *Herrerasaurus* and *Gnathovorax* share the absence of an antorbital fossa on the horizontal process of the maxilla. This condition contrasts with the plesiomorphic presence of such fossa in the common ancestor of Dinosauria.

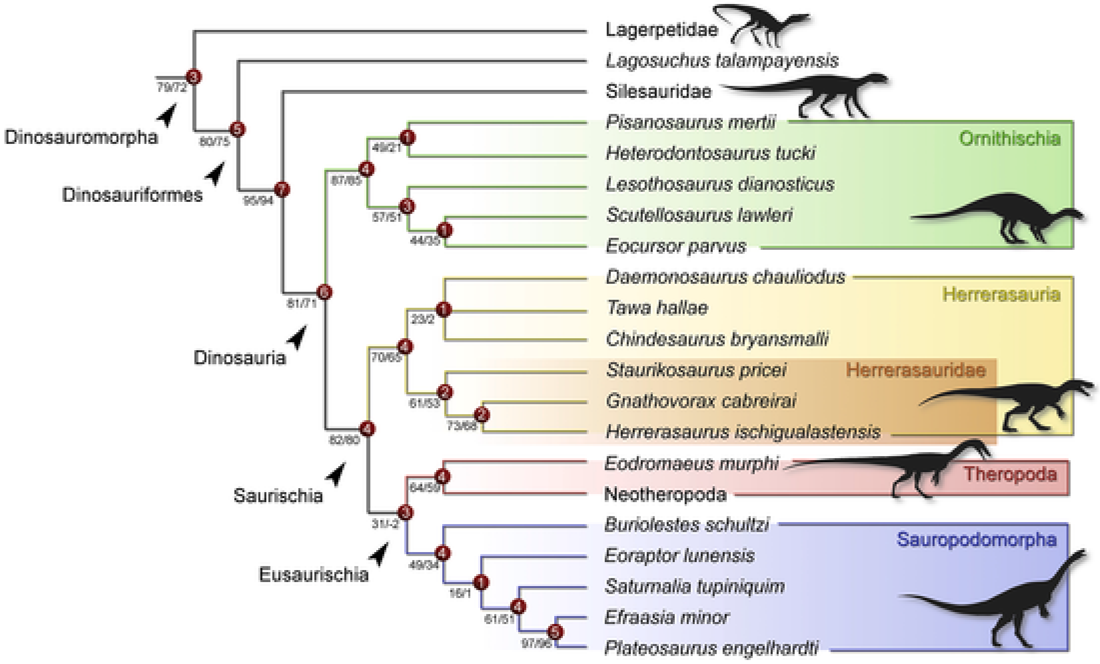

Fig. 7. Reduced strict consensus of the most parsimonious trees found in the phylogenetic analysis. Values on nodes represent Bremer support and values next to each branch represent absolute bootstrap frequency, and GC bootstrap frequency, respectively. Silhouettes based on the artwork by Márcio L. Castro, Andrey Atuchin, and Gabriel Lio.

4) Scapula, entire anterior margin straight/convex or partially concave (ch 153 - 1 → 0). The anterior margin of the scapular blade is distinctly concave in the vast majority of archosauromorphs and this condition is retained in Avemetatarsalia (Nesbitt, 2011; Ezcurra, 2016; Nesbitt et al., 2017a). *Herrerasaurus*, *Gnathovorax* and *Tawa* possess an apomorphically straight/convex anterior margin of the scapular blade, which is a character state independently acquired in early averostrans (e.g., *Ceratosaurus*, *Allosaurus*, *Eoabelisaurus*).

5) Metacarpals, proximal ends abut one another without overlapping (ch 173 - 0 → 1). This character state is present in the ornithischian *Heterodontosaurus*, the herrerasaurs *Herrerasaurus*, *Gnathovorax* and *Tawa*, and neotheropods. However, the presence of a proximal overlapping between metacarpals in *Silesaurus*, *Eocursor*, sauropodomorphs, and *Eodromaeus* results in the optimization of its absence as independent synapomorphies of Herrerasauria and Neotheropoda. However, the distribution of this character among early dinosauriforms has to be further explored because of its apparent high homoplasy.

6) Pubis, distal end strongly expanded relative to the shaft, forming a distinct pubic boot (ch 207 - 1 → 2). It has long been recognized that herrerasaurids share the presence of a strongly anteroposteriorly expanded distal end of pubis, forming a pubic boot similar to that of Jurassic and Cretaceous averostran theropods (Reig, 1963; Benedetto, 1973; Novas, 1992, 1994). As expected, that condition has been reported in the recently described herrerasaurid *Gnathovorax*. *Tawa* possesses a similarly anteroposteriorly expanded distal end of pubis and this character state is optimized as a synapomorphy of Herrerasauria.

7) Mandibular joint, position significantly posterior to the quadrate head (ch 327 - 0 → 1). The herrerasaurs *Herrerasaurus*, *Gnathovorax* and *Taxa* and several early neotheropods (e.g., '*Syntarsus*', *Dilophosaurus*, *Cryolophosaurus*) share a distinctly posteroventrally slanting quadrate in lateral view, contrasting with the subvertical quadrate of other early dinosauriforms.

8) Scapula, distal end of blade poorly anteroposteriorly expanded, without an increased divergence between the anterior and posterior margins with respect to the rest of the blade (ch 385 - 0 → 1). The widespread and plesiomorphic condition of Archosauria is the presence of an anteroposteriorly expanded, usually fan-shaped, distal end of the scapular blade in lateral view. However, *Herrerasaurus*, *Gnathovorax* and *Tawa* share an unexpanded to very slightly expanded distal end of scapula, a condition convergently developed by early averostrans in the Jurassic (e.g., *Allosaurus*, *Eoabelisaurus*).

9) Metacarpus, metacarpal IV versus metacarpal III lengths ratio less than 0.6 (ch 386 - 0 → 1). Metacarpal IV is proportionally reduced in the autopodium of early neotheropod dinosaurs, but it is still longer than 0.6 times the length of the metacarpal III (with the exception of the coelophysids *Coelophysis* and '*Syntarsus*'). Similarly, a proportionally long metacarpal IV is plesiomorphic for Dinosauria, but this bone is apomorphically reduced (less than 0.6 times the length of metacarpal III) in the herrerasaurs *Herrerasaurus*, *Gnathovorax* and *Tawa*.

10) Manual digits, unguals of digits II–IV length distinctly longer than the last phalanx of the same digit (ch 387 - 0 → 1). The presence of a raptorial manus, with elongated and trenchant unguals is well documented in *Herrerasaurus* (Sereno, 1994). This same condition occurs in *Gnathovorax*, *Tawa*, and a few neotheropods (*Coelophysis* and *Allosaurus* among those scored in this data matrix). As a result, the presence of unguals longer than their respective preceding phalanx is here optimized as a synapomorphy of Herrerasauria.

In our results, the branch supports of Herrerasauria are relatively high, with a Bremer value of 4 and bootstrap frequencies >50%. Similarly, well supported branches are found for Ornithischia, Saurischia, Sauropodomorpha and Theropoda. The branch supports of Herrerasauridae and the *Herrerasaurus* + *Gnathovorax* clade are lower (Bremer value of 2 and bootstrap frequencies >50%), and those of the *Tawa* + *Chindesaurus* + *Daemonosaurus* clade are very low. In addition, the differences between the absolute and GC bootstrap frequencies indicate high amount of contradictory information for Herrerasauria and the *Tawa* + *Chindesaurus* + *Daemonosaurus* clade.

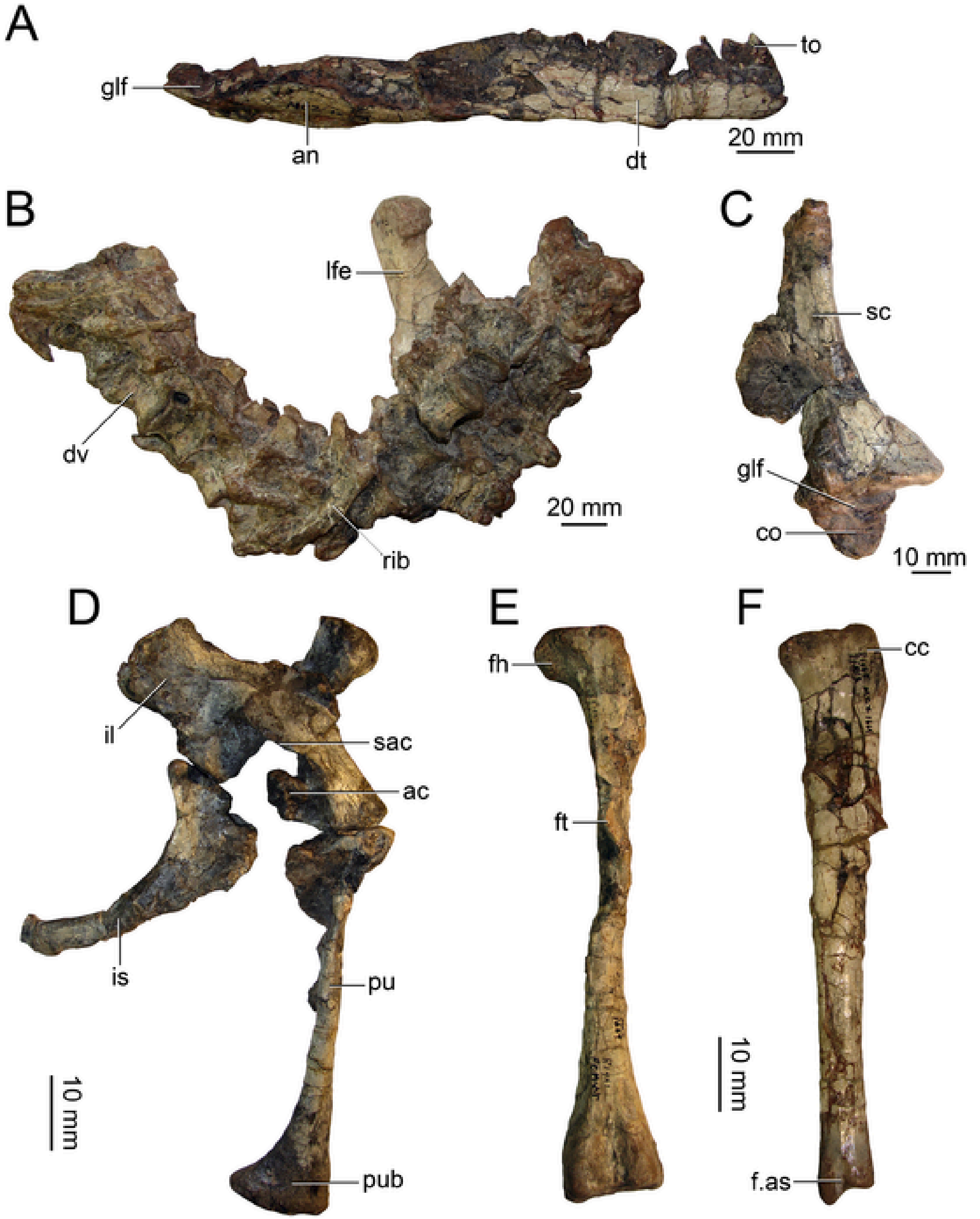

Fig. 8. ***Staurikosaurus pricei*****.** Selected elements of specimen MCZ 1669 (holotype). (A) right hemimandible in lateral view. (B) dorsal vertebrae and ribs, and proximal half of left femur in lateral and posteromedial views, respectively. (C) left scapula and fragment of coracoid in lateral view. (D) right hemipelvis in lateral view; (E) right femur in posterior view; (F) right tibia in lateral view. Abbreviations: ac, acetabulum; an, angular; cc, cnemial crest; co, coracoid; dt, dentary; dv, dorsal vertebra; f.as, facet for astragalus; fh, femoral head; ft, fourth trochanter; glf, glenoid fossa; il, ilium; is, ischium; lfe, left femur; pu, pubis; pub, pubic boot; sac, supraacetabular crest; sc, scapula; to, tooth.

New searches under topological constraints forcing the position of *Tawa* as a theropod (setting *Chindesaurus* and *Daemonosaurus* as floating taxa) found that seven additional steps are necessary to place this species as the sister taxon to the *Eodromaeus* + Neotheropoda clade. In this topology, *Chindesaurus* is recovered as the sister taxon to *Tawa*, and Herrerasauridae and *Daemonosaurus* as the successive earliest branching theropods. Finally, 16 extra steps are required to place herrerasaurids as the sister taxon to Dinosauria. In this latter constrain, *Tawa*, *Daemonosaurus* and *Chindesaurus* were set as floating taxa and have been recovered within a monophyletic Herrerasauria.

Differences among South and North American herrerasaurs - Having discussed the evidence that supports that *Chindesaurus, Tawa, Daemonosaurus* and *"Caseosaurus"* are members of Herrerasauria, there are some character states that unite the North American forms, and separate them from the southern herrerasaurids. The North American herrerasaurs *Daemonosaurus*, *Tawa* and *Chindesaurus* share the following three synapomorphies absent in the South American herrerasaurids: anterior extent of the slot for the quadratojugal at or anterior to the posterior edge of the dorsal process of jugal; anterior to middle cervical vertebrae with diapophysis and parapophysis nearly

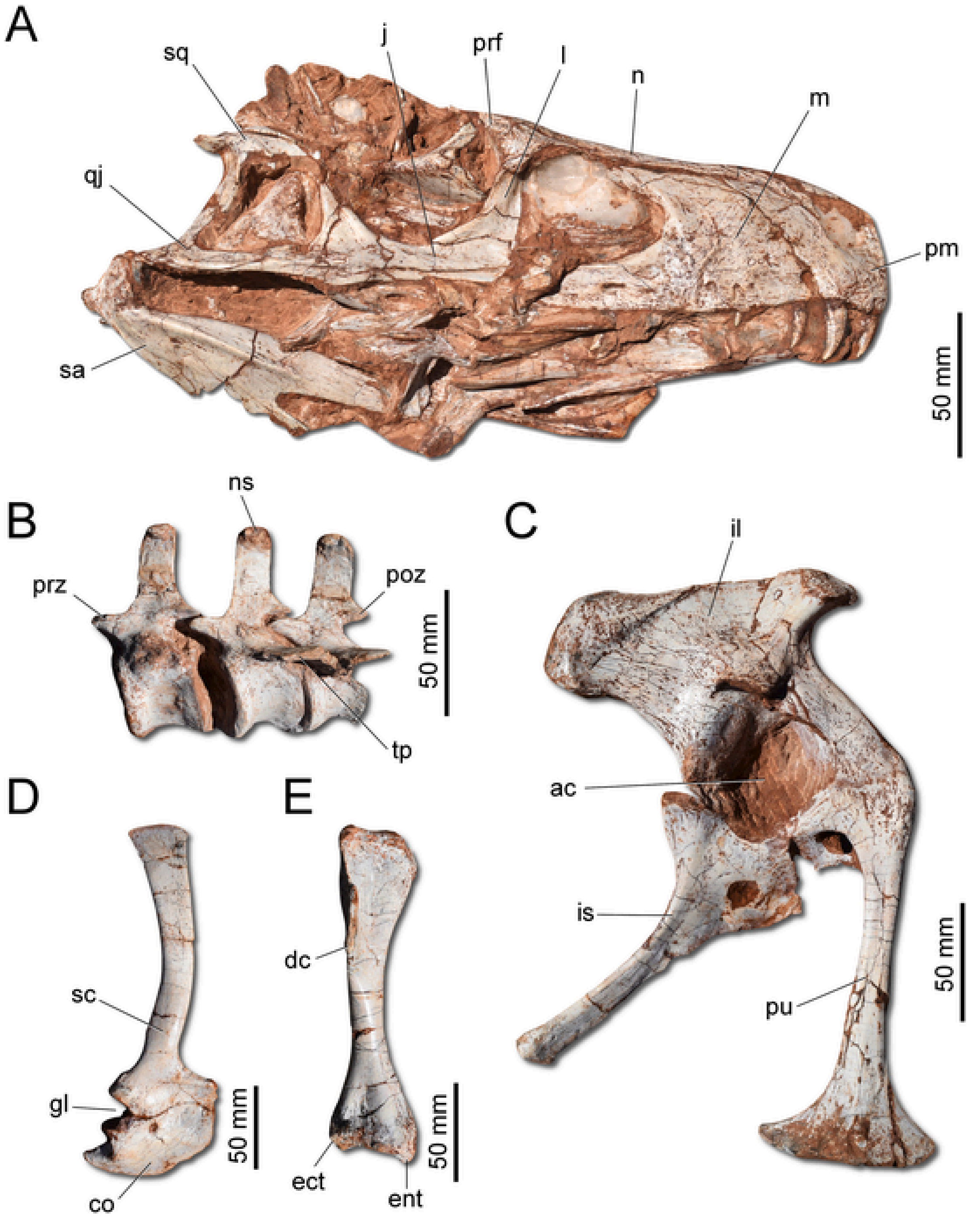

Fig. 9. ***Gnathovorax cabreirai.*** Selected elements of specimen CAPPA/UFSM 0009 (holotype). (A) skull in right lateral view. (B) proximal caudal vertebrae in left lateral view. (C) right pelvic girdle in lateral view. (D) right scapula and coracoid in lateral view. (E) right humerus in anterior view. Abbreviations: ac, acetabulum; co, coracoid; dc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; gl, glenoid; il, ilium; is, ischium; j, jugal; l, lacrimal, m, maxilla; n, nasal; ns, neural spine; pm, premaxilla; poz, postzygapophysis; prf, prefrontal, prz, prezygapophysis; pu, pubis; qj, quadratojugal; sa, surangular; sc, scapula; sq, squamosal; tp, transverse process.

touching; and cervical vertebrae with pneumatic features (= pleurocoels) in the anterior portion of the centrum present as deep fossae.

It is striking to note that these three character states are convergently present (as optimized in our analysis) in neotheropods. This suggests that North American herrerasaurs and neotheropods underwent some degree of convergence, mainly exemplified in the morphology of their cervical vertebrae. On the other hand, the herrerasaurids differ from the North American herrerasaurs in the presence of pubis ventrally or slightly posteroventrally oriented, and tibia with subsquared distal outline (anteroposterior depth to mediolateral width ratio ≥ 0.9).

