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New traversodontid cynodont from the Late Triassic Chañares Formation

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NEW TRAVERSODONTID CYNODONT FROM THE LATE TRIASSIC CHAÑARES FORMATION

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Abstract. The Chañares Formation in north-western Argentina has provided an impressive number of specimens of early archosauriforms, dicynodonts, and non-mammaliamorph cynodonts. However, there is a very low diversity of cynognathian cynodonts. Herein, we report on *Pontognathus ignotus* gen. et sp. nov., a small new traversodontid from the traditional Late Triassic Carnian levels of the unit. It differs from other traversodontids for lacking a maxillary platform lateral to the posterior postcanines and by presenting a unique combination of characters from the premaxilla, maxilla, and dentition (*i.e.*, the precanine diastema; the placement of the paracanine fossa; the number of upper postcanines; the general outline of the upper postcanines crown in occlusal view; the shouldering between adjacent teeth; the expansion of the crown distolateral to the sectorial crest; the extension, limits and deepness of the occlusal basin; the distal ridge-like bulging at the base of the crown; the number and relative placement and development of the cusps). It is a relatively small taxon inferred to have occupied a specialized, small herbivorous/omnivorous role, which in this fauna is otherwise only shared by small individuals of the traversodontid *Massetognathus pascuali*.

Key words. Anatomy. Cynodontia. Traversodontid. Gondwana. Late Triassic. Carnian.

Resumen. NUEVO CINODONTE TRAVERSODÓNTIDO DEL TRIÁSICO TARDÍO DE LA FORMACIÓN CHAÑARES. La Formación Chañares en el Noroeste de Argentina ha proporcionado un impresionante número de especímenes de arcosauriformes tempranos, dicinodontes y cinodontes no mamaliamorfos. Sin embargo, la diversidad conocida de cinodontes cinognatios es muy baja. En este trabajo presentamos *Pontognathus ignotus* gen. et sp. nov., un nuevo traversodóntido de pequeño tamaño proveniente de los tradicionales niveles carnianos (Triásico Superior) de la unidad. Este se diferencia de otros traversodóntidos por carecer de una plataforma maxilar lateral a los postcaninos posteriores y por presentar una combinación única de caracteres del premaxilar, del maxilar y de la dentición (*i.e.*, la diastema precanina; la ubicación de la fosa paracanina; el número de postcaninos superiores; la forma general de la corona de los postcaninos superiores en vista oclusal; la interrelación entre dientes adyacentes; la expansión de la corona distolateral a la cresta sectorial; la extensión, los límites y la profundidad de la cuenca oclusal; el abultamiento distal en forma de cresta en la base de la corona; el número de cúspides y su posición y desarrollo relativo). Se infiere que este pequeño taxón habría ocupado un rol ecológico especializado de pequeño herbívoro/omnívoro que, de otro modo, en esta fauna, es solamente compartido por individuos pequeños del traversodóntido *Massetognathus pascuali*.

Palabras clave. Anatomía. Cynodontia. Traversodóntido. Gondwana. Triásico Tardío. Carniano.

Soon after the discovery of the Chañares Formation in the '60s, several foundational papers established the taxonomic characterization of its tetrapod assemblage (*e.g.*, Romer, 1966, 1967, 1969, 1971a, 1971b, 1972a, 1973a, 1973b; Romer & Jensen, 1966; Cox, 1968; Jenkins, 1970; Romer & Lewis, 1973). The Chañares fauna is represented primarily by archosauromorphs and synapsids, including several species of cynodonts. Among the latter, two genera and three species of probainognathians and two genera and four species of traversodontids were recognized initially (Romer, 1967, 1969, 1970, 1972a, 1973a). It was only several decades later that the taxonomy of the Chañares cynodonts was reviewed. Battail (1991) suggested that only one of the traversodontid species was valid, but did not discuss any evidence supporting his hypothesis. After a detailed morphometric analysis, Abdala and Giannini (2000) concluded that the previously identified Chañares traversodontid taxa (*Massetognathus pascuali* Romer, 1967, *Massetognathus teruggii* Romer, 1967, *Massetognathus major* Romer, 1972a, and *Megagomphodon oligodens* Romer, 1972a) were best interpreted as different ontogenetic stages of a single species, *M. pascuali*. Regarding the probainognathians of this unit, Abdala and Giannini (2002) proposed the synonymy of the genus *Probelesodon* Romer, 1969 with *Chiniquodon* von Huene, 1936, also known from the Brazilian *Dinodontosaurus* Assemblage Zone and from a scarce record from the Ischigualasto Formation of Argentina (Bonaparte, 1966a; see also Martínez & Forster, 1996). Furthermore, Abdala and Giannini (2002) considered both species of *Probelesodon* (*P. lewisi* Romer, 1969 and *P. minor* Romer, 1973b) synonymous with *Chiniquodon theotonicus* von Huene, 1936. Hence, by the early 2000s, the cynodonts of the Chañares Formation were represented only by the herbivorous traversodontid *Massetognathus pascuali* and the faunivorous probainognathians *Chiniquodon theotonicus* and *Probainognathus jenseni* Romer, 1970, which are, according to Ezcurra *et al.* (2017), apparently exclusively present in the traditional (*Massetognathus-Chanaresuchus* Assemblage Zone) levels of the unit (but see Ordoñez *et al.,* 2020 for a different view).