In particular, *Tawa* shows a number of unique features departing from herrerasaurids. For example, it exhibits a low premaxillary body ventral to the external naris and a long edentulous gap on the posterior end of the premaxilla that are absent in *Herrerasaurus, Gnathovorax* and *Daemonosaurus*. In addition, both *Tawa* and *Daemonosaurus* have a notched premaxilla-maxilla suture on the ventral margin of the rostrum that differs from the straight margin of herrerasaurids (Nesbitt and Sues, 2021). The femur of *Tawa* differs from that of *Herrarasaurus* in several aspects: the fourth trochanter is symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft, and the

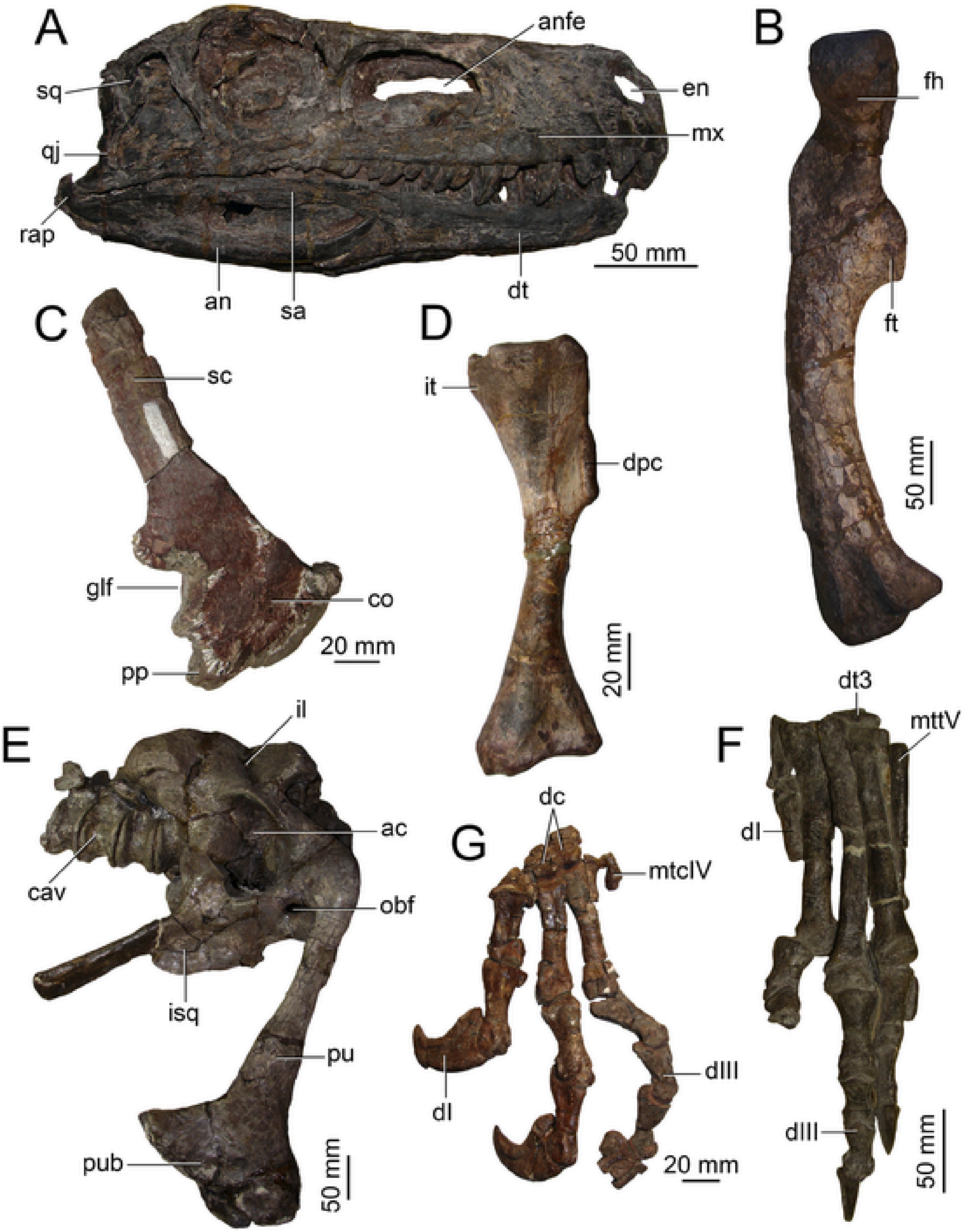

Fig. 10. ***Herrerasaurus ischigualastensis***. Selected elements corresponding to different specimens. (A) skull of PVSJ 407 (referred specimen) in right lateral view. (B) right femur of PVL 2566 (holotype) in anteromedial view. (C) right scapulocoracoid of MCZ 7064 (referred specimen) in lateral view. (D) left humerus of MACN-Pv 18,060 (referred specimen) in anteromedial view; (E) pelvic girdle and anterior caudal vertebrae of PVL 2566 (holotype) in right lateral view; (F) distal tarsal 3 and pes of PVSJ 373 (referred specimen) in dorsal view; (G) left distal carpals and manus of PVSJ 380 (referred specimen in anterior view). Abbreviations: ac, acetabulum; an, angular; anfe, antorbital fenestra; cav, caudal vertebrae; co, coracoid; dI, digit I; dIII, digit III; dc, distal carpals; dpc, deltopectoral crest; dt, dentary; dt3, distal tarsal 3; en, external naris; fe, femur; fh, femoral head; ft, fourth trochanter; glf, glenoid fossa; il, ilium; isq, ischium; it internal trochanter; mtcIV; metacarpal IV; mttV, metatarsal V; mx, maxilla; obt, obturator process; pp, posterior process; pu, pubis; pub, pubic boot; qj, quadratojugal; rap, retroarticular process; sa, surangular; sc, scapula; sq, squamosal.

femur is devoid of the muscle scar on the lateral half of the anterior surface of distal shaft; the distal articular condyles are different in shape and size, and a longitudinal medial crest (and its associated anterior and medial depressions) is present on the distal region of the femur. Whereas in *Herrerasaurus* the tibial condyle is separated from the crista tibiofibularis by a narrow notch, in *Tawa* there is a wide excavation (although this latter condition also applies for *Staurikosaurus*). *Tawa* possesses elongate metatarsals I through V, with metatarsal I notably long, almost equal to metatarsal II. This trait is not recorded in other dinosauriforms, suggesting that it may constitute an autapomorphy of *Tawa*. As mentioned above, the stocky astragalus is a feature shared by *Tawa* and *Chindesaurus* that is absent among herrerasaurids.

6.3. Conclusions on Herrerasauria

In North America, current documentation of herrerasaur fossils come from levels that are younger than those of the currently oldest known neotheropods, *Camposaurus* (*Placerias* Quarry, Chinle Formation) and *Lepidus* (Otis Chalk, Dockum Group). This means that there was a temporal overlap between herrerasaurs and neotheropods up to the end of the Triassic. This is in sharp difference with the South American fossil record, in which Norian beds are so far devoid of herrerasaur remains, but yield different species of neotheropods (e.g., *Zupaysaurus, Powellvenator*, *Lucianovenator*).

The results of our phylogenetic analysis bolster the presence of herrerasaurs outside South America during the Late Triassic (Norian through Rhaetian). Indeed, the presence of herrerasaurs in the Norian beds of the Chinle Formation and Dockum Group of the USA (e.g., Long and Murry, 1995; Irmis et al., 2007; Sarıgül, 2017), and probably in India (ISIR 282; Novas et al., 2011) and Poland (Niedźwiedzki et al., 2014), shows that the group was globally dispersed, contrasting with their apparent South America endemism during the Carnian. As already said, the presence of "*Caseosaurus*" in the late Carnian–early Norian age Tecovas Member suggest that herrerasaurs were already present in North America when those forms still roamed South America.

It has been long recognized that Carnian herrerasaurids present convergent features with neotheropods, especially with Jurassic averostrans (Reig, 1963; Novas, 1994; Sereno, 1994; Sereno and Novas, 1994). For example, the general morphology of the dorsoventrally deep rostrum of herrrerasaurids resembles that of early tetanurans (e.g., *Asfaltovenator*, *Allosaurus*, *Ceratosaurus*), the elongated autopodium with trenchant unguals are similar to those of neotheropods (e.g., *Coelophysis*, *Allosaurus*), and the unexpanded, elongated scapular blade and distal end of pubis developed as a pubic boot also occurs in averostrans (e.g., *Ceratosaurus*, *Allosaurus*). All these features have been interpreted as convergences related to the predation upon medium to large-sized preys (Sereno and Novas, 1994). The evolutionary history of herrerasaurs during the Norian also reveals specializations in the clade that are here optimized as convergences with species of the coeval 'coelophysoid-grade' neotheropod evolutionary radiation, such as the presence of an elongated premaxillary body (*Tawa*), a lower temporal bar formed almost exclusively by the quadratojugal (*Tawa* and *Daemonosaurus*), and pneumatic fossae on the cervical vertebrae (*Tawa*, *Daemonosaurus* and *Chindesaurus*). The evolution of herrerasaurs during the Norian-Rhaetian seems to have increased the number of homoplasies present among Triassic dinosauriforms, which is a pattern also recorded among deeply nested silesaurids (e.g., *Silesaurus*) and early ornithischians and neotheropods (e.g., proximal tibia and ankle morphology) (Nesbitt et al., 2010, 2017a, Baron et al., 2017a). Nevertheless, the post-Carnian evolutionary history of herrerasaurs also resulted in its own specializations, such as the bizarre, short-snouted and large-toothed skull of *Daemonosaurus*, which strikingly differs from the condition in coelophysoids and other early dinosauriforms (Sues et al., 2011). In addition, the recognition of *Daemonosaurus* as a herrerasaurian provides evidence for the first time that this clade survived into the Rhaetian and the group was likely one of the victims of the extinction(s) close to or at the Triassic-Jurassic boundary.

In sum, Herrerasauria was widely geographically distributed, representing a relatively diverse early dinosaur radiation of large-sized predators that prospered mainly before the origin and during the earliest radiation of Neotheropoda. Notably, Marsh et al. (2019: p. 2) concluded that: "the *Chindesaurus* + *Tawa* clade recovered here may represent a potentially diverse group of early theropods prior to the end-Triassic mass extinction". In our view, the triad of North American taxa composed of *Chindesaurus*, *Tawa*, and *Daemonosaurus* are part of Herrerasauria, which –paraphrasing Marsh et al. (2019)– conformed a diverse group of early meat-eating dinosaurs that diversified prior to the end-Triassic mass extinction.

7. Carnian sauropodomorphs

Among Carnian dinosaurs from South America, *Eoraptor, Buriolestes, Panphagia, Pampadromaeus, Saturnalia*, and *Chromogisaurus* are currently considered the earliest branching sauropodomorphs (Langer et al., 1999; Martínez and Alcober, 2009; Ezcurra, 2010; Cabreira et al., 2011; Apaldetti et al., 2013; Otero et al., 2015; Langer et al., 2019; Pretto et al., 2019; Müller, 2020, Fig. 4). Most authors agree in positioning *Buriolestes* and *Eoraptor* outside a clade in which *Panphagia, Pampadromaeus, Saturnalia,* and *Chromogisaurus* are closer to the Norian sauropodomorphs, sometimes joined together in one or more subclades (Cabreira et al., 2016; Langer et al., 2017, 2019, Müller et al., 2018a). A rather common result is the recovery of *Saturnalia* and *Chromogisaurus* as sister-taxa to one another (i.e., Saturnaliidae; Ezcurra, 2010; Martínez et al., 2013b; Langer et al., 2019). The sauropodomorph *Bagualosaurus* comes, together with *Pampadromaeus*, from slightly younger Carnian beds compared to those in which *Buriolestes* and *Saturnalia* were found, and forms with younger sauropodomorphs the clade Bagualosauria (Pretto et al., 2019; Langer et al., 2019; Müller, 2020).

Within such interpretive context, it is worth mentioning that the phylogenetic positions of *Buriolestes* and *Eoraptor* are unstable. Some authors considered *Eoraptor* closer to the remaining sauropodomorphs (e.g., Cabreira et al., 2016; Pacheco et al., 2019; Müller, 2020), whereas others found this taxon as the sister to *Buriolestes* plus the rest of Sauropodomorpha (e.g., Bronzati et al., 2019; Langer et al., 2019). In our analysis, however, *Buriolestes* and *Eoraptor* are found as successive sister taxa of the remaining sauropodomorphs (Figs. 4 and 6).

Below, we review these taxa, discussing the possibility that *Nhandumirim* and *Guaibasaurus* also belong to Sauropodomorpha.

Buriolestes schultzi – *Buriolestes* (Cabreira et al., 2016) is known from two partial skeletons and some fragmentary specimens unearthed from the Buriol site (São João do Polêsine, Rio Grande do Sul, Brazil). One of the specimens (CAPPA/UFSM 0035) preserves a complete skull and partial skeleton, which comprises one of the best-preserved skeletons among the oldest dinosaurs worldwide (Fig. 11; Müller et al., 2018a). The rocks that produced these specimens are part of the Santa Maria Formation (Cabreira et al., 2016; Müller et al., 2018a). *Buriolestes* has been suggested as the sister taxon to all other sauropodomorphs (Cabreira et al., 2016; Müller et al., 2018a; Pacheco et al., 2019; Pretto et al., 2019), the sister taxon to the Saturnaliidae + Bagualosauria clade (Bronzati et al., 2019; Langer et al., 2019), or a saturnaliid (Baron et al., 2017a; Langer et al., 2017; Müller et al., 2018a; Garcia et al., 2019b). This dinosaur differs from coeval sauropodomorphs mainly in the tooth morphology, which lacks omnivorous/herbivorous specialization (Cabreira et al., 2016).

Despite its sharp and blade-like teeth, *Buriolestes* has been consistently recovered as a sauropodomorph (Cabreira et al., 2016; Langer et al., 2017, 2019; Cau, 2018; Müller et al., 2018a; Pacheco et al., 2019). The phylogenetic affinities with the clade are generally supported by the ventrally inclined dorsal surface of the anterior tip of the dentary, mandibular glenoid located ventral relative to the dorsal margin of the dentary, absence of pneumatic features on the cervical vertebrae, neural arch of the cervical vertebrae higher than the posterior articular facet of the centrum, asymmetrical fourth trochanter of the femur, and fibular condyle of the tibia offset anteriorly from the medial condyle (Cabreira et al., 2016; Müller et al., 2018a). However, most of these traits are variably spread among ornithischians, herrerasaurids, and non-dinosaurian dinosauriforms. For instance, the low mandibular articulation is present in ornithischians, pneumatic features are absent in several non-theropod dinosaurs, and the asymmetrical fourth trochanter is recorded in herrerasaurids and ornithischians. Therefore, the ventrally bent dorsal margin of the dentary tip is the only character that is shared solely by *Buriolestes* and other sauropodomorphs (Cabreira et al., 2016; Müller et al., 2018a,c). Also, the skeleton of this

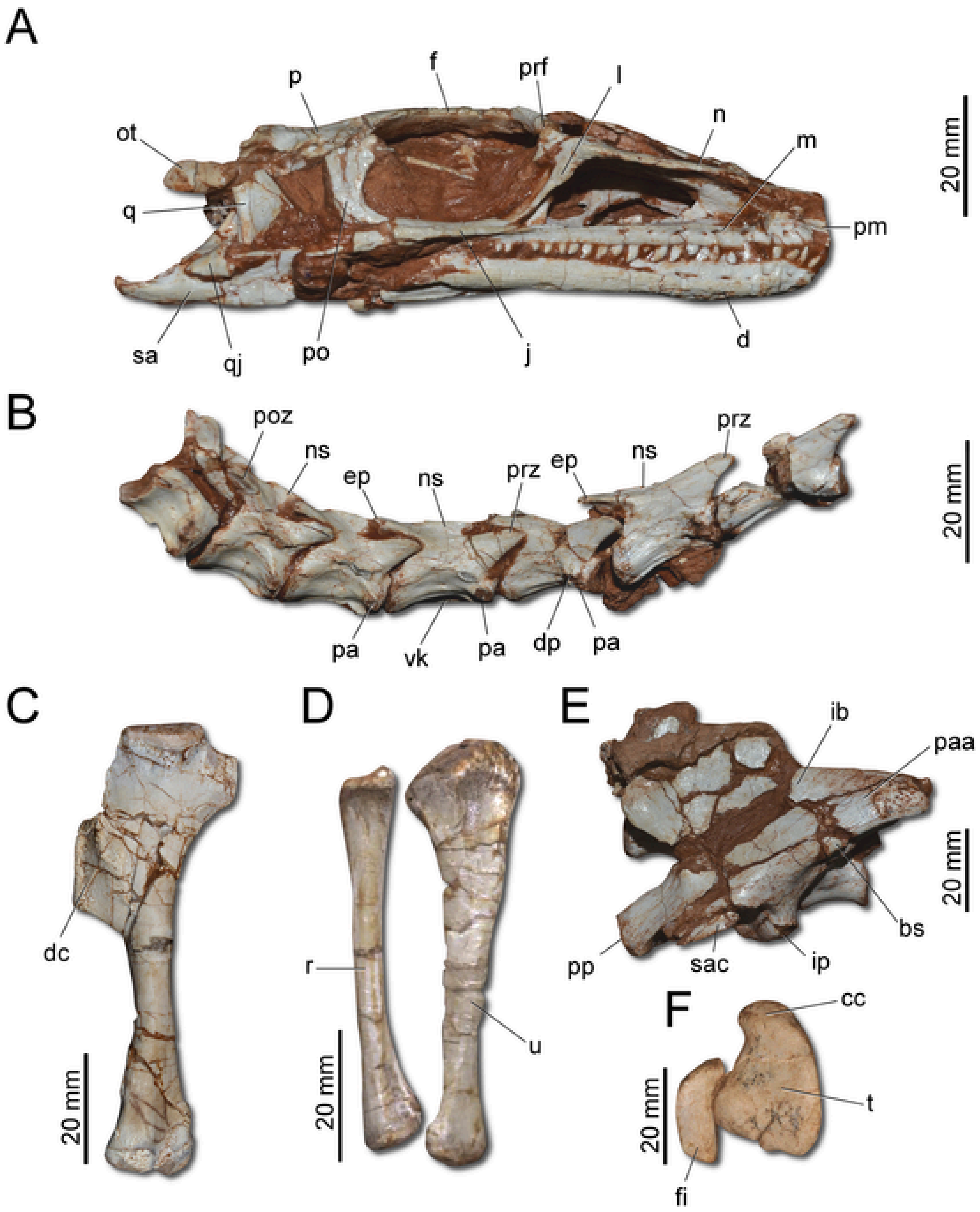

Fig. 11. ***Buriolestes schultzi***. Selected elements corresponding to different specimens. (A) skull of CAPPA/UFSM 0035 in right lateral view. (B) postaxial cervical vertebrae and ribs of CAPPA/UFSM 0035 in right lateral view. (C) left humerus of ULBRA- PVT280 in posterolateral view. (D) left radius and ulna of ULBRA-PVT280 in anterior view. (E) left ilium of CAPPA/UFSM 0035 in lateral view. (F) left tibia and fibula of ULBRA-PVT280 in proximal view. Abbreviations: bs, brevis shelf; cc, cnemial crest; d, dentary; dc, deltopectoral crest; dp, diapophysis; ep, epipophysis; f, frontal; fi, fibula; ib, iliac blade; ip, ischiadic peduncle; j, jugal; l, lacrimal; m, maxilla; n, nasal; ns, neural spine; ot, otoccipital; p, parietal; pa, parapophysis; pm, premaxilla; poz, postzygapophysis; pp, pubic peduncle; prf, prefrontal; prz, prezygapophysis; q, quadrate; qj, quadratojugal; r, radius; sa, surangular; sac, supracetabular crest; t, tibia; u, ulna; vk, ventral keel.

dinosaur bears some unusual traits among coeval sauropodomorphs, which include a short external naris, a gap between the premaxilla and maxilla articulation, a deltopectoral crest that is less than 43% the length of the humerus, the pubis not contacting its counterpart at the distal edge, and the presence of a posterior projection of the medial condyle of the tibia. Most of these conditions are plesiomorphies for sauropodomorphs. A morphological disparity analysis failed to find *Buriolestes* closer to the theropod morphospace in distinct partitions of the skeleton (Müller et al., 2018a).

Additional sauropodomorph characteristics present in *Buriolestes* include teeth with marked distinction between root and crown, and presence of a ridge on their outer surface. Besides, the ulna of *Buriolestes* is distally expanded, a condition contrasting with that of silesaurids, herrerasaurids, and most neotheropods, in which the distal end of that bone is more cylindrical and less expanded. Although the distal ulnar expansion in *Buriolestes* is similar to that of *Plateosaurus*, it is absent in Carnian sauropodomorphs such as *Eoraptor* and *Pampadromaeus* (the condition is unknown in *Saturnalia* as the preserved ulnae lack the distal end).

Plesiomorphic features present in *Buriolestes*, shared with other early dinosaurs but absent in other sauropodomorphs are identified in the skull, dentition, and postcranium. *Buriolestes* retained a plesiomorphically large skull, representing approximately 80% of the length of the femur, as in *Silesaurus* (82%), *Asilisaurus* (estimated in 83%), *Heterodontosaurus* (100%), *Eodromaeus* (85%), *Pampadromaeus* (estimated in 86%), *Eoraptor* (81%), *Gnathovorax* (91%), and *Eocursor* (73%; Butler et al., 2007). In contrast, the skull is about to 60–70% of the femur length in *Saturnalia* (Bronzati et al., 2019). *Buriolestes* also exhibits proportionally small external nares, as in herrerasaurids. The supraoccipital of *Buriolestes* is wider than tall, with an "M"-shaped dorsal contour and a pair of notches flanking the medial eminence of the bone, as in *Silesaurus*, *Saturnalia* and *Thecodontosaurus*.

The teeth of *Buriolestes* are plesiomorphically curved, transversely compressed, and serrated. Premaxillary teeth in *Buriolestes* bear serrations on the distal edge. In contrast, in *Coelophysis* and *Syntarsus* premaxillary teeth lack serrations (Colbert, 1989), whereas in *Eoraptor* and *Pampadromaeus* the premaxillary teeth are serrated. Anterior maxillary teeth have crown and root separated by a constriction, thus being similar to the condition in *Eoraptor, Bagualosaurus,* and *Panphagia*. Also, the teeth of *Buriolestes* resemble those of *Eoraptor* in having a longitudinal bulge on its labial surface. Maxillary teeth count is about to 24, similar to that of *Coelophysis*, thus clearly surpassing the tooth number of other early dinosauriforms. *Buriolestes* has pterygoid teeth, as in *Eoraptor* and *Pampadromaeus*, but also in *Eodromaeus*. Regarding the postcranium, *Buriolestes* retained cervical vertebrae with strongly developed longitudinal crests on the ventral surface of the centrum, as in *Panphagia* and *Herrerasaurus*. Mid-to distal caudal vertebrae are low and elongate, as in *Lagosuchus, Silesaurus,* and *Herrerasaurus*, but different from the shorter and deeper condition present in *Eoraptor* and Norian sauropodomorphs. The caudal series of one of the specimens include 27 mid-distal elements that probably correspond to the sector between caudal vertebrae 20 to 47 (assuming a total of 50 caudal vertebrae). If this counting is correct, the neural spine gets very low and the transverse processes reduce between caudal vertebrae 20 and 25. Yet, as the series is not complete, it is not possible to recognize the features of any particular clade. When compared to *Plateosaurus* (von Huene, 1926), the caudal vertebra 27 of *Buriolestes* is lower and longer, and the prezygapophyses are horizontal, whereas in *Plateosaurus* those elements project anterodorsally until caudal vertebra 39. The same applies to the postzygapophysis, which has a high position and is separated from the vertebral body. Likewise, the distal caudal vertebrae of *Buriolestes* resemble those of *Silesaurus* in terms of lengthening of the center and the strong reduction or absence of neural spines in the elements interpreted here as caudal vertebrae 20–25. Transverse processes disappear in *Silesaurus* after caudal vertebra 24, and this seems to be also the case for *Buriolestes*. An important difference is the presence in *Silesaurus* of elongated prezygapophyses around caudal vertebrae 27, as also occurs in *Herrerasaurus*. It is notable that caudal vertebra 20 of *Lagosuchus* (Sereno and Arcucci, 1994a) is already very elongated and devoid of a neural spine and transverse processes, unlike *Silesaurus, Herrerasaurus*, and *Buriolestes*.

The scapular blade of *Buriolestes* is much wider than in *Silesaurus, Tawa, Eodromeus,* and *Herrerasaurus*, thus resembling those of *Eoraptor* and *Panphagia*. Medially, it exhibits a notable longitudinal buttress reminiscent of that seen in *Eodromaeus* and *Herrerasaurus*. The humerus of *Buriolestes* has poorly transversely expanded proximal and distal ends, as in *Herrerasaurus* (MACN-Pv, 18,060), but different from the more expanded ends of the humerus of *Saturnalia*. In *Buriolestes*, the humerus is longer than 60% the length of the femur, and the deltopectoral crest is 40% of the humeral length, conditions that Cabreira et al. (2016) interpreted as typical of sauropodomorphs. Although the former ratio is common among early sauropodomorphs (e.g., *Pampadromaeus*, estimated in 74% by Langer et al., 2019), a humerus longer than 60% the length of femur is also seen in *Heterodontosaurus* (74%), *Lesothosaurus* (64%; Baron et al., 2017c), *Eocursor* (approximately 68%; Butler et al., 2007), *Lagosuchus* (63%), *Silesaurus* (64%), and *Asilisaurus* (62%). Notably, it is 56% in *Eoraptor*. Regarding the proximodistal extension of the deltopectoral crest, that of *Buriolestes* is similar to the condition in *Coelophysis* (39%; Colbert, 1989), *Heterodontosaurus* (40%), *Leosothosaurus* (34%; Baron et al., 2017c), *Eodromaeus* (37%), *Herrerasaurus* (40%), *Eoraptor* (35%), and *Eocursor* (35%).

In the ilium of *Buriolestes*, the medial wall of the acetabulum is poorly perforated (as in *Bagualosaurus*, *Saturnalia*, and *Pampadromaeus*). The postacetabular blade is similar to that of other early dinosaurs, especially saturnaliids, being elongated, with squared posterior portion and laterally ornamented by muscle scars. In ventral view, it can be seen that the supraacetabular crest of *Buriolestes* is more convex and laterally projected compared with those of *Lewisuchus, Panphagia,* and *Eoraptor*, in which that crest is more elongated and the acetabular roof has an elliptical contour. As for the semicircular contour of the acetabular roof, *Buriolestes* shares this condition with *Silesaurus, Herrerasaurus*, *Saturnalia*, *Megapnosaurus*, and *Liliensternus*. Thus, the anteroposteriorly short and laterally expanded supraacetabular crest could be interpreted as a plesiomorphic condition of *Buriolestes*.

Each of the hindlimb bones of *Buriolestes*, especially the femur, is notably similar to those in herrerasaurids and coeval sauropodomorphs. The tibia exhibits a very low fibular crest closely resembling the condition of *Eoraptor* (Sereno et al., 2013), but the fibular crest of *Silesaurus* and neotheropods is much better developed. In *Chromogisaurus* and *Saturnalia*, this area is marked by a strong rugosity (Langer, 2003; Ezcurra, 2010). The distal end of the tibial shaft bears a sharp posteromedial edge, which clearly separates both the medial and posterior faces, forming a square-shaped cross section. At its posterolateral edge, there is a defined longitudinal ridge that was probably located behind the distal end of the fibula. The tibia of *Eoraptor, Panphagia*, and *Herrerasaurus* also have a distal end with a quadrangular contour, with ridges and edges similar in position to those of *Buriolestes*, although less marked. In *Buriolestes*, the fibula has the distal end similar to that of *Herrerasaurus*. As in the latter taxon, it is only slightly narrower than the distal end of the tibia. The astragalus of *Buriolestes* is block-like, similar to those of *Herrerasaurus, Eoraptor*, and *Panphagia*, with a trapezoid-shaped medial surface, proximodistally deep, and with a straight dorsal margin, different from early core-sauropodomorphs and neotheropods, in which this margin is concave.

Features present in *Buriolestes* that are unlike those of silesaurids, herrerasaurids, and *Lesothosaurus*, approaching the eusaurischian condition are: 1) postnarial process of the premaxilla projected horizontally backwards, as in *Pampadromaeus, Macrocollum, Coelophysis* (Sereno, 2012, Fig. 98A), and *Notatesseraeraptor*, unlike *Herrerasaurus, Eodromaeus, Daemonosaurus, Lesothosaurus*, and *Silesaurus*, in which the latter is dorsally tilted, flanking the nostril from behind; 2) antorbital fossa very broad anteroposteriorly (as in most dinosaurs, *Lesothosaurus* included, but unlike herrerasaurs, which retain the plesiomorphic condition); 3) maxilla possesses a longitudinal rim along the ventral margin of the antorbital fossa as in *Lewisuchus, Eoraptor*, and *Coelophysis*; 4) lacrimal with a ventral ramus dorsoventrally taller than in *Herrerasaurus* and *Lesothosaurus*; 5) jugal excluded from the antorbital fenestra, unlike herrerasaurids and *Silesaurus*, but similar to remaining dinosaurs; 6) sacrum composed of three vertebrae; 7) pubic peduncle of ilium with an anteriorly oriented articular surface, as in *Eoraptor* and *Liliensternus,* whereas it is more ventrally oriented in other early dinosaurs; 8) distal articular condyles of femur globose, as in *Eoraptor, Saturnalia, Coelophysis*, and *Liliensternus*, being different from the more flattened condition seen in herrerasaurids and *Silesaurus*.

Buriolestes exhibits the following features indicating that it is not a neotheropod: 1) articulation between quadratojugal and jugal posteriorly displaced from the ascending ramus of the jugal, as in *Eoraptor* and other early dinosaurs, but different from *Daemonosaurus*, *Tawa* and neotheropods; 2) vertebral column composed of nine cervical, 15 dorsal, and three sacral vertebrae; and 3) the longest cervical vertebrae are the third and fourth, as in *Eoraptor*. In *Pantydraco* (Galton and Kermack, 2010) the longest cervical vertebra is the fifth. In other Norian sauropodomorphs the neck becomes proportionally two times longer in comparison to that of *Buriolestes* (Müller et al., 2018a). In contrast, a tall preacetabular process in *Buriolestes* resembles those of neotheropods, as is the case in the even deeper preacetabular blade of *Coelophysis* and *Dilophosaurus*. Martínez et al. (2011) indicated that *Eodromaeus* exhibits a tall preacetabular blade, as in *Buriolestes*. Also interesting is that the preacetabular process of *Buriolestes* is wider and with a clear differentiation from the medial surface of the ilium, more than in other early dinosaurs.

Müller et al. (2018a) show that disparity morphological analyses fail to place *Buriolestes* in an area occupied by theropods, suggesting that its skeleton is not marked by a mosaic of theropod and sauropodomorph traits. As Cabreira et al. (2016) pointed out, there are several features distinguishing *Buriolestes* from sauropodomorphs, including a proportionally large skull, with an elongate rostrum, armed with curved and transversely compressed blade-like teeth. Under the current phylogenetic context, the most supported hypothesis is that *Buriolestes* represents one of the earliest diverging, perhaps the earliest diverging, sauropodomorphs. Despite the fact that the almost whole skeleton of *Buriolestes* is known, there are no complete manus, which hosts important sauropodomorph traits (Martínez et al., 2011). Therefore, additional specimens with this anatomical region preserved are still necessary in order to further scrutinize the phylogenetic affinities of this dinosaur.

Eoraptor lunensis - in the original description, *Eoraptor* (Fig. 12) was allied with Theropoda mainly because of the 'tridactyl, grasping hand' (Sereno et al., 1993). More than two decades later, the phylogenetic affinities of *Eoraptor* are still controversial (Langer, 2014). In the years following the original description, several studies agreed with its theropod affinity (e.g., Novas, 1994; Tykoski, 2005; Nesbitt et al., 2009), whereas others suggested a position outside the Theropoda-Sauropodomorpha split (Langer, 2004; Langer and Benton, 2006; Martínez and Alcober, 2009; Martínez et al., 2013a; Otero and Pol, 2013). However, the discovery of the putative theropod *Eodromaeus murphi* (Martínez et al., 2011) lead to a new interpretation of the phylogenetic affinities of *Eoraptor*. The description of *Eodromaeus*, also from the Ischigualasto Formation, revealed anatomical traits shared with theropods, which are absent in *Eoraptor* (Martínez et al., 2011). Moreover, new interpretations and discoveries improved the knowledge on the anatomy of *Eoraptor*

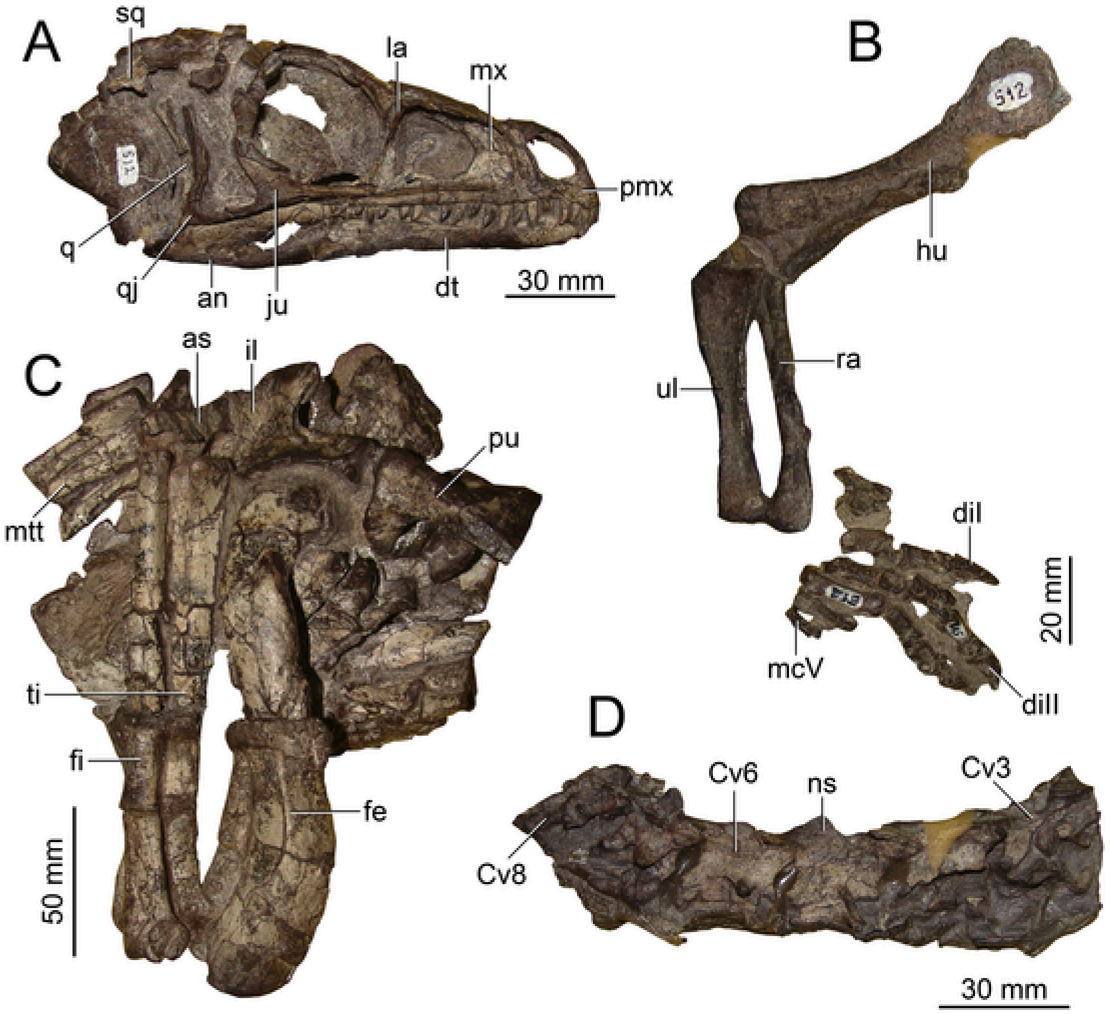

Fig. 12. ***Eoraptor lunensis***. Selected elements of specimen PVSJ 512 (holotype). (A) skull in right lateral view. (B) left humerus, ulna and radius, and right manus in anterior views. (C) right hemipelvis and hindlimb in mainly lateral view. (D) cervical vertebrae 3–8 in right lateral view. Abbreviations: an, angular; as, astragalus; Cv3; cervical vertebra 3; Cv6; cervical vertebra 6; Cv8; cervical vertebra 8; diI, manual digit I; diII, manual digit II; dpc, deltopectoral crest; dt, dentary; fe, femur; fi, fibula; hu, humerus; il, ilium; ju, jugal; la, lacrimal; mcV; metacarpal V; mtt, metatarsus; mx, maxilla; ns, neural spine; pmx, premaxilla; pu, pubis; q, quadrate; qj, quadratojugal; ra, radius; sq, squamosal; ti, tibia; ul, ulna.