Intensive fieldwork was performed in the Chañares Formation since the early 1970s after the discovery of its paleontological potential. This led to the worldwide recognition of its importance for understanding the evolution of terrestrial biotas (see Mancuso *et al.,* 2014). However, only four tetrapod taxa were nominated after a 20-year-gap: the proterochampsid *Tropidosuchus romeri* Arcucci, 1990, the pseudosuchian *Tarjadia ruthae* Arcucci and Marsicano, 1998, the ornithodiran *Lagosuchus lilloensis* Romer, 1972b (a combination changed to *Marasuchus lilloensis* Sereno and Arcucci, 1994), and the dinosauriform *Pseudolagosuchus major* Arcucci, 1987. However, it has been proposed that *Marasuchus lilloensis* is a junior synonym of *Lagosuchus talampayensis* Romer, 1971c (Agnolin & Ezcurra, 2019) and *Pseudolagosuchus major* junior synonym of *Lewisuchus admixtus* Romer, 1972c (Ezcurra *et al.,* 2020). Since then, it was recently when Ezcurra *et al.* (2017, 2020) presented findings of new archosauromorphs, dicynodonts, and cynodonts from the basal portion of the Chañares Formation (*Tarjadia* Assemblage Zone *sensu* Ezcurra *et al.,* 2017). Among the latter, they reported the presence of two cynodont taxa, one of them allied with the probainognathian *Aleodon* Crompton, 1955, previously known from the *Dinodontosaurus* Assemblage Zone in Brazil, the Omingonde Formation in Namibia, and the Manda Beds in Tanzania, and the other to the traversodontids *Scalenodon* Crompton, 1955 or *Mandagomphodon* Hopson, 2014, up to then only known from the Manda beds in Tanzania and the *Dinodontosaurus* Assemblage Zone in Brazil (see Parrington, 1946; Crompton, 1955; Abdala & Smith, 2009; Hopson, 2014; Martinelli *et al.,* 2017; Melo *et al.,* 2017). It was some years later that Martinelli *et al.* (2024) formalized some of the new findings with the erection of the new aleodontine probainognathian taxon *Riojanodon nenoi* Martinelli *et al.*, 2024. In addition, Mancuso and Irmis (2020) described a new large-bodied dicynodont, *Stahleckeria* sp., from the lower levels of the Chañares Formation, another taxon affiliated with the *Dinodontosaurus* Assemblage Zone (AZ) of the lower Santa Maria Formation in Brazil and the uppermost part of the Omingonde Formation in Namibia. Otherwise known from the *Santacruzodon* AZ in Brazil (Melo *et al.,* 2015) and the Isalo II levels in Madagascar (Flynn *et al.,* 2000; Kammerer *et al.,* 2008), the presence of the genus *Menadon* Flynn *et al.*, 2000 was reported from the upper Chañares Formation, above the *Massetognathus-Chanaresuchus* Assemblage Zone (Martinelli *et al.,* 2023, 2024, fig. 1). Here we report the finding of a new traversodontid from the Chañares Formation, the first new traversodontid named from this unit in the last 53 years and the first new cynodont reported from the traditional fossiliferous levels (*Massetognathus-Chanaresuchus* Assemblage Zone *sensu* Ezcurra *et al.*, 2017) since the ’70s.

GEOLOGICAL BACKGROUND

The worldwide known Chañares Formation is part of an entirely continental succession deposited in the Ischigualasto-Villa Unión Basin (Fig. 1). The basin infill represents one of the most continuous continental Triassic successions in western Gondwana, with a diverse vertebrate fauna that includes actinopterygian and sarcopterygian fishes, temnospondyl amphibians, non-mammalian therapsids, lepidosauromorphs, various archosauromorphs (*e.g.*, rhynchosaurs), early crocodylomorphs, dinosaurian precursors, ornithischian, sauropodomorph, and theropod dinosaurs, and possibly the oldest dinosaur footprints (*e.g.*, Arcucci *et al.*, 2004; López-Arbarello *et al.*, 2006; Marsicano *et al.*, 2007; Mancuso & Marsicano, 2008; Martinez *et al.*, 2013; Mancuso *et al.*, 2014; Ezcurra *et al.*, 2017, 2020; Abdala *et al.*, 2020; Desojo *et al.*, 2020; Leardi *et al.*, 2020; Mancuso & Irmis, 2020; Kammerer & Ordoñez, 2021; Gaetano *et al.*, 2022). Equally abundant and diverse are the micro- and macro-floral assemblages (*e.g.*, Zavattieri & Melchor, 1999; Artabe *et al.*, 2001, 2003; Ottone *et al.*, 2005; Ottone & Mancuso, 2006; Colombi & Parrish, 2008; Arce & Lutz, 2010; Lutz *et al.*, 2011; Césari & Colombi, 2016; Perez Loinaze *et al.*, 2018; Pedernera *et al.*, 2020, 2022).

The Chañares Formation is part of the Agua de la Peña Group (Chañares, Los Rastros, Ischigualasto, and Los Colorados formations) (Mancuso, 2005) and overlies the Tarjados red beds. The lower Carnian Chañares Formation (Marsicano *et al.*, 2016; Irmis *et al.*, 2022) is dominated by tuffaceous sandstones and siltstones deposited in a fluvio-lacustrine environment, as well as orthoconglomerates and paraconglomerates representing alluvial fan systems (Rogers *et al.*, 2001; Mancuso *et al.*, 2014, 2020). These fluvial and lake-margin settings suggest more humid conditions relative to older deposits (Mancuso *et al.*, 2020) and contain a diverse tetrapod assemblage that includes a high diversity of archosauriforms (*e.g.*, proterochampsians, pseudosuchians, ornithodirans) and very abundant synapsids (large dicynodonts and small- to medium-sized cynodonts) (Rogers *et al.*, 2001; Mancuso *et al.*, 2014; Marsicano *et al.*, 2016; Ezcurra *et al.*, 2017, 2020; Ordoñez *et al.*, 2020; Martinelli *et al.*, 2024). This tetrapod assemblage was interpreted to represent a single faunal association dubbed *Dinodontosaurus* Assemblage Zone (*e.g.*, Rogers *et al.*, 2001; Mancuso *et al.*, 2014; Marsicano *et al.*, 2016; Mancuso & Irmis, 2020; Ordoñez *et al.*, 2020; Irmis *et al.*, 2022). On

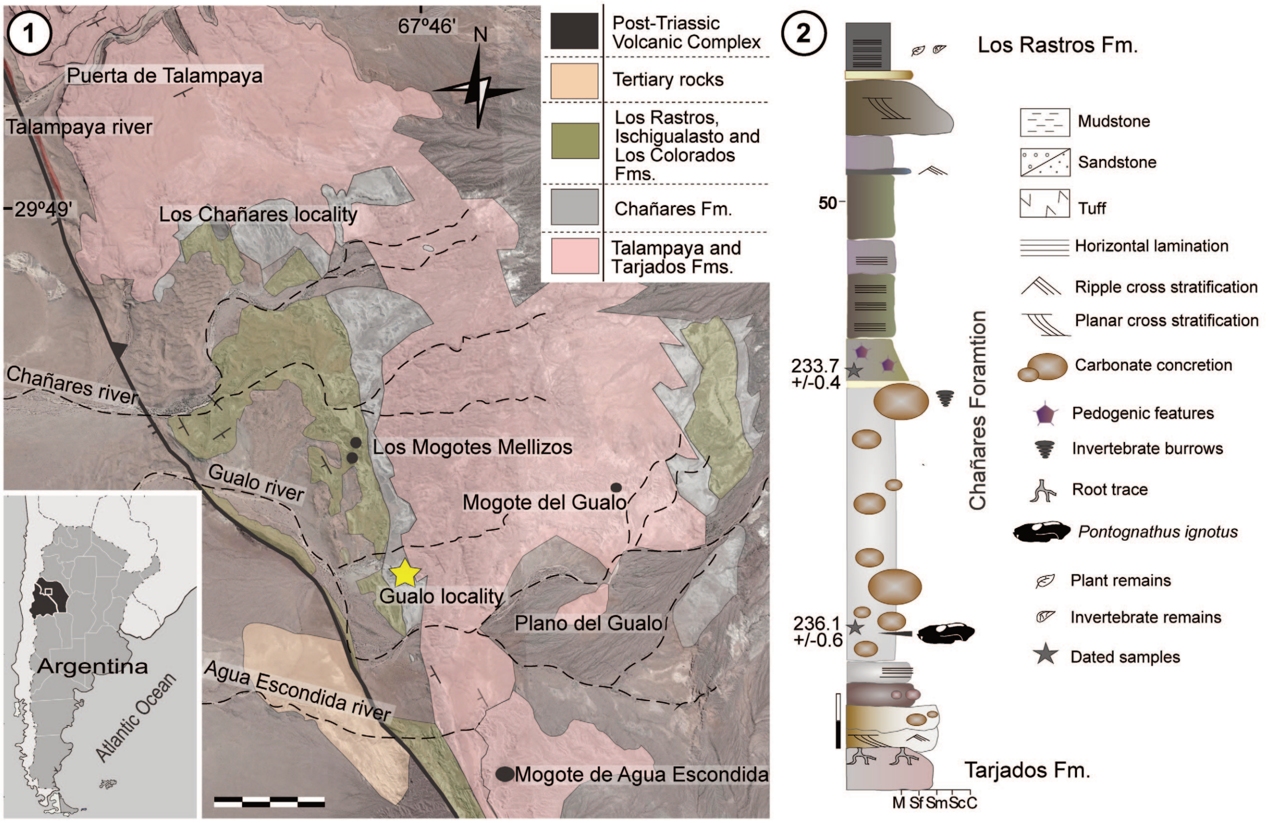

Figure 1. 1, Geological map of the Ischigualasto-Villa Unión Basin in Talampaya National Park area (modified from Caselli, 1998) on a satellite image taken from Google Earth. Yellow star indicates the quarry area. **2,** Stratigraphic section of the Chañares Formation at the Río Gualo locality with ***Pontognathus ignotus*** gen. et sp. nov. location. Scale bar= 2 km in 1 and scale bar= 5 m in 2.

the other hand, the fossiliferous levels of the Chañares Formation have also been interpreted to comprise different assemblage zones, from bottom to top: the *Tarjadia* Assemblage Zone, the *Massetognathus*-*Chanaresuchus* Assemblage Zone, and a still not defined, unnamed Assemblage Zone (Ezcurra *et al.,* 2017; Martinelli *et al.,* 2023, 2024). Considering the cynodont content of the unit, the traditional representatives (*i.e.*, *Massetognathus pascuali*, *Chiniquodon theotonicus*, and *Probainognathus jenseni*) are recovered from the *Massetognathus*-*Chanaresuchus* Assemblage Zone (*sensu* Ezcurra *et al.,* 2017; contra Ordoñez *et al.,* 2020), as well as the new taxon described in this work. *Massetognathus pascuali*, *Chiniquodon theotonicus*, and *Probainognathus jenseni* have been suggested to be absent from the *Tarjadia* and the uppermost (not yet defined and unnamed) assemblage zones, which alternatively include *Riojanodon nenoi* and two indeterminate taxa belonging to the Aleodontinae and Traversodontidae, on the one hand, and *Menadon* sp. on the other (Ezcurra *et al.,* 2017; Martinelli *et al.,* 2023, 2024; but see Ordoñez *et al.,* 2020 for a different interpretation).

MATERIALS AND METHODS

High-resolution micro-computed tomography. PULR-V 287 (holotype of *Pontognathus ignotus*) and PULR-V 289 (here referred to *Massetognathus pascuali*) were analysed through X-ray micro-tomography using a Nikon XT225ST 2X micro-CT scan at the Laboratorio Argentino de Haces de Neutrones (Centro Atómico Constituyentes, Comisión Nacional de Energía Atómica). In the case of the PULR-V 287, the equipment was set up to 80 kV and 201 μA. A total of 1000 projections of the specimen were captured with an exposure time of 500 ms. In the case of the mandible PULR-V 289, the parameters were set to 80 kV and 261 μA. A total of 600 projections of the specimen were captured with an exposure time of 250 ms. In both cases, a 1 mm aluminium filter was employed. The experimental design resulted in a 19.7 μm voxel size for PULR-V 287 and 16.2 μm for PULR-V 289. 3D digital models of the specimens are available on MorphoMuseuM (Gaetano *et al.,* 2025).