(Sereno et al., 2013). This combination of factors, lead Martínez et al. (2011) to suggest that *Eoraptor* was a sauropodomorph dinosaur.

Martínez et al. (2011), Sereno et al. (2013), and Müller et al. (2018a) nested *Eoraptor* within Sauropodomorpha on the basis of derived features that include: medially rotated manual phalanx I-1, with the ungual phalanx internally oriented; lower jaw tooth series shorter than the maxillary tooth series; vertebrae from the posterior half of the tail notably shortened; large narial aperture; elongate ventral process of squamosal; first dentary tooth not reaching the anterior margin of the dentary; and ventrally inclined dorsal surface of the anterior tip of the dentary. The history of the phylogenetic affinities of *Eoraptor* has been complicated by the presence of rampant homoplasy among early dinosauriforms (Nesbitt, 2011; Sereno et al., 2013; Baron et al., 2017a; Langer et al., 2017).

Eoraptor has maxillary and dentary tooth crowns that are labiolingually expanded in distal/mesial view and have few denticles per millimeter. This is shared with sauropodomorphs, contrasting with the blade-like morphology present in faunivorous forms, such as *Lewisuchus*, *Tawa*, *Coelophysis*, and *Buriolestes* (Müller et al., 2018a; Ezcurra et al., 2020b). Vertebrae belonging to the distal half of the tail are elongate in *Lagosuchus*, *Silesaurus*, Herrerasauridae, and *Buriolestes*, but not in *Eoraptor* and other more deeply nested sauropodomorphs.

Martínez et al. (2011) recognized a medially rotated manual phalanx I-1 in an angle of 35° or more as a feature uniting *Eoraptor* and Sauropodomorpha, differing from the condition observed in theropods and *Eodromaeus*. A twisted phalanx I-1 is traditionally considered typical of Sauropodomorpha (Gauthier, 1986; Sereno, 2007b), but it was regarded by Galton (1977) as present in most saurischians. In *Herrerasaurus* (Sereno, 1994), the distal end of phalanx I-1 rotates 15° with respect to the proximal end, in an opposite direction as compared with that of its respective metacarpal. In *Heterodontosaurus* (Sereno, 2012; Galton, 2014) phalanx I-1 has a slight torsion on its longitudinal axis, as in other dinosaurs: *Chilesaurus, Herrerasaurus*, and neotheropods. Thus, a slight phalangeal twisting seems to be diagnostic of one of the earliest clades within Avemetatarsalia or even Dinosauria, whereas a stronger twisting (> 35°) seems to be exclusive to *Eoraptor* and sauropodomorphs among early dinosaurs. In contrast, *Eoraptor* shows some character states that are present in neotheropods or sauropodomorphs. For example, the manual unguals of *Eoraptor* are proportionally shorter than those of *Herrerasaurus*, *Tawa*, *Heterodontosaurus,* and early sauropodomorphs (e.g., *Efraasia*).

Eoraptor shares with *Buriolestes* and other non-bagualosaurian sauropodomorphs a very similar morphology of the pelvic girdle, especially in the ilium. In agreement with the analysis of Martínez et al. (2011), this is consistent with the position of *Eoraptor* among sauropodomorphs, but the affinities within the clade are at first hand far from evident. For example, it seems clear that *Saturnalia* and *Chromogisaurus* are closer to one another than to *Eoraptor* because of the presence of an ulna with an extremely enlarged olecranon process with a strongly striated posterolateral surface (see below for discussion of the proximal end of the ulna), iliac postacetabular process with a pointed posteroventral corner and a rounded posterodorsal margin, and a strong and anterodorsally tapering trapezoidal rugosity for the origin of the *Mm. flexor tibialis* and *iliotibialis* (Ezcurra, 2010). However, the diversity of phylogenetic results recovered in recent years shows that the position of *Eoraptor* within Sauropodomorpha is still controversial. For instance, the taxon has been considered the sister group of all other sauropodomorphs (McPhee and Choiniere, 2018; Bronzati et al., 2019; Langer et al., 2019); the sister group of all other Saturnaliidae (Langer et al., 2017), or the sister group of all other sauropodomorphs expect for *Buriolestes* (Cabreira et al., 2016; Pacheco et al., 2019; Müller, 2020). In addition, despite the large number of studies favoring sauropodomorph affinities, other recent analyses still ally *Eoraptor* to Theropoda (Baron et al., 2017a; Nesbitt et al., 2017a; Sarıgül et al., 2018; Martz and Small, 2019). This latter position generally relies on the raptorial arm, composed of a short humerus associated with a long manus with reduced outer digits (Langer, 2014). However, no other coeval sauropodomorph preserves a complete hand. Furthermore, studies that favor theropod affinities generally do not include the complete set of currently known Carnian sauropodomorphs. This is also true for analyses were *Eoraptor* nests as a saurischian outside the Theropoda-Sauropodomorpha dichotomy (= Eusaurischia). Indeed, *Eoraptor* has plesiomorphies absent in Eusaurischia, such as a long postnarial process of the premaxilla and short posterior cervical vertebrae (Langer, 2004). The long postnarial process is unusual compared to other early sauropodomorphs. On the other hand, a recently described specimen referred to *Buriolestes* (CAPPA/UFSM 0035) preserves the entire cervical series, which shares the short posterior vertebrae of *Eoraptor*. So, both, a position outside Eusaurischia or inside Theropoda seems unlikely for *Eoraptor* under the current scenario.

Saturnalia tupiniquim – this taxon was named by Langer et al. (1999), based on three partially preserved skeletons from the upper part of Santa Maria Formation, Rio Grande do Sul, Brazil (Langer et al. 1999, 2007; Langer, 2003; Bronzati et al., 2017, 2018, 2019). It comes from the *Hyperodapedon* Acme Zone (ca. 233 ma; Langer et al., 2018), along with *Buriolestes, Nhandumirim*, *Staurikosaurus*, and *Gnathovorax*. *Saturnalia* was the first sauropodomorph recognized from the Carnian (Langer et al., 1999, Fig. 13) and its phylogenetic position within the clade has been stable in most subsequent analyses (e.g., Langer, 2004; Langer and Benton, 2006; Martínez and Alcober, 2009; Ezcurra, 2010; Martínez et al., 2013a; Otero and Pol, 2013; Cabreira et al., 2016; Müller et al., 2018a). Detailed descriptions of the available cranial material (Bronzati et al., 2017, 2019); pectoral girdle and forelimb (Langer et al., 2007), and sacral vertebrae, pelvic girdle, and hindlimb (Langer, 2003) are available, but a comprehensive description of the vertebral column and comparison between the three known specimens is still lacking.

Recent studies of the cranial material and endocast (Bronzati et al., 2017, 2019) allowed the estimation of a reduced skull length for *Saturnalia*, about two thirds of the femoral length, a ratio that is shared only by bagualosaurian sauropomorphs. An efficient predatory feeding behaviour, including fast movements of the head in order to capture small prey, such as insects or small vertebrates, was suggested by information from the brain endocast, including a relatively large floccular lobe of the cerebellum, and by the morphology of the teeth, which retain presiomorphic features typical of faunivorous taxa (e.g., *Buriolestes*, *Herrerasaurus*, *Coelophysis*). The maxilla of *Saturnalia* has a long and thin posterior ramus extending below the antorbital fenestra, with about ten tooth positions. The frontals are broader posteriorly and form the skull roof between the orbits. The parietals are not co-ossified and bear long posterolateral processes. The lacrimal is 'L-shaped', with a shorter anterior ramus and a subvertical ventral ramus, which forms about three-quarters of the preorbital height and is markedly expanded in its ventral portion. The antorbital fossa excavates the entire lacrimal, but is more expanded at its ventral portion. The squamosal has a slender ventral ramus that is narrower than a quarter of its length, as typical of Sauropodomorpha. The braincase of *Saturnalia* has a semilunar depression on the lateral face of the parabasisphenoid, the ventral margin of the occipital condyle is placed dorsal to the ventral margin of the cultriform process of the parabasisphenoid, the preotic pendant is poorly developed, and the basipterygoid processes are anteriorly oriented. The dentary is elongate and its anterior tip not ventrally curved. The entire tooth series of the dentary is composed of over ten 'leaf-shaped' elements, which are more slender towards the anterior tip of the bone. The crowns are latermedially flattened and the carina bear about ten denticles per millimeter, unlike the coarser denticles of most sauropodomorphs.

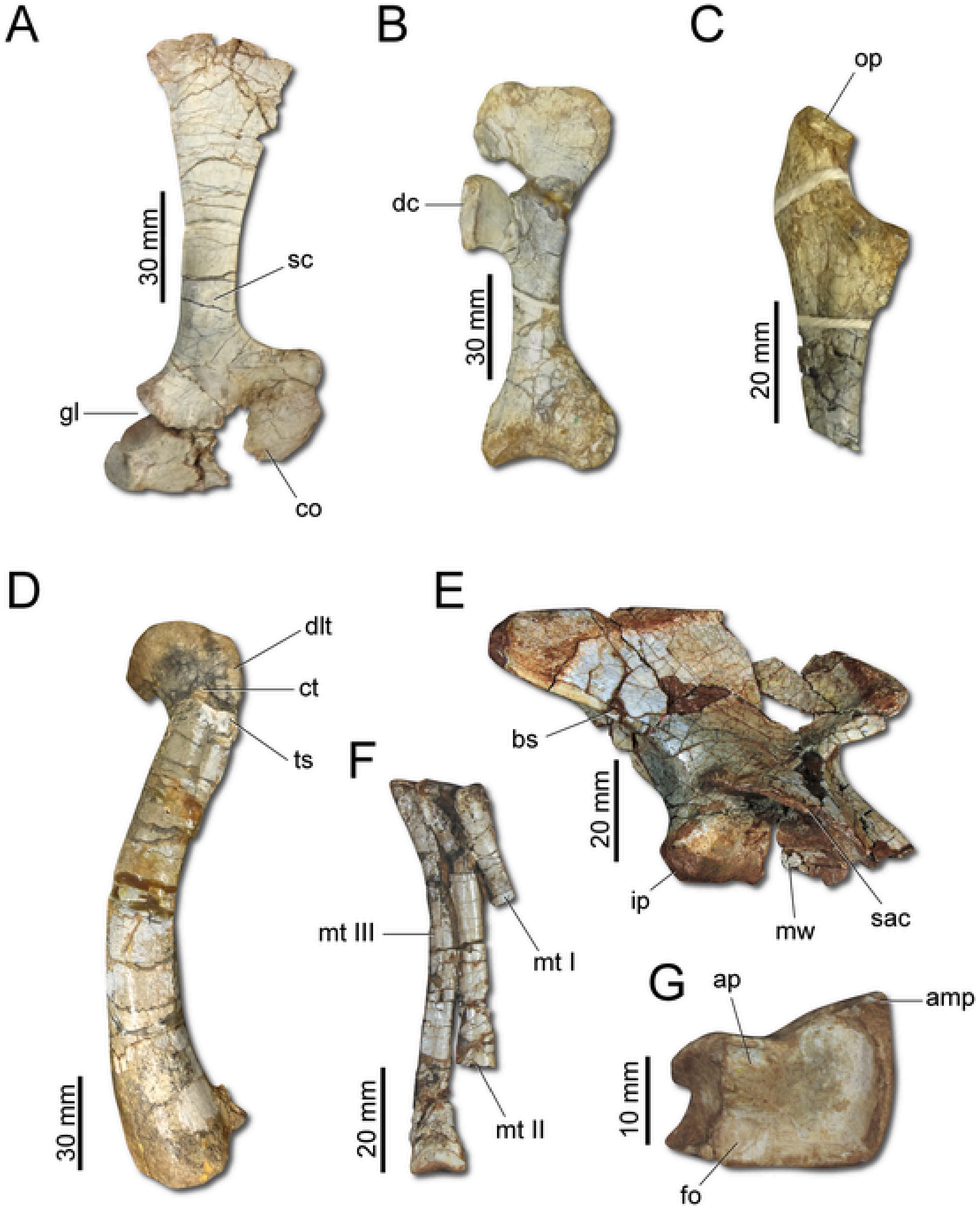

Fig. 13. ***Saturnalia tupiniquim***. Selected elements corresponding to different specimens. (A) right scapula and coracoid of MCP 3845-PV in lateral view. (B) right humerus of MCP 3845-PV in anterior view. (C) right ulna of MCP 3845-PV in lateral view. (D) left femur of MCP 3845-PV in lateral view. (E) right ilium of MCP 3846-PV in lateral view. (F) right metatarsals of MCP 3845-PV in anterior view. (G) left astragalus of MCP 3846-PV in proximal view. Abbreviations: amp, anteromedial process; ap, ascending process; bs, brevis shelf; co, coronoid; ct, anterior trochanter; dc, deltopectoral crest; dlt, dorsolateral trochanter; fo, fossa; gl, glenoid; ip, ischiadic peduncle; mt, metatarsal; mw, medial wall; op, olecranon process; sac, supracetabular crest; sc, scapula; ts, trochanteric shelf.

Saturnalia has ten cervical vertebrae, but the atlas–axis complex is unknown. Cervical vertebrae 3–9 are longer than the anterior trunk vertebrae, but the tenth element is subequal to those in length and is considered equivalent to the first trunk vertebra described for *Buriolestes* (Müller et al., 2018a). All cervical vertebrae have low neural spines and ventrally keeled centra. There are 14 trunk vertebrae, the neural spines of which are deeper and more robust than those of the cervical series. The three anteriormost elements are shorter than the mid-cervical vertebrae, but more posterior trunk vertebrae are longer and subequal to mid-cervical elements. Only the two anterior-most trunk centra have ventral keels, but hyposphene–hypantrum auxiliary articulations are seen through the series. The diapophyses bear strong laminae, forming well-developed anterior, ventral and posterior fossae. The holotype of *Saturnalia* has the two primordial sacral vertebrae of archosaurs forming most of the sacral articulation, but an element from the caudal series has the transverse process articulating to the ilium. On the other hand, the paratype MCP 3845-PV has a trunk element incorporated into the sacrum (Marsola et al., 2019a). Posterior trunk vertebrae and proximal caudal vertebrae show no signs of axial shortening, whereas vertebrae from the distal part of the tail have typically short prezygapophyses.

The pectoral girdle of *Saturnalia* (Langer et al., 2007) has scapula and coracoid attached in an immovable articulation. The angle between acromion and the scapular blade varies from less than 90° to about 115° among specimens. The more robust posterior portion of the body of the scapula includes a glenoid, forming an angle of ca. 45° to the bone long axis. The scapular blade gradually expands dorsally and the coracoid is ovoid in shape and medially concave. The coracoid is thicker posteriorly, where there is a well-developed posterior process. The humerus has a well-developed deltopectoral crest, separated from the proximal margin of the bone, that extends for about 45% of the humerus length. The transverse width of the distal articulation corresponds to about 35% of the length of the bone. Both of these latter features are typical of sauromopodomorph dinosaurs (Sereno, 1999). The radius is about 60% the humeral length. The ulna of *Saturnalia* has a very long olecranon process, with a heavily striated posterior surface, as also seen in *Chromogisaurus*.

As for the pelvic girdle and limb (Langer, 2003), the ilium of *Saturnalia* has an expanded medial acetabular wall with a straight ventral margin. The preacetabular process is pointed, whereas the postacetabular process is well developed and bears an expanded brevis shelf. The pubis has a deep ischio-acetabular groove and a laminar medial portion. The ischium has a large antitrochanter, which occupies the entire acetabular incisure of that bone. The femur is sigmoid, with a semi-pendant fourth trochanter and variably developed anterior and dorsolateral trochanters among specimens. The tibia is straight, with a well-developed cnemial crest. The distal end of the bone has various degrees of lateromedial expansion among specimens. The descending process does not distinctly expand laterally to cover the fibula. The astragalus is lateromedially expanded, with a clear lateral basin for the reception of the fibula, differing from the more restricted facet in most sauropodomorphs. Distal tarsal 3 and 4 are known, and the elongated metatarsals have the typical pattern of early dinosaurs. The pedal phalangeal formula is ?-3-4-5-0 for MCN PV 3855.

Chromogisaurus novasi - this taxon was named by Ezcurra (2010) based on a partially preserved skeleton coming from the Cancha de Bochas Member, Ischigualasto Formation (Ezcurra, 2010; Martínez et al., 2013a,b; Fig. 14), from approximately the same levels and a nearby locality as *Panphagia protos* (Ezcurra, 2010; Martínez et al., 2013a,b).