Institutional abbreviations. BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **MCZ,** Museum of Comparative Zoology, Harvard University, Cambridge, USA; **PULR-V,** Colección Paleontología de Vertebrados, Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL,** Paleontología de Vertebrados Lillo, Instituto Miguel Lillo, Tucumán, Argentina.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
CYNODONTIA Owen, 1861
EUCYNODONTIA Kemp, 1982
CYNOGNATHIA Seeley, 1908
TRAVERSODONTIDAE von Huene, 1936

Genus ***Pontognathus*** gen. nov.

LSID urn:lsid:zoobank.org:act:7DB4433E-F7F7-4A04-AD5F-948240070801

Type species. *Pontognathus ignotus* sp. nov.

Derivation of name. *Ponto* from the Greek "sea", the name given to vast land extensions, in reference to the large, very fossiliferous outcrops of the Chañares Formation, where the holotype was found; and *gnathus* from the Greek "jaw", in reference to the characteristic lower jaw of cynodonts and a common ending for cynodont genera.

Diagnosis. Same as for the type species.

Pontognathus ignotus sp. nov.

Figure 2

LSID urn:lsid:zoobank.org:act:0FDF5202-9672-4760-B6BD-E450A32F21CE

Type Material. Holotype PULR-V 287, partial snout preserving the lateralmost incisor, the base of the canine, and several postcanines.

Derivation of name. *Ignotus* from the Latin "unknown", in reference to the long time before the recognition of this species despite the intensive paleontological exploration of the Chañares Formation.

Geographic and Stratigraphic Occurrence. PULR-V 287 was found in outcrops of the Chañares Formation west to El Portillo, between the northern unnamed affluent of the Gualo river to the north and the Agua Escondida river to the south (29° 53.085′ S; 67° 46.406′ W). In the study area, tetrapod fossils are confined to the lowermost 15 m of the Chañares Formation, within sediments that belong to a fining-upward sequence of channels. Specifically, PULR-V 287 specimen was found 9.4 m above the contact with the Tarjados Formation, within the laterally persistent, structureless, light-grey mudstone layers attributed to low-energy littoral mudflats of the Chañares Formation. This fossil-bearing horizon was dated to 236.1 ± 0.6 Ma (early Carnian) by Marsicano *et al.* (2016) and later recalculated to 236.5 ± 1.4 Ma by Irmis *et al.* (2022).

Diagnosis. Small cynodont with lateral platform of the maxilla absent unlike in other traversodontids; presence of a precanine diastema (unlike *Massetognathus* spp., *Santacruzodon hopsoni*, and *Scalenodon ribeiroae*); paracanine fossa medial to the upper canine (shared with *Massetognathus* spp., *Santacruzodon hopsoni*, *Dadadon isaloi* and *Paratraversodon franciscaensis*); nine upper postcanines (less than *Massetognathus* spp., and *Scalenodon* spp.); ovoid upper postcanines, wider labiolingually than mesiodistally in occlusal view; absence of shouldering between adjacent teeth (unlike in *Dadadon isaloi*, *Santacruzodon hopsoni*, and *Massetognathus* spp.); expansion of the crown distolateral to the sectorial crest very poorly developed (differing from *Dadadon isaloi*, *Santacruzodon hopsoni*, and *Massetognathus* spp.); occlusal basin mesiodistally shorter, relatively shallow, and limited by a less developed anterior crest than in *Massetognathus pascuali*; similar to *Massetognathus pascuali*, in the location and degree of development of the transversal crest, with the central and internal cusps very close; presence of a distal ridge-like bulging at the base of the crown (absent in *Massetognathus* spp., *Dadadon isaloi*, *Scalenodon* spp., and *Santacruzodon hopsoni*.

Associated fauna. Intensive prospection of the type locality of *P. ignotus* resulted in the finding of several specimens in a 1.5 m stratigraphic interval centred around the levels containing PULR-V 287. They are represented by fragmentary postcranial and cranial remains of archosauriforms and synapsids, including dinosauromorphs, proterochampsians, the cynodonts *Massetognathus pascuali* (including the specimens PULR-V 288 and PULR-V 289, see below) and *Probainognathus jenseni*, and dicynodonts.

Description. The skull PULR-V 287 is poorly preserved, represented by fragmentary portions of the snout, including part of both premaxillae and maxillae with signs of dorsoventral postmortem compression. It is inferred to have been approximately 9 cm in basal skull length. The absence of a maxillary platform lateral to the postcanines is the most distinctive trait (Fig. 2.5). PULR-V 287 only preserves the lateralmost incisor (Fig. 2.1). Although this tooth is badly damaged, it can be recognized that the crown is compressed labiolingually, with a main central cusp and a mesial accessory cusp. The distal margin of the crown is not well preserved, precluding the identification of further accessory cusps. The snout bulges laterally at the level of the canines (Fig. 2.2). The left canine is broken at the level of the root, but it is inferred to have been a relatively large tooth. The right canine is not preserved and only the posterior region of its alveolus is recognizable. Posterolaterally to this alveolus, the root of a smaller tooth is preserved, probably representing the replacing right canine (Fig. 2.1). A second tooth posteromedially adjacent to the replacing canine revealed by CT-scan images is interpreted as a second-generation replacement canine.