The proximal end of the ulna of *Chromogisaurus* was recently reinterpreted as the posterior region of a rhynchosaur hemimandible

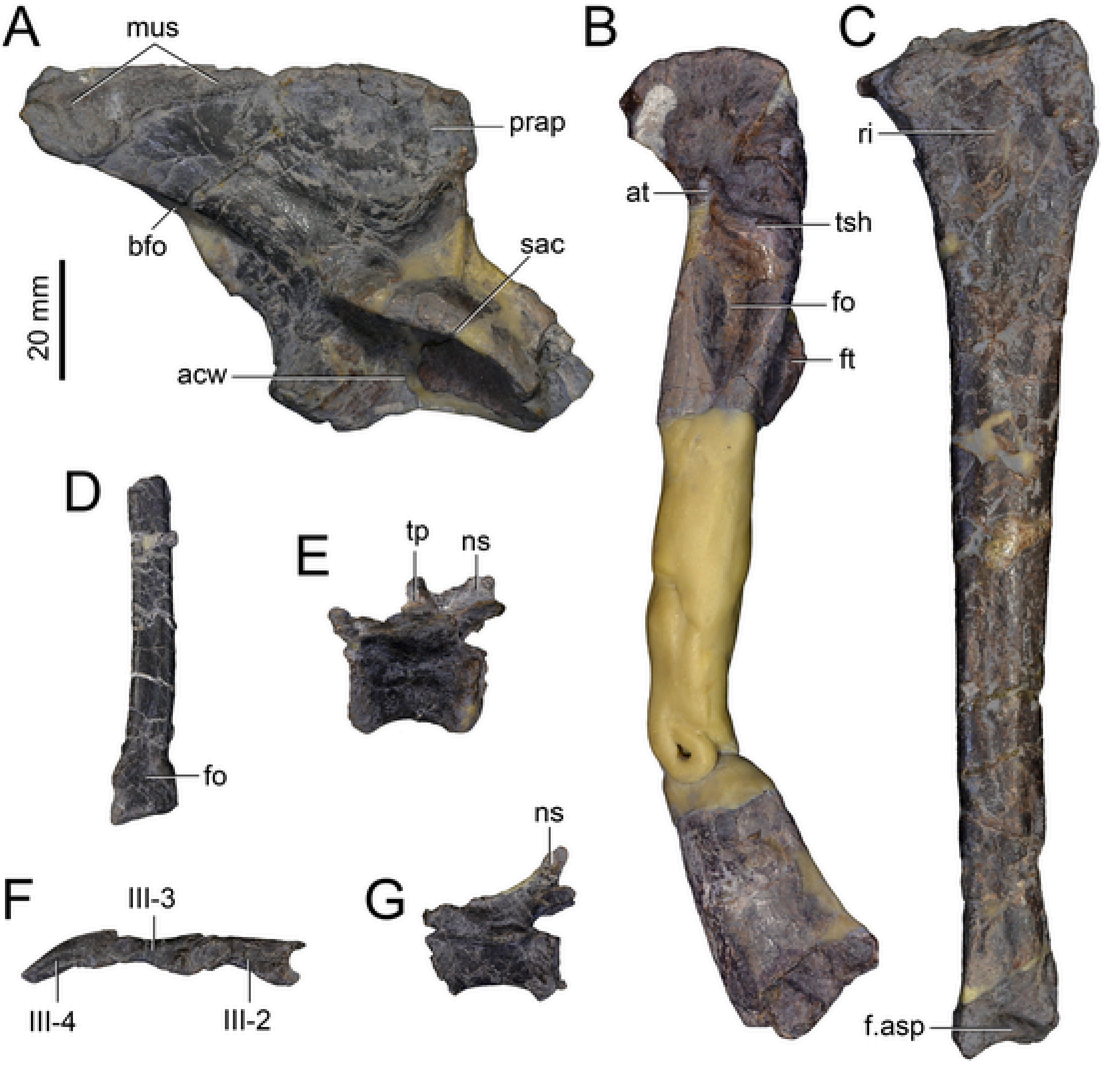

Fig. 14. ***Chromogisaurus novasi.*** Selected elements of specimen PVSJ 845 (holotype). (A) right ilium in lateral view. (B) left femur in lateral view. (C) right tibia in lateral view. (D) right metatarsal II in dorsal view. (E) anterior caudal vertebra in left lateral view. (F) phalanges 2–4 of pedal digit II in left lateral view. (G) middle caudal vertebra in left lateral view. Abbreviations: acw, acetabular wall; at, anterior trochanter; bfo, brevis fossa; f.asp, facet for ascending process of astragalus; fo, fossa; ft, fourth trochanter; mus, muscle scar; prap, preacetabular process; ri, ridge; sac, supraacetabular crest; tsh, trochanteric shelf.

(Martínez et al., 2013a). However, this region of the rhynchosaur skeleton differs from the referred bone in the presence of a mostly flat articular surface of the mandibular glenoid fossa, a glenoid region distinctly transversely broader than the retroarticular process, a squared, non-tapering retroarticular process in lateral view, and the absence of a densely striated surface. In contrast, the morphology of this bone is almost identical to that of the proximal end of the ulna of *Saturnalia*, only mainly differing in the presence of a more anteriorly expanded base of the olecranon process in *Chromogisaurus*. *Panphagia* differs from the sympatric *Chromogisaurus* (and also from *Saturnalia*) in the absence of an iliac postacetabular process with a pointed posteroventral corner and a rounded posterodorsal margin, and a strong and anterodorsally tapering trapezoidal rugosity for the origin of the *Mm. flexor tibialis* and *iliotibialis* (Ezcurra, 2010).

The inclusion of *Chromogisaurus* among sauropodomorphs has been based on the presence of elongate neural spines of proximal caudal vertebrae, laterally curved iliac blade, elongate pubic peduncle, and lateral condyle of proximal end of tibia more anteriorly placed than the medial one (Ezcurra, 2010). The distribution of these character states is complex among early dinosauriforms and their optimization potentially variable among different topological arrangments. In this regard, a laterally curved iliac blade and elongate pubic peduncle, as well as the morphology of the proximal tibia are shared with silesaurids, whereas elongate neural spines of proximal caudal vertebrae are widespread among dinosauriforms, including *Silesaurus* and *Asilisaurus*. Indeed, the second and third of the above-mentioned character states have a wide distribution within early dinosaurs, and even among dinosauriforms, such as *Silesaurus* and *Lewisuchus*. On the other hand, the first character state is clearly present and widely distributed in non-dinosaur dinosauriforms such as *Silesaurus* and *Asilisaurus*. Likewise, the fourth character state exhibits a wide distribution in early dinosauriforms (e.g., *Lagosuchus, Lewisuchus*).

Regarding the diagnostic features of *Chromogisaurus*, Martínez et al. (2013a) pointed out that the elliptical fossa distal to the trochanteric shelf (initially identified by Ezcurra, 2010, as autapomorphic for this species) are the result of crushing and collapse of the internal structures of the femur, an interpretation followed later by Müller and Garcia (2019). However, we consider that new specimens are needed because the fossa possesses the same size and depth in both right and left femora and a similar, but shallower, fossa is present in referred specimens of *Eodromaeus*.

Panphagia protos – this taxon was described by Martínez and Alcober (2009) on the basis of a single partial skeleton (Fig. 15). The only known specimen comes from Valle Pintado, lower levels of Cancha de Bochas Member, Ischigualasto Formation, Agua de la Peña Group (Martínez and Alcober, 2009; Martínez et al., 2013a, b). The sauropodomorph affinities of this taxon is consensual across several phylogenetic analyses (Martínez and Alcober, 2009; Ezcurra, 2010; Cabreira et al., 2011, 2016, Martínez et al., 2011; Bittencourt et al., 2015; Agnolin and Rozadilla, 2017; Müller et al., 2018a; Langer et al., 2019). In contrast, the phylogenetic position of *Panphagia* within Sauropodomorpha is slightly variable. When *Panphagia* was originally described, it was proposed as the sister taxon to all other Sauropodomorpha by Martínez and Alcober (2009). However, at that time, *Eoraptor* was generally considered an early theropod (e.g., Sereno et al., 1993; Nesbitt et al., 2009) or a saurischian outside the Theropoda-Sauropodomorpha dichotomy (e.g., Langer and Benton, 2006).

Several derived features have been interpreted to unite *Panphagia* and *Saturnalia* with Sauropodomorpha, including: constricted tooth crowns, tooth crowns of lanceolate contour, and a short lamina located at the posterolateral end of the distal end of tibia (Martínez and Alcober, 2009). On the other hand, the distally curved crows of the dentary teeth, semicircular distal outline of the ischium, and lateral condyle of the tibia posteriorly located were considered as evidence to place *Panphagia* external to the clade composed of *Saturnalia* and other sauropodomorphs (Martínez and Alcober, 2009). However, these conditions also occur in sauropodomorphs that were described more recently, such as *Buriolestes*. So, *Panphagia* has been recovered in a polytomy with some other coeval sauropodomorphs (Martínez et al., 2011; Bittencourt et al., 2015; Langer et al., 2017; Agnolin and Rozadilla, 2018; Garcia et al., 2019b), whereas some studies suggested a sister-taxa relationship between *Panphagia* and *Pampadromaeus* (Cabreira et al., 2011; Müller et al., 2018a; Bronzati et al., 2019; Pacheco et al., 2019). The latter hypothesis relies on the absence of a bony sheet between the anterior and ventral processes of the prefrontal. Additional specimens will be welcomed to verify the validity of this trait as the prefrontal is disarticulated from the lacrimal in both taxa and the bony sheet may be susceptible to damage during taphonomic processes.

An alternative hypothesis considers *Panphagia* more closely related to post-Carnian sauropodomorphs than to coeval taxa (Baron et al., 2017a). However, a revised and more comprehensive version of the former dataset places *Panphagia* within an unresolved Saturnaliidae (Baron et al., 2017b; Langer et al., 2017), a scenario also recovered in other datasets (Müller et al., 2018a,c). Moreover, new findings have demonstrated that some traits are deeply controlled by ontogeny. It is the case of the strong rugose areas present in the ilia of saturnaliids (Garcia et al., 2019b). Actually, ontogenetic series of the oldest sauropodomorphs are scarce, but these rugose areas on the iliac blade seem to be absent in more mature specimens of *Lewisuchus*, *Asilisaurus*, bagualosaurians, herrerasaurids, ornithischians, and neotheropods (Ezcurra, 2010; Ezcurra et al., 2020b; Nesbitt et al., 2020). Nevertheless, the inner affinities of the less inclusive clades (e.g., Saturnaliidae) of early sauropodomorphs should be carefully reconsidered.

The acetabulum of *Panphagia* is almost medially closed, with the medial acetabular wall strongly developed, in which the ventral margin of the wall is almost straight and at level of the distal ends of both pubic and ischadic peduncles. This condition resembles that of *Pampadromaeus, Buiriolestes,* and *Saturnalia*, and indicates that these taxa are more plesiomorphic regarding that character than most other dinosaurs. In *Bagualosaurus, Chromogisaurus* and *Eoraptor*, the ventral margin of the medial acetabular wall seems slightly more notched (concave), whereas in *Pantydraco* the medial acetabular wall is strongly notched (Yates, 2003). The most important conclusions on this aspect are that most early dinosaurs had an almost closed acetabulum; the distinction between Dinosauria ancestrally with respect to Silesauridae is that the ventral margin of the acetabular wall in the latter forms a ventral triangular projection, whereas in early dinosaurs the ventral border is straight to concave; and a fully open acetabulum evolved probably independently in different dinosaurian groups, namely Herrerasauridae (e.g., *Herrerasaurus*), Sauropodomorpha (e.g., *Pantydraco*), Neotheropoda (e.g., Coelophysis), and Ornithischia (e.g., *Eocursor*).

Panphagia differs from *Eoraptor* in several features (Martínez and Alcober, 2009). Its scapular blade is proportionally shorter and wider. The distal end of ischium is dorsally expanded as in *Saturnalia*, differing from the much less expanded distal end of the bone in *Eoraptor* and *Herrerasaurus*. The proximal end of the tibia in *Panphagia* has the lateral condyle located close to the posterior border, similar to that in *Eoraptor*, but differing from the more anterior condyle of *Saturnalia* and later sauropodomorphs (Martínez et al., 2011).

In conclusion, the sauropodomorph affinities of *Panphagia* seem robust and stable among the phylogenetic analyses. However, its affinities among Carnian members of the group are uncertain, altougth it is generally recovered as closer to norian sauropodomorphs that to *Buriolestes* and *Eoraptor*.

Pampadromaeus barberenai – this taxon was described by Cabreira et al. (2011) on the basis of a partially preserved skeleton including a nearly complete skull (Fig. 16). The specimen comes from Janner site or Várzea do Agudo, Alemoa Member, Santa María Formation, Rosário do Sul Grup, about 2 km west of Agudo, Rio Grande do

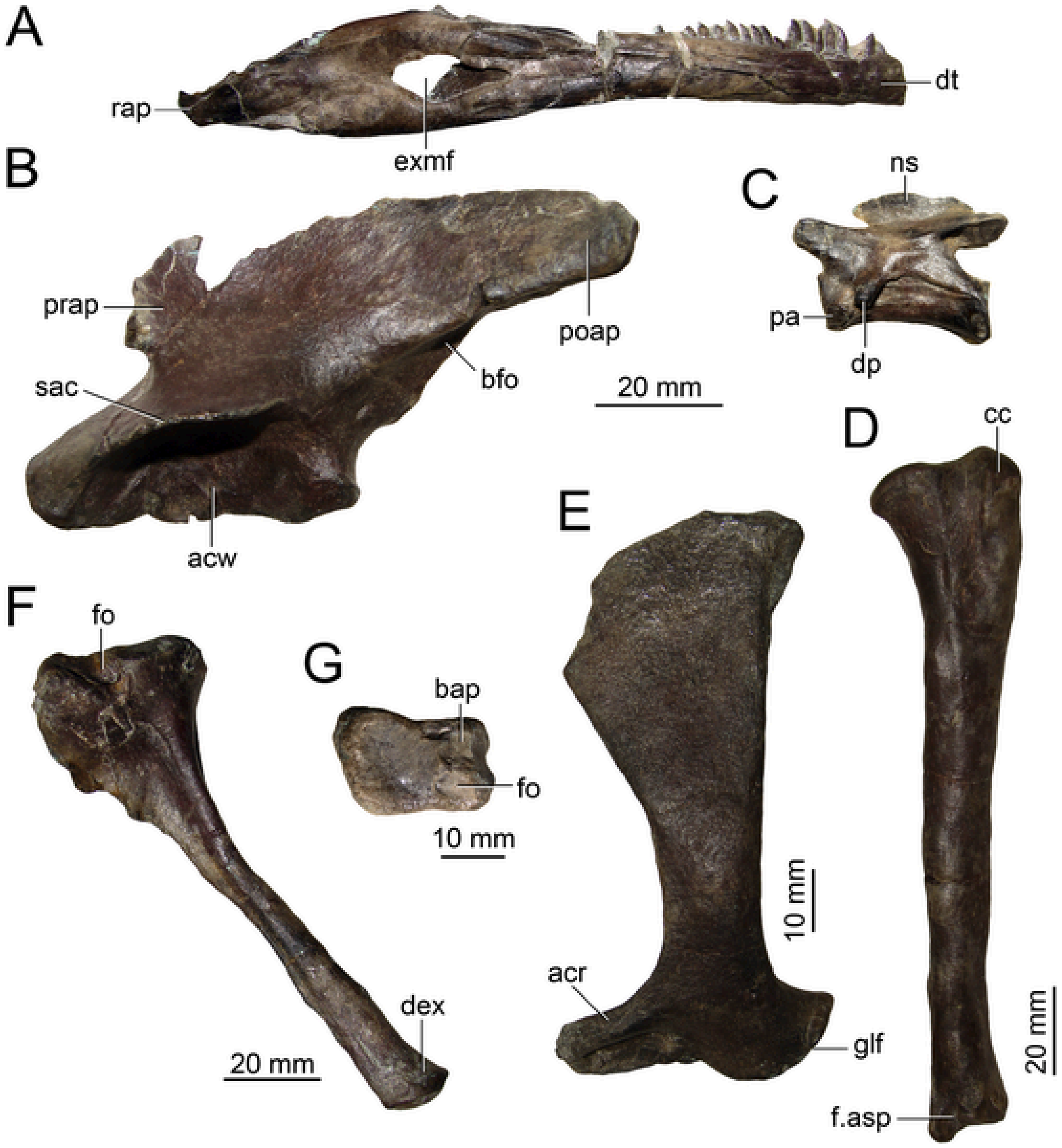

Fig. 15. ***Panphagia protos***. Selected elements of specimen PVSJ 874 (holotype). (A) right hemimandible lacking anterior end in lateral view. (B) left ilium in lateral view. (C) anterior cervical vertebra in left lateral view. (D) right tibia in lateral view; (E) left scapula in lateral view; (F) left ischium in lateral view; (G) right astragalus in dorsal view. Abbreviations: acr, acromion; acw, acetabular wall; bap, base of ascending process; bfo, brevis fossa; cc, cnemial crest; dex, distal expansion; dp, diapophysis; dt, dentary; exmf, external mandibular fenestra; f.asp, facet for ascending process of astragalus; fo, fossa; glf, glenoid fossa; ns, neural spine; pa, parapophysis; poap, postacetabular process; prap, preacetabular process; rap, retroarticular process; sac, supraacetabular crest.

Sul, Brasil. More recently, Langer et al. (2019) described in detail the available bones of the specimen. It comes from the *Exaeretodon* sub-assemblage zone of the *Hyperodapedon* AZ (~228 Ma; Müller and Garcia, 2019), overlying the *Hyperodapedon* Acme zone; these levels also yielded *Bagualosaurus*.

Cabreira et al. (2011) sustained the affinities of *Pampadromaeus* with sauropodomorphs on the basis of ventral process of squamosal extensive and strap-shaped, anterior caudal vertebrae with neural spines anteroposteriorly extended, distal end of humerus transversely wide, ilium with subtriangular-shaped preacetabular process, and elongate pubic peduncle. The only character state that may be considered as exclusively shared by *Pampadromaeus* and sauropodomorphs is the transversely expanded distal end of humerus and the optimization of the others may change among the alternative early dinosaurian topologies. In sum, the relationship of *Pampadromeus* with Sauropodomorpha is mainly supported by the transverse expansion of distal humerus and the morphology of the leaf-shaped tooth crowns.

Bagualosaurus agudoensis – this taxon is known from a single partial skeleton unearthed from the Janner site (Agudo, Rio Grande do Sul, Brazil; Pretto et al., 2019). Specimen UFRGS-PV-1099-T is composed of a partial skull associated with partially articulated post-cranial elements (Fig. 17). This material combines anatomical traits with coeval and post-Carnian sauropodomorphs. As a result, *Bagualosaurus* has been recovered as the sister taxon to post-Carnian sauropodomorphs (Bronzati et al., 2019; Langer et al., 2019; Pacheco et al., 2019; Pretto et al., 2019; Müller, 2020), within Bagualosauria.