The upper postcanine tooth row is approximately straight, diverging posteriorly from the midline of the skull (Fig. 2.1). It is composed by nine postcanines. On the right side, PC1 and PC2 are only represented by the roots inside the alveoli whereas the crowns of PC3 to PC9 are preserved. On the left side, the crowns of PC1 to PC4 are missing and those of PC5 to PC7 are damaged. The roots of the left PC2 and PC4 and the tip of the root of the left PC3 are preserved inside the corresponding alveoli. There is a precanine diastema and a larger postcanine diastema. On the left side, the postcanine diastema is approximately the length of the canine alveolus whereas on the right side it seems to be longer. The postcanines are ovoid, wider labiolingually than mesiodistally. There is a large distolabial cusp, which is continuous with a mesially directed high sectorial crest (Fig. 2.3). Although not preserved in all the teeth, a mesiolabial cusp is inferred to be present from the third postcanine onward (Fig. 2.3). In postcanines anterior to PC5, the distolabial sector is projected labially relative to the mesiolabial cusp or mesiolabial region of the tooth, whereas in the sixth to eight teeth this region of the sectorial crest is less projected labially. A posteriorly placed transverse crest is present, with the central and lingual cusps occupying approximately the lingual half of the crown and separated by a large notch from the distolabial cusp (Fig. 2.5). PC4 to

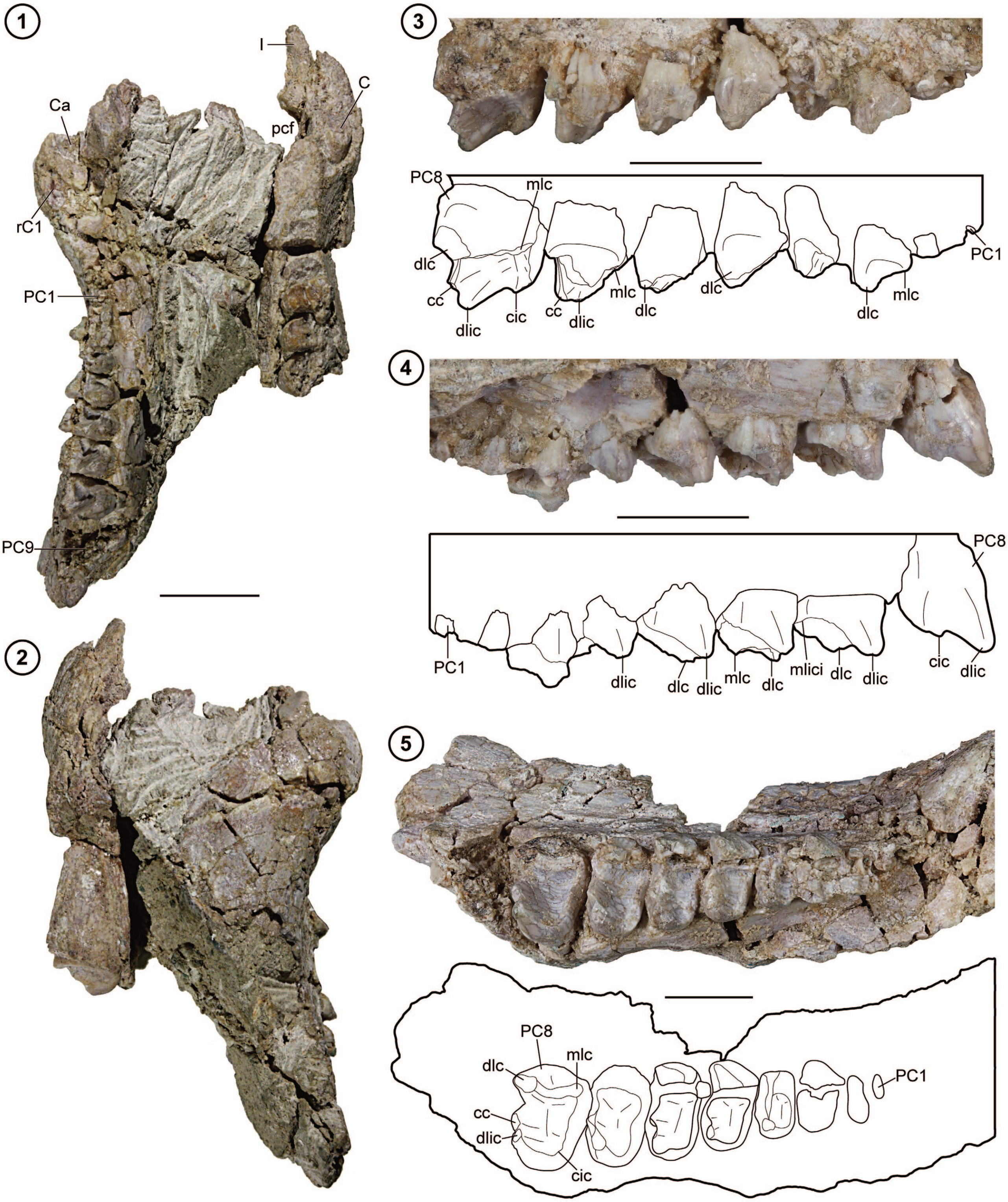

Figure 2. *Pontognathus ignotus* gen. et sp. nov. holotype specimen (**PULR-V 287**). **1–2,** Fragmentary skull; **1,** ventral view; **2,** dorsal view. **3–5,** Detail of the preserved upper postcanines; **3,** labial view; **4,** lingual view; **5,** occlusal view. Abbreviations: **C,** upper canine; **Ca,** upper canine alveolus; **cc,** central cusp; **cic,** cingular cusp; **dlc,** distolabial cusp; **dlic,** distolingual cusp; **I,** upper incisor; **mlc,** mesiolabial cusp; **mlici,** mesiolingual cingulum; **PC1,** first upper postcanine; **PC8,** eighth upper postcanine; **PC9,** ninth upper postcanine; **pcf,** paracanine fossa; **rC1,** first upper canine replacement. Scale bar= 10 mm in 1–2 and scale bar= 5 mm in 3–5.

PC8 show a mesiolingual cingulum represented by a well-developed crest, with PC5 to PC8 featuring several small cuspules or crenulations on this crest. In PC8, the crest ends lingually in a somewhat larger cusp (Fig. 2.4). This crest limits an occlusal basin, which is mesiodistally shallow, short on the lingual margin, and becomes deeper and longer labially, close to the sectorial ridge. A distal cingulum is not developed although a ridge-like bulging of the base of the crown is observed in PC6 to PC8. The shouldering is absent in the posterior better preserved postcanines. In PC5 and PC6, there is an apparent presence of this feature, but preservation is not good enough and may represent an impression after breakage of the crown. The PC9 is only represented by the poorly preserved transverse crest (Fig. 2.1), which conforms to the morphology observed in more anterior postcanines.