The most striking feature of *Bagualosaurus* is the large body size when compared to coeval forms. The femoral length of *Bagualosaurus* is 215 mm (Pretto et al., 2019), whereas the femoral length of coeval sauropodomorphs is about 150 mm (Ezcurra, 2010; Sereno et al., 2013; Cabreira et al., 2016; Müller et al., 2018a; Langer et al., 2019). There-

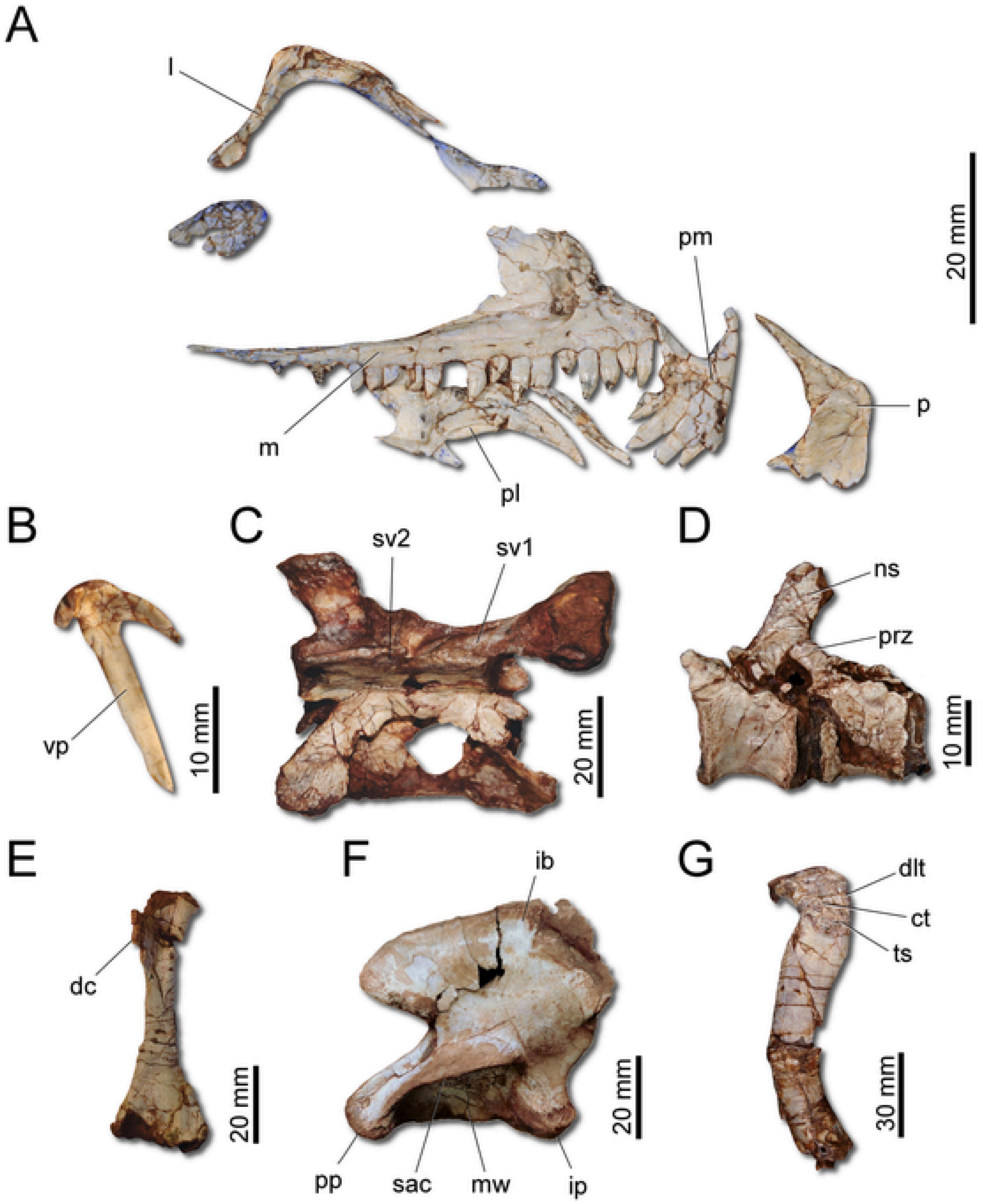

Fig. 16. ***Pampadromaeus barberenai***. Selected elements of Pampadromaeus barberenai (ULBRA-PVT016). (A) partial skull in right lateral view. (B) left squamosal in medial view. (C) sacrum in dorsal view. (D) caudal vertebrae in left lateral view. (E) right humerus in anterior view. (F) left ilium in lateral view. (G) left femur in lateral view. Abbreviations: ct, anterior trochanter; dc, deltopectoral crest; dlt, dorsolateral trochanter; ib, iliac blade; ip, ischiadic peduncle; l, lacrimal; m, maxilla; mw, medial wall; ns, neural spine; p, parietal; pl, palatine; pm premaxilla; pp, pubic peduncle; prz, prezygapophysis; sac, supracetabular crest; sv, sacral vertebra; ts, trochanteric shelf; vp, ventral process.

fore, *Bagualosaurus* was ca. 25–50% larger than any other Carnian sauropodomorph (Pretto et al., 2019). On the other hand, sauropodomorphs with longer femora (c. 335 mm) are reported from the upper beds of the Candelária Sequence (Müller et al., 2018a), which are early Norian in age (Langer et al., 2018). Thus, the body size of *Bagualosaurus* lies on the midway between the small Carnian forms and the relatively larger Norian sauropodomorphs.

In addition to the relatively large body size, another unusual trait when compared to coeval sauropodomorphs is the proportionally small skull of *Bagualosaurus*, representing less than two-thirds of the femoral length. This is the condition present in all post-Carnian sauropodomorphs (e.g., Yates, 2007a; Langer et al., 2010), whereas the earliest members generally have proportionally larger skulls (Cabreira et al., 2011, 2016; Sereno et al., 2013). An exception is *Saturnalia*, which shares with *Bagualosaurus* a small skull (Langer et al., 1999; Bronzati et al., 2019), suggesting that the skull reduction is not an unequivocal synapomorphy of Bagualosauria.

The tooth morphology of *Bagualosaurus* includes some adaptations related to the acquisition of an omnivorous diet, such as the presence of serrations forming oblique angles relative to the main axis of the crown. However, this is also present in *Pampadromaeus* and *Panphagia*. In contrast, as in *Plateosaurus*, *Efraasia*, and other post-Carnian

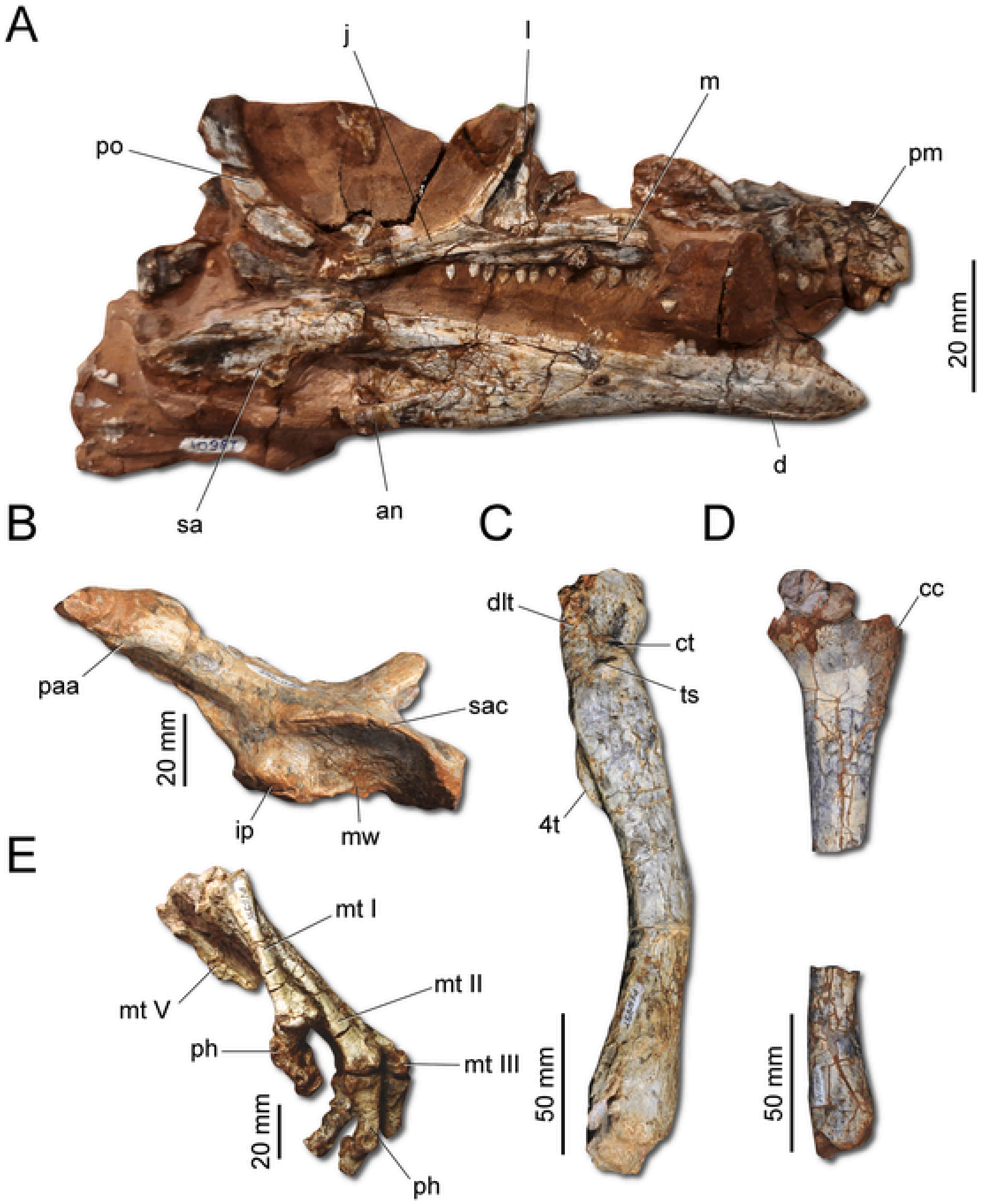

Fig. 17. ***Bagualosaurus agudoensis***. Selected elements of specimen UFRGS-PV-1099-T. (A) partial skull in right lateral view. (B) right ilium in lateral view. (C) right femur in lateral view. (D) left tibia in medial view. (E) left pes in medial view. Abbreviations: 4t, fourth trochanter; an, angular; cc, cnemial crest; ct, anterior trochanter; d, dentary; dlt, dorsolateral trochanter; ip, ischiadic peduncle; j, jugal; l, lacrimal; m, maxilla; mt, metatarsal; mw, medial wall; paa, postacetabular ala; ph, phalanx; pm, premaxilla; po, postorbital; sa, surangular; sac, supracetabular crest; ts, trochanteric shelf.

sauropodomorphs (e.g., Prieto-Márquez and Norell, 2011), the first premaxillary tooth of *Bagualosaurus* has a relatively high crown, which does not occur in other Carnian forms (Pretto et al., 2019). Moreover, the dentary is a dorsoventrally tall and robust bone, unlike the gracile bone of coeval sauropodomorphs. Despite these traits, *Bagualosaurus* also bears a suit of character states that resembles the earliest members of the clade. For instance, the jugal is excluded from the antorbital fossa, the dentary lacks a buccal emargination, the iliac acetabulum is poorly perforated, and the femur is markedly sigmoid and bears a trochanteric shelf. This combination of plesiomorphic and derived traits reflects the key-position of this taxon in the phylogenetic tree of sauropodomorphs. Unfortunately, there are no cervical vertebrae or manual elements preserved for *Bagualosaurus*.

7.1. *Probable early sauropodomorphs*

Nhandumirim waldsangae – this taxon was recently described by Marsola et al. (2019a) from Cerro da Alemoa, in the urban area of Santa Maria. It comes from upper levels of the Alemoa Member of the Santa Maria Formation. The only known specimen is composed of the hindlimb and ilium as well as posterior dorsal and caudal vertebrae.

Marsola et al. (2019a) carried out two different phylogenetic analyses for assessing the phylogenetic relationships of *Nhandumirim*:

in one of the analyses, it resulted in a polytomy with other saurischians, including saturnaliids, but in a second analysis, based on the dataset of Cabreira et al. (2016), *Nhandumirim* was positioned as a theropod. Theropod affinities stand on the following three synapomorphies: posteriorly extended ischiadic peduncle; a mediolaterally expanded distal end of the tibia; and a tabular posterolateral flange of the tibia. The general contour and topography of distal end of tibia is closely similar to that of *Herrerasaurus* (Novas, 1989, 1994) and *Eoraptor* (Sereno et al., 2013), with a posteroloteral flange not laterally surpassing the facet for the astragalar ascending process. This latter condition sharply differs from neotheropods, in which such flange is prominently developed laterally (Novas, 1989).

Contrary to the theropod affiliation proposed for *Nhandumirim*, the morphology of all the available bones of its holotype is very similar to those of *Saturnalia, Chromogisaurus,* and *Eoraptor*. This includes the conformation of the brevis shelf and fossa of ilium, the elongate postacetabular blade, and incipiently opened acetabular wall. The femur of *Nhandumirim* lacks a trochanteric shelf, which is present in *Saturnalia* (and coeval sauropodomorphs). However, the presence and shape of the trochanteric shelf is controlled by maturation degree in several Triassic dinosauriforms (Nesbitt, 2011; Piechowski et al., 2014; Griffin and Nesbitt, 2016), in which the younger individuals generally lack that structure. *Nhandumirim* was considered a juvenile specimen on the basis of histological analysis (Marsola et al., 2019a) and, therefore, the absence of a trochanteric shelf seems related to its ontogenetic status. A recent phylogenetic analysis found *Nhandumirim* as a sauropodomorph dinosaur nested within Saturnaliidae (Müller and Garcia, 2020). As a result, the affinities of this probable theropod, sauropodomorph or early saurischian taxon seem to need a detailed revision.

Guaibasaurus candelariensis - this dinosaur was originally described by Bonaparte et al. (1999) on the basis of a partial postcranial skeleton and an articulated and nearly complete left hindlimb (Fig. 18), which were discovered in the Sesmaria do Pinhal 2 locality near Candelária, Rio Grande do Sul, in Brazil. Later, articulated and nearly complete postcranial skeleton was referred to *Guaibasaurus* (Bonaparte et al., 2007), collected from the Linha São Luiz locality near the town of Faxinal do Soturno, Rio Grande do Sul (Bonaparte et al., 2010; Langer et al., 2011). These strata are early Norian in age (Langer et al., 2018).

Guaibasaurus shows a striking combination of plesiomorphic features that makes its taxonomic referral a difficult task. Because of its uniqueness, it was referred to its own family, Guaibasauridae, interpreting *Guaibasaurus* as “less derived” than Herrerasauridae and representing an “ancestral form” to Theropoda and Sauropodomorpha (Bonaparte et al., 1999, 2007). Guaibasauridae was originally a monotypic group, but later Bonaparte et al. (2007) included *Saturnalia tupiniquim* and the dinosauriform *Agnosphitys cromhallensis* from the Late Triassic of the United Kingdom (Fraser et al., 2002), within this clade. However, a recent phylogenetic analysis found *Agnosphitys* within Silesauridae (Baron et al., 2017a). Since then, phylogenetic interpretations on *Guaibasaurus* have depicted the taxon either as a theropod (e.g., Langer, 2004; Langer et al., 2007, 2011; Yates, 2007b; Bittencourt and Kellner, 2009) or as a sauropodomorph (e.g., Ezcurra, 2006, 2010; Ezcurra and Novas, 2009; Novas, 2009). More recently, it has been proposed that the clade formed by *Chindesaurus bryansmalli* and *Tawa hallae* may also include *Guaibasaurus* (Marsh et al., 2019). We will discuss these main alternatives, but it is worth mentioning that the main reason for the phylogenetic instability of *Guaibasaurus* is probably not character conflict, but the damage undergone to the bones during preparation (Langer et al., 2011).

A detailed analysis extended the taxonomic composition of Guaibasauridae with the inclusion of *Saturnalia, Panphagia, Guaibasaurus*, and *Chromogisaurus* (Ezcurra, 2010). However, differences between *Guaibasaurus* and other guaibasaurids has been noted in this study, thus coining the term Saturnaliinae for the clade gathering *Saturnalia, Panphagia*, and *Chromogisaurus*. Similarly, a subsequent study concluded that *Saturnalia, Panphagia*, and *Eoraptor* may be grouped into a monophyletic group of early sauropodomorphs (Martínez et al., 2011), an interpretation that was later adopted by other authors (e.g., Baron and Williams, 2017; Müller et al., 2018a,c; Bronzati et al., 2019a; Langer et al., 2019; Garcia et al., 2019b). Subsequently, Saturnaliinae was modified as to family rank (Langer et al., 2019) and Saturnaliidae was employed since then.

The inclusion of *Guaibasaurus* among theropods was sustained by Langer et al. (2011; see also Upchurch et al., 2007, and Yates, 2007b), while refuting in detail those character states recognized by Ezcurra (2010) in support of a sauropodomorph affiliation. Langer et al. (2011) listed for *Guaibasaurus* the presence of six theropodan synapomorphies mainly restricted to the forelimb (e.g., proximal end of metacarpals in wide contact but lacking extensive overlapping, humerus represents 0.6 of total femoral length, hand representing more than 0.4 of humerus + radius length, metacarpal IV narrow). It is important to say that such forelimb features are also present in other early dinosaurs such as *Herrerasaurus* and *Eoraptor*.

There are some general similarities that *Guaibasaurus* shares with *Saturnalia*. The deltopectoral crest of the humerus of *Guaibasaurus* is proximodistally elongate and strongly anteriorly projected, as occurs in basal sauropodomorphs (Langer et al., 2007). Both ulna and radius are short and stout, as typically occurs among sauropodomorphs. Although the manual elements are not well preserved, the available metacarpals and phalanges are stouter and more robust than those of herrerasaurids, *Heterodontosaurus, Eodromaeus* and *Coelophysis*, but congruent with the robustness seen in early sauropodomorphs. The general shape of the ilium of *Guaibasaurus* (especially the lateral expansion of the supracetabular crest and its strongly convex outer margin), the pubis (bearing an ischio-pubic groove) and ischium (bearing a distally expanded foot, which expands mainly dorsally; Langer et al., 2011) are very similar to *Saturnalia* and kin. In contrast, the transverse expansion of the outer malleoulus of the tibia of *Guaibasaurus*, similar to that of *Tawa* and *Riojasaurus* (Novas, 1989), may be reinterpreted as autapomorphic of *Guaibasaurus*. In addition, the recent described *Macrocollum* (Müller et al., 2018c) shares a general morphology with *Guaibasaurus*, such as similar limb proportions, poorly excavated acetabulum, femur without a trochanteric shelf, well-developed anterior margin of the medial condyle of the astragaulus, and slender foot with an elongated digit I. This shared general anatomy might suggest affinities of *Guaibasaurus* with Unaysauridae (Müller and Garcia, 2020). However, the poorly preserved condition and lack of more comparative elements (e.g., cranial parts) of the specimens precludes a more precise comparison. In sum, we consider more likely that *Guaibasaurus* is nested among early sauropodomorphs, in opposition to its inclusion within Theropoda.