COMPARATIVE ANALYSIS

We performed comparisons with relevant traversodontids. For that purpose, we followed the descriptions and illustrations previously published (mainly von Huene, 1936; Crompton, 1955, 1972; Brink, 1963; Bonaparte, 1966b; Romer, 1967, 1972a; Kemp, 1980; Hopson, 1984; Goñi, 1986; Goñi & Goin, 1988; Sues *et al.,* 1992; Flynn *et al.,* 2000; Abdala & Ribeiro, 2003; Abdala & Sa-Teixeira, 2004; Liu *et al.,* 2008; Liu & Powell, 2009; Martinelli, 2010; Ranivoharimanana *et al.,* 2011; Kammerer *et al.,* 2012; Hopson, 2014; Melo *et al.,* 2017, 2022; Schmitt *et al.,* 2019; Hendrickx, *et al.,* 2020; Kerber *et al.,* 2024; Martinelli *et al.,* 2024) as well as personal observations of key specimens.

Pontognathus ignotus gen. et sp. nov. is distinctive among traversodontids for lacking a maxillary platform lateral to the posterior postcanines and by presenting a unique combination of characters from the premaxilla, maxilla, and dentition. Particularly relevant are comparisons with *M. pascuali*, the other traversodontid found in the same levels as *P. ignotus.* Similarities of their dentition suggest that these taxa might be closely related. However, *P. ignotus* can be clearly differentiated from *M. pascuali*, mainly by the absence of a maxillary platform, the reduced number of upper postcanines (nine *vs* 11 or more in similar sized and even in smaller individuals; Tab. 1), absence of shouldering between adjacent postcanines, the presence of only two cusps (instead of three) in the sectorial crest, poorly developed lateral expansion of the crown distolateral to the sectorial crest, mesiodistally shorter occlusal basin with a less developed anterior crest, presence of a distal ridge-like bulging, and presence of a precanine diastema (Fig. 3). Notable features also differentiate *P. ignotus* from traversodontids reported from purportedly coetaneous faunal associations from Western Gondwana, including *Dadadon isaloi* Flynn *et al.*, 2000, *Massetognathus ochagaviae* Barberena, 1981, *Santacruzodon hopsoni* Abdala and Ribeiro, 2003, *Traversodon stahleckeri* von Huene, 1936, and *Paratraversodon franciscaensis* Kerber *et al.,* 2024 (see below).

In *P. ignotus*, the maxillary lateral platform is absent unlike in other traversodontids, including small individuals of *M. pascuali*. Among traversodontids, *Scalenodon angustifrons* (Parrington, 1946) and *Paratraversodon franciscaensis* show a maxillary platform that is relatively poorly developed. The constriction in the snout posterior to the canine highlighted in *P. franciscaensis* and *Traversodon stahleckeri* (see Kerber *et al.,* 2024) is also present in *Pontognathus ignotus*. *Massetognathus* spp., *Santacruzodon hopsoni*, and *Scalenodon ribeiroae* Melo *et al.,* 2017 differ from *P. ignotus* in the absence of a precanine diastema. Unlike *P. ignotus*, only very short pre- and postcanine diastemata are present in *Scalendon angustifrons* and *Paratraversodon franciscaensis*. In *Scalenodon riberoae* and *P. franciscaensis*, the length of the postcanine diastema is comparable to that of *P. ignotus*. In *Mandagomphodon hirschsoni* (Crompton, 1972) and *P. ignotus*, there are pre- and postcanine diastemata; however, the postcanine diastema is comparatively longer in *M. hirschsoni*. *Luangwa drysdalli* Brink, 1963 and *Luangwa sudamericana* Abdala and Sa-Teixeira, 2004 differ from *P. ignotus* in the absence of postcanine diastema. The placement of the paracanine fossa in *P. ignotus* is medial to the upper canine as is the case in *Massetognathus* spp., *Santacruzodon hopsoni*, *Dadadon isaloi* and *Paratraversodon franciscaensis* (Abdala & Ribeiro, 2003; Ranivoharimanana *et al.,* 2011; Melo *et al.,* 2022, fig. 3; Kerber *et al.*, 2024, fig. 16b).

Pontognathus ignotus bears fewer postcanines (nine) than *Scalenodon spp.* (11 to 13), and *Massetognathus* spp. (11 to 19). The sample of *Massetognathus pascuali* is quite large, presenting variation in the number of upper postcanines according to the individual size. Nevertheless, in specimens approximately of the same size as *Pontognathus ignotus*, there are more postcanines in *Massetognathus pascuali* (Tab. 1). The number of upper postcanines varies from seven to 10 in *Dadadon isaloi*, from eight to 13 in *Santacruzodon hopsoni*, and from seven to nine in *Luangwa.* spp. *Paratraversodon franciscaensis* has nine upper postcanines. The last two postcanines of *P. ignotus* are the largest as in most other traversodontids, except for *Mandagomphodon attridgei* in which the last two postcanines are smaller than the previous teeth (Crompton, 1972, fig. 10A). This condition was also reported for "many specimens of *Scalenodon angustifrons*" (Crompton, 1972, p. 53) and, as an unusual condition, in one specimen of *Dadadon isaloi* with the posteriormost alveolus smaller than the previous one (Kammerer *et al.*, 2012, p. 115). In *Paratraversodon franscicaensis* the last postcanine, in eruption, is smaller than the previous teeth (Kerber *et al.*, 2024, fig. 8a).

The general outline of the upper postcanine crown in occlusal view is similar in *P. ignotus* and *Massetognathus pascuali*, *Traversodon stahleckeri*, and *Dadadon isaloi.*

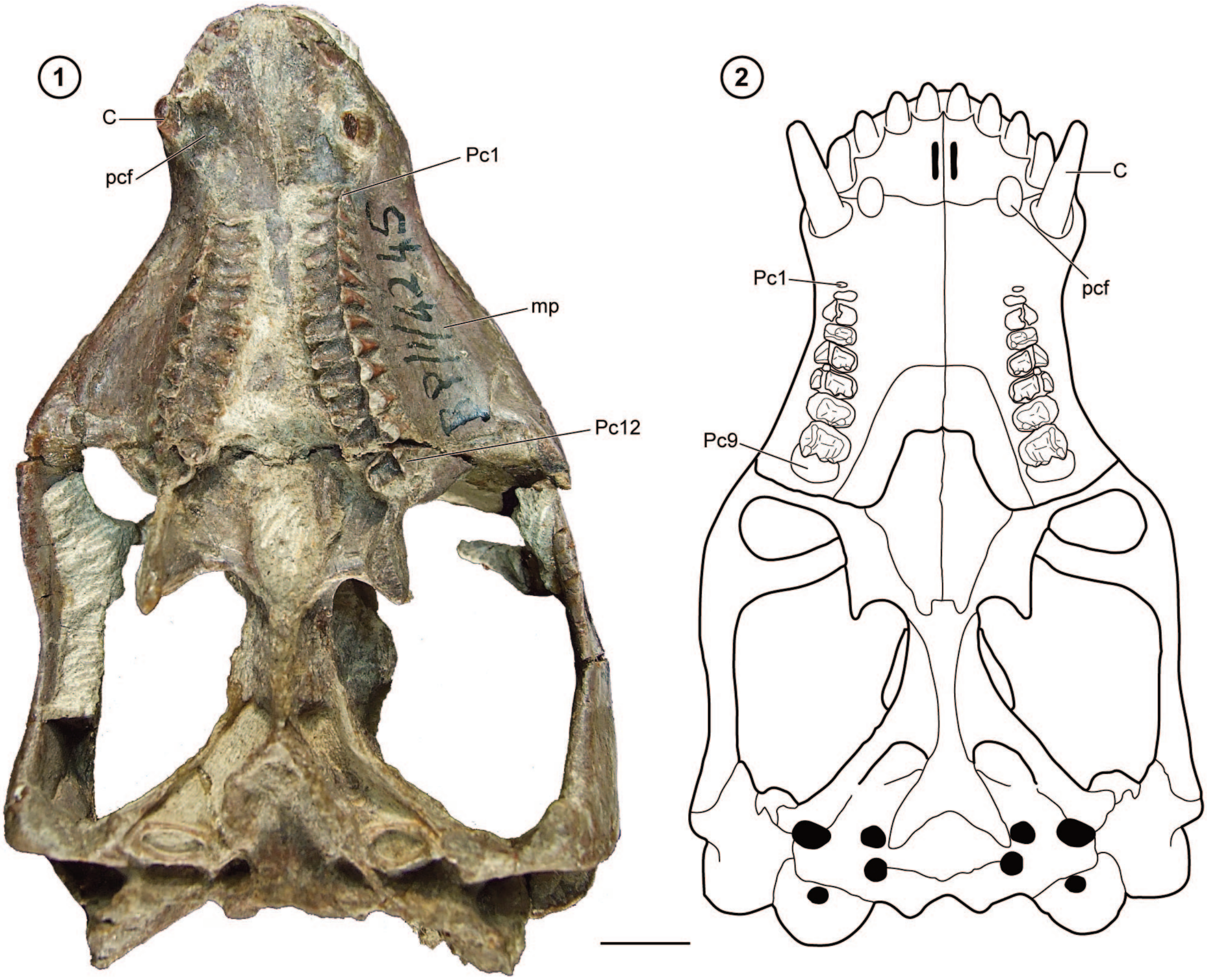

Figure 3. Comparison between a reconstruction of ***Pontognathus ignotus*** gen. et sp. nov. and a similar sized skull of ***Massetognathus pascuali***. **1,** ***Massetognathus pascuali*** skull (**BP/1/4245**) in ventral view. **2,** Reconstruction of ***Pontognathus ignotus*** in ventral view based on the holotype and only known specimen (**PULR-V 287**) and in ***Massetognathus pascuali*** specimens. Note the well-developed maxillary platform in ***Massetognathus pascuali*** (absent in ***Pontognathus ignotus***), the higher number of postcanines (12 *vs* 9 in ***Pontognathus ignotus***), and the different position of the paracanine fossa (slightly more anterior in ***Pontognathus ignotus***). Abbreviations: **C,** upper canine; **mp,** maxillary platform; **PC1,** first upper postcanine; **PC9,** ninth upper postcanine; **PC12,** twelfth upper postcanine; **pcf,** paracanine fossa. Scale bar= 10 mm.

TABLE 1 – Skull length and postcanine number of *Massetognathus pascuali*.

Specimen number	Skull length (cm)	Upper postcanine number	Lower postcanine number	Observations
MCZ 4212	~6.6	12		
PVL 4613	7.2	12-13	13-14	
MCZ 4221	7.6	12		
MCZ 4214	7.9	13	9	
MCZ 4219	8.1	12		
MCZ 4215	8.1	11		
MCZ 4216	8.1	11+1 e.t.		
PULR-V 10	8.3	?12		*M. pascuali* ty. s.
MCZ 4218	8.4	11		
PVL 3903	9	13		
PVL 4727	9	12+1 e.t.		
MCZ 3801	9.3	13+1 e.t.	14	
PVL 4729	9.6	11+1 e.t.		
MCZ 4208	10.1	13+1 e.t.		
PVL 3904	10.5	13+1 e.t.	12-13	
BP/1/4245	10.6	12	11+1 e.t.	
MCZ 3795	10.9	13		
MCZ 3798	11.4	12		
PVL 3901	12.4	14+1 e.t.	15	
PVL 4726	12.6	14	13	
PVL 3902	12.7	14	14	
MCZ 3806	13	?13		
MCZ 3804	13.2	13		
PVL 3906	14.2	13		
MCZ 4021	14.9	14+1 e.t.	10+1 e.t.	
PVL 4728	16	?13		
MCZ 4265	16.6	16		
PULR 65	18.6	17-18	19	*Me. oligodens* ty. s.
MCZ 4138	19.1	13-14		
PULR-V 11	20.4	13		*M. major* ty. s.