7.2. Conclusions on early sauropodomorphs

Saturnaliids share with other sauropodomorphs some features that are absent in theropods and non-dinosaurian dinosauriforms, including a ventrally bent dorsal margin of anterior end of dentary, low mandibular articulation, long deltopectoral crest on humerus, expanded distal end of humerus, and ilium with elongated pubic peduncle greater than twice the anteroposterior depth of its distal end (Ezcurra, 2010; Cabreira et al., 2016).

Bagualosaurian sauropodomorphs (*sensu* Langer et al., 2019; Pretto et al., 2019), includes *Bagualosaurus* and post-Carnian sauropodomorphs, which show a combination of features, including relatively large body size (30% more than saturnaliid body size), reduced skull size (present also in *Saturnalia*), notably elongate cervical vertebrae (unknown for *Bagualosaurus* and *Unaysaurus*), short epipodium, relatively straight femur (absent in *Bagualosaurus*), possi-

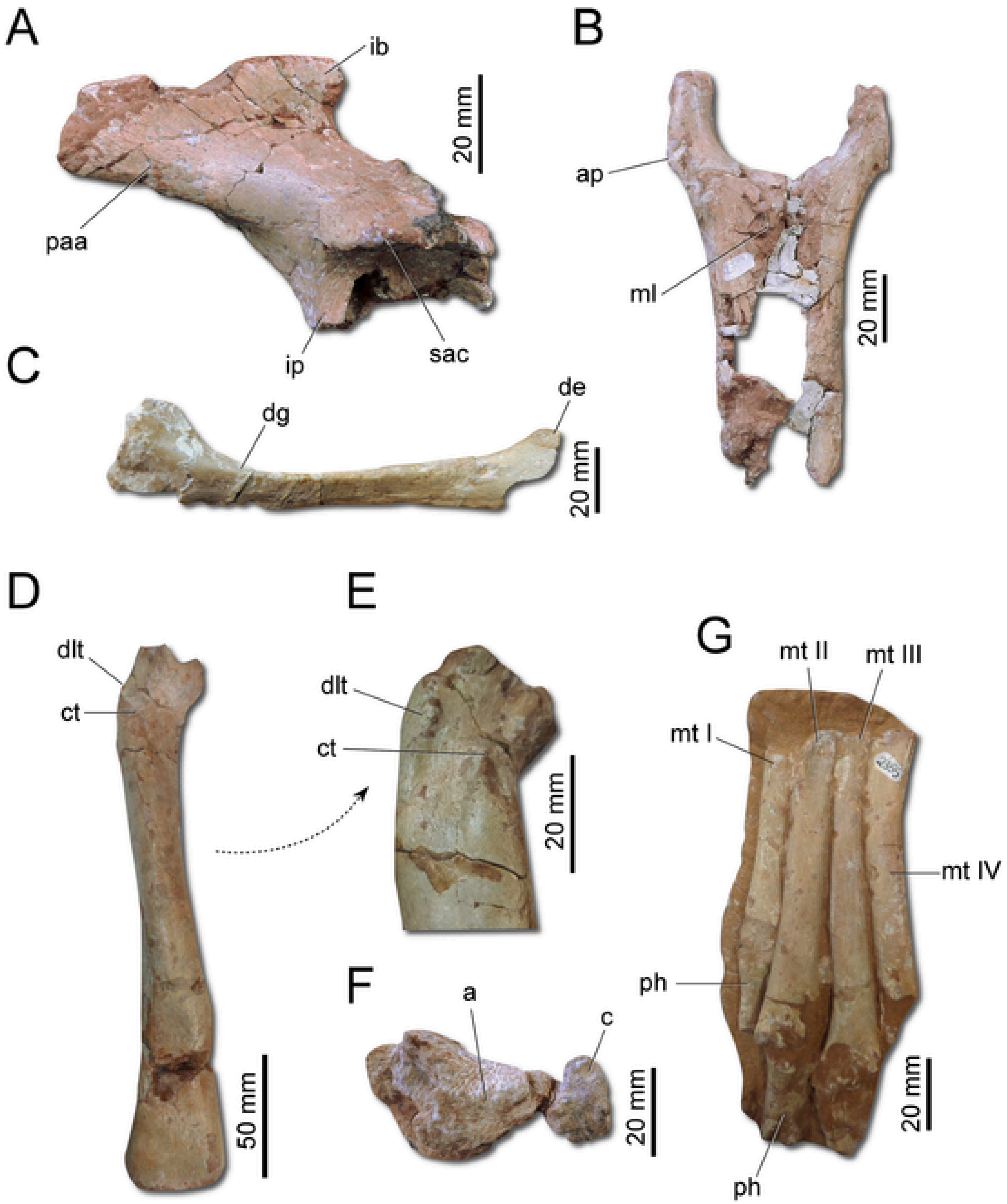

Fig. 18. ***Guaibasaurus candelariensis***. Selected elements of Guaibasaurus candelariensis. (A) right ilium of MCN PV2355 in lateral view. (B) pubes of MCN PV2355 in anterior view. (C) left ischium of MCN PV2355 in lateral view. (D) right femur of MCN PV2355 in anterior view. (E) proximal portion of the right femur of MCN PV2355 in anterolateral view. (F) left astragalus and calcaneum of MCN PV2356 in distal view. (G) left pes of MCN PV2355 in anterior view. Abbreviations: a, astragalus; ap, ambiens process; c, calcaneum; ct, anterior trochanter; de, distal expansion; dg, dorsal groove; dlt, dorsolateral trochanter; ib, iliac blade; ip, ischiadic peduncle; ml, medial lamina; mt, metatarsal; paa, postacetabular ala; ph, phalanx; sac, supracetabular crest.

ble rhamphoteca on premaxilla (based on the presence of a concentration of foramina and/or parasagittal ridges along the anterior portion of the bone), and absence of a subnarial gap in the upper alveolar margin, among others (Leal et al., 2004; Müller et al., 2018a; Pretto et al., 2019).

The results of the present analysis indicate that the early evolution of Saurischia included branches that did not belong to the main lineages into which Dinosauria is usually divided: Neotheropoda and core-Sauropodomorpha. Herrerasauria and saturnaliids represent evolutionary radiations that started before the flowering of neotheropods and core-sauropodomorphs and became extinct during the early Norian and Rhaetian, respectively. In addition, the fossil record of sauropodomorphs from Carnian and Norian beds is far more abundant and diverse than that of the other dinosaur groups (an exception is the abundant record of *Herrerasaurus* from the Ischigualasto Formation; Martínez et al., 2013b). This record associated with more refined ages (e.g., Martínez et al., 2011; Kent et al., 2014; Langer et al., 2018) allows the establishment of macroevolutionary patterns that controlled the early evolution and initial radiation of sauropodomorphs (Fig. 19). For instance, the oldest sauropodomorphs are small, bipedal, and possibly faunivorous animals (Cabreira et al., 2016; Bronzati et al., 2017) that occupied a small parcel of the terrestrial ecosystems from southern Pangea, which were dominated by rhynchosaurs and herbivorous/omnivorous synapsids (Martínez et al., 2013b). In contrast, during the No-

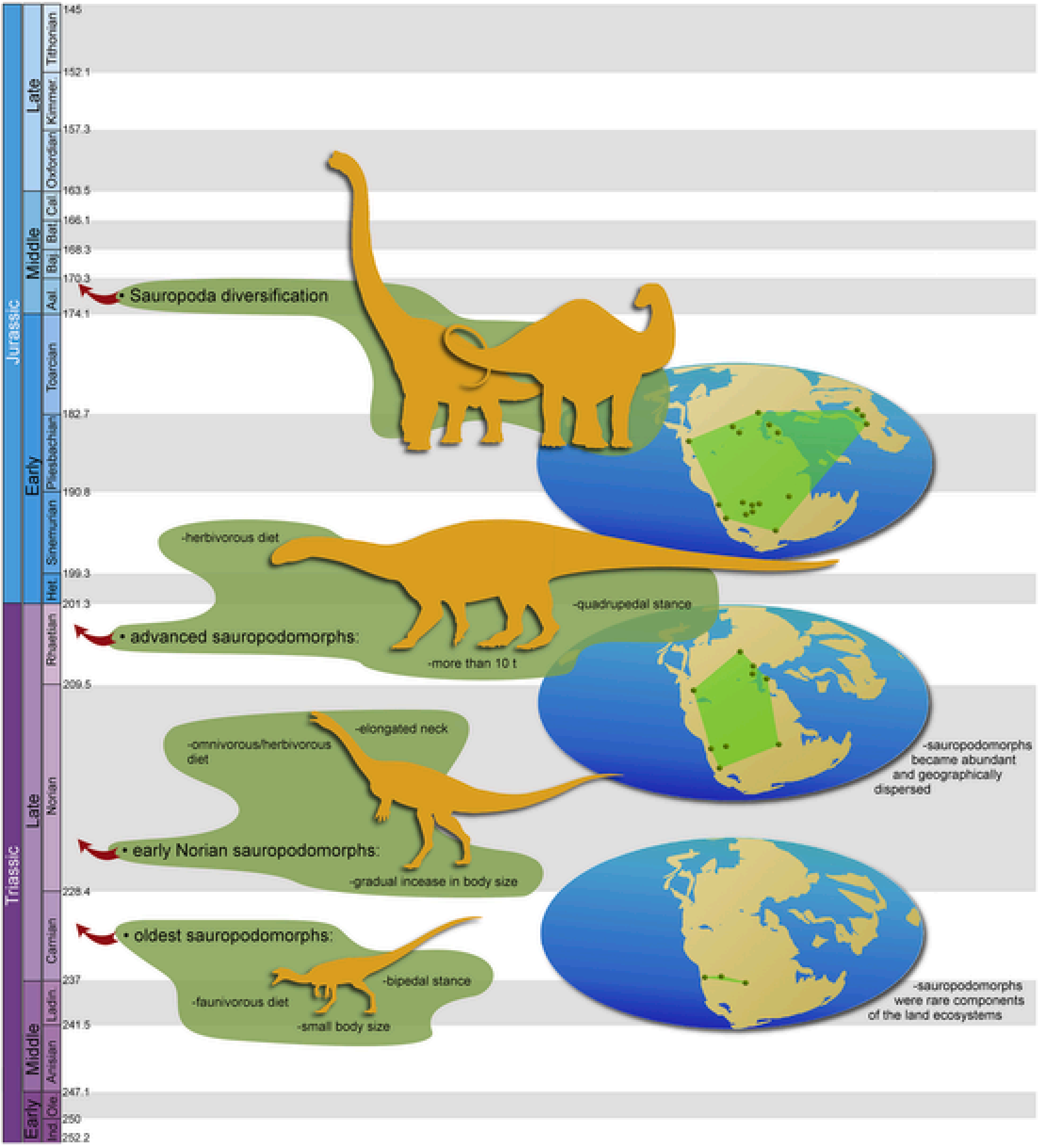

Fig. 19. Macroevolutionary trends among sauropodomorphs during Triassic and Jurassic Periods. Convex hull geographic range maps for sauropodomorphs from Müller et al. (2017). Silhouettes based on the artwork by Márcio L. Castro and Jorge A. Gonzalez.

rian, the fossil record of the group became far more abundant and spread across the world (Benton, 2014), where sauropodomorphs became the most abundant large vertebrates in their ecosystems. This was the first time that a dinosaur group ruled the terrestrial ecosystems. Later, those relatively small animals adopted a quadrupedal stance (McPhee et al., 2018) and became far larger, reaching more than 10 tons before the Early Jurassic (Apaldetti et al., 2018). The cursoriality of the earliest forms was gradually abandoned by Norian forms, which is evident by their straight femur that is longer than the tibia, whereas in the earliest and cursorial forms the femur is sigmoid and shorter than the tibia. This drastic turnover accompanied the dietary shift experienced by early Norian sauropodomorphs, which acquired dental traits related to an herbivorous/omnivorous diet and a longer neck (Müller et al., 2018a) that facilitated reaching tall vegetation. The cranial endocasts also support a behavioral shift. The earliest sauropodomorphs have a well-developed flocculus of the cerebellum, which is significantly reduced in Norian forms (Bronzati et al., 2017; Müller et al., 2020). This structure has been associated with the coordination of eye, head, and neck movements, and also in gaze stabilization in extant vertebrates (Witmer et al., 2003; Voogd and Wylie, 2004; Stocker et al., 2016). Its reduction is tentatively associated with the loss of predatory behaviors (Bronzati et al., 2017). Therefore, the fossil record of sauropodomorphs from South America provides crucial clues on the first steps taken by the group before reaching their evolutionary success.

8. *Eodromaeus*, a Carnian theropod?

Although definitive theropods are known from Norian beds, the presence of Carnian sauropodomorphs requires that the theropod line also extended at least into the Carnian (e.g., Langer et al., 1999; Martínez and Alcober, 2009). However, unambiguous Triassic representatives of Theropoda other than coelophysoid-grade (i.e., non-averostran neotheropods) species remain unknown (except for *Eodromaeus*), as the historically interpreted members of this clade, the herrerasaurids, are better positioned outside Eusaurischia, and the North

American taxa *Tawa, Chindesaurus* and *Daemonosaurus* have been here hypothesized as members of Herrerasauria (see above). Thus, the only putative Carnian theropod is the Ischigualastian aged *Eodromaeus murphi* (Fig. 20).

Eodromaeus exhibits some morphological features of Theropoda, but its general appearance still differs from that of neotheropods. On the contrary, its pelvic girdle and hindlimb retained most of the plesiomorphies that are widely present among other Carnian dinosaurs. Thus, an important morphological gap separates *Eodromaeus* from neotheropods. *Eodromaeus* is represented by five specimens, coming from the lower third of the Ischigualasto Formation. The holotype consists of a partially articulated skeleton that shows a gross morphology and proportions similar to those of *Eoraptor* (Martínez et al., 2011).

Eodromaeus had been originally described as an early member of Theropoda, closer to Neotheropoda than to Herrerasauridae (Martínez et al., 2011), a hypothesis also shared by other authors (e.g., Nesbitt and Ezcurra, 2015; Ezcurra and Martínez, 2016). More recently, however, *Eodromaeus* has been alternatively interpreted as sister to Eusaurischia (Baron and Williams, 2017; Marsola et al., 2019a; Müller and García, 2020), and as sister to Herrerasauridae (Nesbitt et al., 2020). Character states originally recognized in support of the theropodan affinities of *Eodromaeus* (Martínez et al., 2011) deserve the following comments:

1) Promaxilary fenestra: the presence of this opening is a feature historically interpreted as diagnostic of Theropoda (Gauthier, 1986; Rauhut, 2003). Nevertheless, such a fenestra has been documented among other early dinosauriforms including *Herrerasaurus* (Martínez et al., 2011, SI), *Sanjuansaurus* (Alcober and Martínez, 2010), *Pampadromeus* (Cabreira et al., 2011), *Macrocollum* (Müller, 2020), *Heterodontosaurus* (Sereno, 2012), and the silesaurid *Sacisaurus* (Langer and Ferigolo, 2013). On the contrary, *Tawa, Gnathovorax, Buriolestes* and *Eoraptor* lack a promaxilary fenestra (Martínez et al., 2011; Sereno et al., 2013; Müller et al., 2018a; Pacheco et al., 2019). This feature seems to be rather homoplastic among Dinosauriformes.
2) Basisphenoidal fossa: *Eodromaeus* exhibits a deep fissure on the ventral surface of the parabasisphenoid (Martínez et al., 2011, SI), as occurs in many neotheropods. In contrast, the ventral surface of the parabasisphenoid in *Lewisuchus* (Bittencourt et al., 2015), *Silesaurus* (Dzik, 2003), *Gnathovorax* (CAPPA/UFSM 0009), *Eoraptor* (Sereno et al., 2013) and *Buriolestes* (Müller et al., 2018a) has a shallow concavity. Available information suggests this is a synapomorphic feature within Theropoda.
3) Pleurocoels on cervical vertebrae: as in *Herrerasaurus*, a system of longitudinal crests is present on the lateral surface of the centrum and base of the neural arch, with three of these crests separating two elongate depressions. However, cervical vertebrae 7 and 8 have a deep blind excavation immediately posterodorsal to the parapophysis (PVSJ 562), similar in position to the anterior

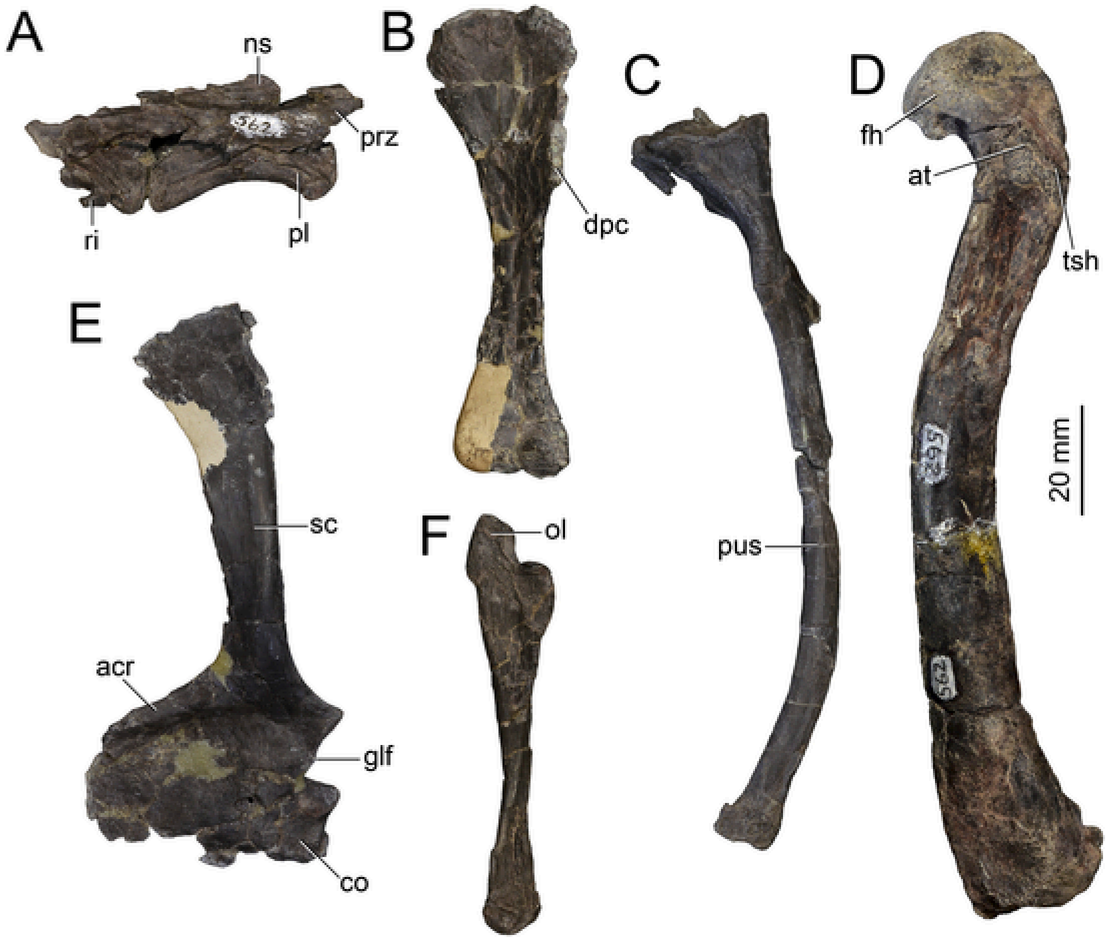

Fig. 20. ***Eodromaeus murphi***. Selected elements of Eodromaeus murphi (PVSJ 562: referred specimen). (A) cervical vertebrae 7 and 8, and right cervical rib 8 in right lateral view. (B) left humerus in anterior view. (C) right pubis in lateral view. (D) left femur in anterolateral view. (E) left scapula and coracoid in lateral view. (F) left femur in medial view. Abbreviations: acr, acromion; at, anterior trochanter; co, coracoid; dpc, deltopectoral crest; fh, femoral head; ft, fourth trochanter; glf, glenoid fossa; ns, neural spine; ol, olecranon; pl, pleurocoel; prz, prezygapophysis; pus, pubic shaft; ri, rib; sc, scapula; tsh, trochanteric shelf.

pleurocoel of Neotheropoda (e.g., *Coelophysis*, *Liliensternus*, *Lucianovenator*) and the fossa present in *Tawa* (Nesbitt et al., 2009). Such a depressions are absent in more anterior cervical vertebrae (PVSJ 562). As a result, the presence of anterior pleurocoels in *Eodormaeus* seems to support its affinities with theropods.

4) Caudal prezygapophyses elongate: elongate prezygapophyses are present in Herrerasauridae, *Silesaurus*, and pterosaurs (Dalla Vecchia, 2013). Current documentation of this feature does not permit us to determine if it evolved early in Avemetatarsalia or Dinosauriformes, and was retained by herrerasaurids and neotheropods. Therefore, it does not necessarily warrant by itself the theropodan affinities for *Eodromaeus*.
5) Close apposition of ulna and radius: this condition is present in Herrerasauridae (Sereno, 1993), *Silesaurus* (Dzik, 2003), and early Pterosauria (Padian, 1983), but not in ornithischians (e.g., heterodontosaurids, *Lesothosaurus*) and early sauropodomorphs (e.g., *Eoraptor, Saturnalia*). As with the previous character, homoplasy blurs the optimization of this character state following the multiple alternative phylogenetic relationships proposed for early dinosaurs in recent years.
6) Manual penultimate phalanges elongate: this feature is also present in *Tawa* and Heterodontosauridae (Sereno, 2012; Galton, 2014). Furthermore, the hand is still unknown in most early dinosauriforms, and thus, the distribution of this trait remains uncertain at the base of avemetatarsalians.
7) Pubic apron transversely narrow towards the distal half: as shown by Martínez et al. (2011), the pubes of *Eodromaeus* are elongate and narrow, resembling the condition in herrerasaurids and coelophysoids, thus differing from the proportionally broader end of that bone in *Silesaurus* and early sauropodomorphs. The pubic apron is also elongate and narrow among ornithischians (Sereno, 1986; Galton, 2014).
8) Expansion on distal end of the pubis: a modest knob on the distal end of pubis is present in *Eodromaeus,* similar to that of *Coelophysis, Dilophosaurus* and *Plateosaurus* (von Huene, 1926). Because a distal knob is not observed in silesaurids or other non-dinosaurian dinosauriforms, this condition may stand as a possible synapomorphic feature of Theropoda in the future.
9) Extensor depression on the distal end of the femur: the presence of a well-defined extensor groove on the distal end of the femur is present in several neotheropods, and was considered variously as synapomorphic of different clades within Neotheropoda (Rauhut, 2003; Ezcurra, 2017). In *Eodromaeus* the anterior aspect of the distal end of the femur shows a subtriangular and rugose area that forms a shallow fossa. This condition is present in several theropods, but also in *Gnathovorax, Buriolestes* and *Eoraptor* (Sereno et al., 2013), and the ornithischian *Scelidosaurus* (Norman, 2020).
10) Fibular crest on the proximal tibia: although this is a classic feature of Neotheropoda, *Silesaurus* and ornithischians (e.g., *Lesothosaurus, Heterodontosaurus, Fruitadens, Tianyulong*; Sereno, 2012; Galton, 2014; Baron et al., 2017a) also bear a well-defined fibular crest on the proximal part of the tibia.

Eodromaeus retained several features that may be interpreted as plesiomorphic for Dinosauria. They include: pterygoid teeth (as in *Buriolestes, Eoraptor,* and *Pampadromaeus*); humerus with cone-like proximally projected internal tuberosity, separated from humeral head by a deep and anteroposteriorly oriented concavity (as in *Eoraptor, Herrerasaurus* and *Buriolestes*); ulna with prominent olecranon process, similar to *Saturnalia*, *Chromogisaurus* and more mature forms of *Megapnosaurus*; carpus formed by several elements, the largest ones being the ulnare and radiale (as in *Herrerasaurus* and *Heterodontosaurus*, but *Eodromaeus* exhibits an enlarged medial distal carpal, as in neotheropods); tibia sub-triangular in proximal contour; distal tibia anteroposteriorly elongate and transversely narrow, resembling *Herrerasaurus* in the general profile, with a poorly developed outer malleolus; and distal fibula enlarged, with anteroposterior diameter subequal to that of tibia.

Notably, *Eodromaeus* exhibits some traits reminiscent of herrerasaurids, including: premaxilla anteroposteriorly very short (also seen in *Daemonosaurus*), maxilla with convex ventral margin, anterior maxillary teeth fang-like, scapula with a narrow blade at its base and very high acromion, and pubis with a sigmoid external margin in anterior view.

Phylogenetic analysis carried on for the present paper places *Eodromaeus* as sister of Neotheropoda, as originally proposed by Martínez et al. (2011). The following synapomorphies support this node: maxilla with promaxillary foramen; medial wall of the antorbital fossa extends along the entire ventral border of the internal antorbital fenestra as a broad lamina, higher than the height of the horizontal process below the antorbital fossa; cervical vertebrae with pleurocoels in the anterior portion of the centrum; trunk vertebrae incorporated into the sacrum; medialmost distal carpal significantly larger than other distal carpals; iliac pubic peduncle ventral extension similar to that of the ischiadic peduncle; iliac ischiadic peduncle well expanded posteriorly to the anterior margin of the postacetabular embayment; femur longer or about the same length as the tibia/fibula; femoral proximal portion with anteromedial tuber offset medially (or posteriorly) relative to the posteromedial tuber; tibia with concave posterolateral margin of the distal end; and tibia with inflexion between the posterolateral process and medial portion of the distal end.

The Bremer value of 4 for Theropoda (i.e., the *Eodromaeus* + Neotheropoda clade) is considerably high. However, both bootstrap frequencies are relatively low (<70%). The difference between the absolute and GC bootstrap frequencies is only 6%, indicating the lack of a high amount of contradictory phylogenetic signal for the position of *Eodromaeus* as the sister taxon to Neotheropoda. Under topological constraints (setting *Tawa*, *Chindesaurus* and *Daemonosaurus* as floating taxa), nine additional steps are required to force the position of *Eodromaeus* within Sauropodomorpha (being recovered as its earliest branching member), and twelve extra steps to place it as an herrerasaurian (sister taxon to other members of the clade) or the sister taxon to all other saurischians. Thus, the position of *Eodromaeus* in our phylogenetic dataset is quite robust based on these branch support parameters.

In sum, *Eodromaeus* exhibits theropod features (e.g., deeply excavated parabasisphenoid, enlarged medial distal carpal, pubis with distal knob), but in joint with a large number of notable plesiomorphic traits (e.g., short premaxilla, humeral internal tuberosity, metacarpal III slightly longer than III, distal end of tibia rectangular-shaped and with poorly developed outer malleolus, fibula distally enlarged, astargalus and calcaneum herrerasaurid-like).

9. Discussion

Based on the phylogenetic hypothesis proposed here (Figs. 1 and 6) and the chronological distribution of dinosauriform taxa (Figs. 2 and 4), we will make some considerations about the early radiation of this archosaur clade.

Non-dinosaurian dinosauromorphs (with the exception of *Asilisaurus* and more deeply nested silesaurids) have recurved teeth, indicating they were faunivorous. In the case of the small-sized (50 cm long) *Lagerpeton* and *Lagosuchus* they were probably insectivorous, but larger forms such as *Lewisuchus* (reaching approximately 1 m long), with proportionally large heads and teeth (skull length subequal to femur length), were probably able to prey on other vertebrates. It is interesting to note that similar-sized predatory animals that lived alongside *Lewisuchus* were probainognathian cynodonts (e.g., *Probainognathus,* *Chiniquodon*; Abdala et al., 2020), representing the best candidates for being competitors. Althought they may have similar feeding habits, the locomotor apparatus of early dinosauromorphs and early probainognathians were conspicuously dissimilar with long and slender limbs and bipedal to semibipedal postures in the former group, and fully quadrupedal with robust fore and hindlimbs in probainognathians (Abdala et al., 2020). At this point, ecological innovations in cynodonts are seen in their craniodental morphology (Kemp, 2005; Martinelli et al., 2016), whereas in early dinosauromorphs much of their anatomical innovations are concentrated on the locomotory apparatus (Benton, 1983; Novas, 1996).

Dinosauriforms of Ischigualastan age were larger and more robust than their Chañarian predecesors, but also more diversified in their diets: ornithischians (accepting *Pisanosaurus* as part of this group) and sauropodomorphs occupied the niche of omnivore/herbivores of modest size, ranging from 1.20 (*Eoraptor*) to 2 m long (*Saturnalia*). Notably, during Ischigualastian-Coloradian times no other tetrapod groups (probably excepting for aetosaurs) played the role of modest sized omnivore/herbivores as that occupied by sauropodomorphs. However, rhynchosaurian archosauromorphs (e.g., *Hyperodapedon*) and traversodontid cynodonts (e.g., *Exaeretodon*) were numerically abundant during the Ischigualastian, and at least the latter group had omnivore-herbivore habits (Abdala et al., 2020). Yet, these clades were drastically affected by the late Carnian biotic turnover, being absent during the Norian (Bonaparte, 1982; Benton et al., 2014; Abdala et al., 2020; Ezcurra et al., 2020c). Whereas silesaurids apparently retained the insectivorous diet of early ornithodirans (Qvarnström et al., 2019), herrerasaurs became hyperpredators and the largest dinosaurs of Ischigualastian times, ranging from 2 m (*Staurikosaurus*) up to 6 m long (*Frenguellisaurus*), probably preying upon other tetrapods. Aside from herrerasaurs, the predatory guild of Ischigualastian-age faunas also included ornithosuchids of small size (*Venaticosuchus*) and large-sized loricatan pseudosuchians (*Saurosuchus;* approximately 8 m long), the latter ones being the top predators of Chañarian, Ischigualastian and Coloradian times (Nesbitt et al., 2013b). It must be pointed out that several cases of extreme morphological convergences with dinosaurs are recorded among the pseudosuchian archosaurs, such as Poposauridae (Nesbitt, 2011), including the Ischigualastian *Sillosuchus*, reaching 9 m long (Nesbitt, 2011). However, the faunal census of tetrapods from the Ischigualasto Formation indicates that herrerasaurs were numerically more abundant (and taxonomically more diverse) than other contemporary carnivorous archosaurs (Martínez et al., 2013b). Aside from herrerasaurs, a hidden diversity of small predatory dinosaurs emerged in recent years with the discovery of *Eodromaeus* and *Buriolestes*, which may have competed with comparably sized faunivorous cynodonts such as *Trucidocynodon, Ecteninion,* and *Chiniquodon*. It seems clear that dracohors (with faunivorous, omnivorous and herbivorous diets) evolved and diversified not as the result of an opportunistic radiation following an extinction event, but contrarily in the context of a process involving highly diverse faunas, including archosauromorphs and synapsids of different kinds. Evidence at hand demonstrates that evolutionary radiation of Carnian dinosaurs was variegated in sizes and morphology, and occurred in the context of a “crowded ecospace”, in which morphologically disparate and taxonomically diverse tetrapods flourished at that time. In sum, the flourishing of Carnian tetrapod faunas from South America were probably driven by favourable climatic and paleoenvironmental conditions related to the “Carnian Pluvial Event” (Simms and Ruffell, 1989; Roghi et al., 2010; Ezcurra, 2012; Bernardi et al., 2018; Mancuso et al., 2020).

During the early Norian, early sauropodomorphs (*Macrocollum, Unaysaurus*) acquired longer necks, smaller heads and more specialized herbivorous dentitions, but although they were diverse and numerically abundant, remained small in size. During this time, herrerasaurs apparently became extinct alongside rhynchosaurs and traversodontids in South America. In the middle-late Norian, carnivorous dinosaurs were represented by neotheropods of large (*Zupaysaurus*) and small (*Powellvenator*) size in this continent. Large pseudosuchians (*Fasolasuchus*) survived up to the middle Norian (Kent et al., 2014), retaining the role of top predators. Nevertheless, sauropodomorphs became the most numerically abundant archosaur clade during Coloradian times, represented by several specimens corresponding to species of modest size (*Coloradisaurus*) as well as larger forms reaching 12 m long (*Riojasaurus*) or even larger (*Lessemsaurus*). The sauropodomorph diversification (involving size increase, numerical abundance and taxonomic diversity) may have responded to a climatic shift towards more arid conditions (Bonaparte, 1982).

The evolutionary split among dinosauriforms such as *Lagosuchus*, silesaurids and dinosaurs occurred before Carnian times. These evolutionary radiations occurred previous to the first Late Triassic mass extinction event, which occurred around the Carnian-Norian boundary (Benton, 1983; Dal Corso et al., 2020). Carnian times also witnessed the early diversification of different amniotan clades, including traversodontid and probainognathian cynodonts, rhynchosaurs, sphenodontians, aetosaurs, and crocodylomorphs (Evans, 2003; Desojo et al., 2013; Abdala et al., 2020; Ezcurra et al., 2020c; Leardi et al., 2020). This indicates that the early radiation of dinosaurs and their closest relatives started well before the disappearance of other potential amniotan competitors, an evidence that clearly counters the opportunistic model (Benton, 1983, 1990).

An extinction at the Carnian-Norian boundary was recognized by Bonaparte (1982), who described an important faunal replacement associated with major climatic-environmental changes between the Ischigualasto and Los Colorados formations. Previously, Bakker (1977) in a general work on the mass extinctions of Tetrapoda, indicated an important change in the composition of the fauna during that time. Subsequently, Benton (1983, 1986, 1989, 1994) argued that the change in terrestrial fauna during the Carnian-Norian limit was of great importance, even greater than in the Triassic-Jurassic boundary. In this regard, Brusatte et al. (2010) indicated that the main jump in the occupation of the morphospace in Dinosauria occurred between the Carnian and Norian. Several lineages of Carnian ornithodrians (Lagerpetidae, Silesauridae, Herrerasauria) crossed the Carnian-Norian boundary, disappearing between the late Norian and Rhaetian, when the dinosaurian faunas were composed, at least mostly, of bagualosaurian sauropodomorphs and neotheropods. In other words, the great faunal change that occurred at the Carnian-Norian boundary unevenly affected various dinosaur lineages, in part depending on the geographical distribution (Marsola et al., 2019b): whereas in South America herrerasaurs became extinct before Coloradian times, and replaced by coelophysoid theropods, in North America archaic dracohors (Herrerasauria and Silesauridae) persisted well into the latest Triassic, and sauropodomophs were absent.

10. Conclusions

The early diversification of Dinosauria looks, at first sight, as a simple pattern of branching into its three main constituting clades: Sauropodomorpha, Theropoda and Ornithischia. The oldest known dinosaurs, recorded in Carnian and early Norian beds, have been usually referred to one of these main groups. However, with the exception of Sauropodomorpha, the oldest unambiguous representatives of Theropoda and Ornithischia remain ellusive. All indicates that our current knowledge of early dinosauriform diversity is far from comprehensive, with few taxa that allow hypothesizing a rather simple evolutionary history channeled within three main lineages. To have a better grasp of this situation, available list of Late Triassic dinosaur species employed in discussions on the origins of the group spans roughly 35 million years, from the beggining of the Carnian (beggining of deposition of the *Massetognathus-Chanaresuchus* Assemblage Zone of the Chañares Formation, ca. 237 Ma), up to the end of the Rhaetian (ca.

201 Ma). This time span is roughly equivalent to the latest Eocene to Recent, when South American native notoungulate mammals are represented by ~140 species distributed in more than ten families, with exquisitely preserved fossils (e.g., Croft et al., 2020). We think that future discoveries will modify this simple pattern of dinosaur origins, and that a more complex branching sequence will emerge.

Author statement

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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.

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Appendix A. Supplementary data

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Uncited reference

Nesbitt et al., 2015, Bronzati et al., 2018

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