Specimens ordered from smaller to larger. Abbreviations: **e.t.**, erupting tooth; ***M.***, *Massetognathus;* ***Me.***, *Megagomphodon;* **ty. s.**, type specimen.

When compared to the quadrangular-shaped upper postcanines of *Pascualgnathus polanskii* Bonaparte, 1966b and *Santacruzodon hopsoni*, those of *P. ignotus* are more ovoid (relatively longer labiolingually than mesiodistally) in occlusal view. In addition, the upper postcanine series of *Santacruzodon hopsoni* shows triangular shaped anterior teeth and more enlarged labiolingually posterior postcanines. Even when the preservation in *P. ignotus* is incomplete, lacking the two most anterior postcanines, all the preserved crowns are labiolingually expanded. The upper postcanines of *Scalenodon angustifrons* are ovoid and relatively wider labiolingually than those of *P. ignotus*, even when considering the anterior teeth. In *Scalenodon ribeiroae,* there is a prominent change in the labiolingual extension of the upper postcanines between PC7 and PC8 and the posterior PC8 to PC11 are greatly expanded labiolingually whereas the more anterior are relatively narrow, similar to those of *P. ignotus*. *Luangwa* spp. show upper postcanines that are relatively larger, mesiodistally longer, and more separated from each other when compared to *P. ignotus*.

In *Dadadon isaloi*, *Santacruzodon hopsoni*, and *Massetognathus* spp., there is shouldering between adjacent teeth, more evident in the posterior teeth. This is not observed in *P. ignotus*, where the upper postcanines are slightly separated from each other. However, the last right upper postcanine preserved shows a distal embayment like that involved in the shouldering in *Massetognathus*. *Luangwa* spp., *Mandagomphodon hirschsoni*, *Scalenodon* spp., and *Paratraversodon franciscaensis* share with *P. ignotus* the lack of shouldering.

The expansion of the crown distolateral to the sectorial crest in the upper postcanines observed in *Dadadon isaloi*, *Santacruzodon hopsoni*, and *Massetognathus* spp. is less developed in *P. ignotus*. This expansion is shaped as an isosceles triangle in *Massetognathus ochagaviae*. The occlusal basin of *P. ignotus* is not as deep as in *Massetognathus* spp. When compared to *M. pascuali*, the occlusal basin of *P. ignotus* is mesiodistally shorter and bears a less developed anterior crest. On the other hand, *P. ignotus* occlusal basin appears to be better delimited by conspicuous labial, mesial, and lingual crests than in *Scalenodon*. The occlusal basin in *P. ignotus* is also better delimited than in *Mandagomphodon hirschsoni*, showing a more developed mesiolingual rim and mesiolabial cusp. The occlusal basin appears to be shallower and mesiodistally longer in *Luangwa* than in *P. ignotus*.

The posterior upper postcanines of *P. ignotus* show a distal ridge-like bulging at the base of the crown as in *Luangwa* spp., *Mandagomphodon hirschsoni*, and *Traversodon*. A distal cingulum is absent in *Massetognathus* spp., *Dadadon isaloi*, *Scalenodon* spp., and *Santacruzodon hopsoni*. Mesiolabial cingula are present in *Dadadon*, *Luangwa* spp., and *Scalenodon* spp. but absent in *P. ignotus*.

In *Andescynodon mendozensis* Bonaparte, 1969, *Luangwa* spp., *Pascualgnathus polanskii,* and *Scalenodon angustifrons*, the transverse crest is located more mesially on the crown, unlike *P. ignotus*. In *P. ignotus* there are three cusps in the transverse crest whereas the central cusp is absent in *Andescynodon mendozensis*, *Pascualgnathus polanskii*, and *Paratraversodon franciscaensis*. In *Scalenodon angustifrons* and *Luangwa drysdalli*, the central and lingual cusps of the transverse crest are farther away from each other than in *P. ignotus*. On the other hand, in *Traversodon stahleckeri* the central cusp of this crest is placed much closer to the lingual one when compared to *P. ignotus*. In *Mandagomphodon attridgei,* these cusps, only preserved complete in the last tooth in eruption, are relatively set apart from each other when compared to *P. ignotus* and *Mandagomphodon hirschsoni*. Unlike in *P. ignotus* and *Mandagomphodon hirschsoni*, in *Mandagomphodon attridgei* (Crompton, 1972) there are two mesial accessory cusps lingually (although in the last tooth there is only one).

Pontognathus ignotus has two cusps in the sectorial border of the upper postcanines, instead of the three of *Santacruzodon*, *Traversodon, Massetognathus* spp. (after Crompton, 1972; Schmitt *et al*., 2019; contra Romer, 1967), and of some postcanines of *Dadadon*. The last two postcanines of *Mandagomphodon attridgei* also features two cusps but surprisingly lack the mesiolabial one.

NEW MATERIALS OF *MASSETOGNATHUS PASCUALI*

Associated with *P. ignotus*, two small specimens (PULR-V 288 and PULR-V 289) attributable to *Massetognathus pascuali* were found. PULR-V 288 is a left partial snout and orbit, and PULR-V 289 is a partial lower jaw (Fig. 4). These specimens belong to small, similar sized individuals. With approximately 9 cm in basal skull length estimated for PULR-V 288, they are among the smallest specimens sampled (Tab. 1). Despite the impressive abundance of *M. pascuali* remains in the Chañares Formation, small individuals have not been properly described or illustrated. Hence, we present here a detailed description of PULR-V 288 and PULR-V 289.

PULR-V 288 - skull

The left side and part of the dorsal surface of the snout and orbital region are preserved in PULR-V 288 (Fig. 4.1). The snout is somewhat deformed and laterally compressed, which is particularly evident on the top of the skull, the

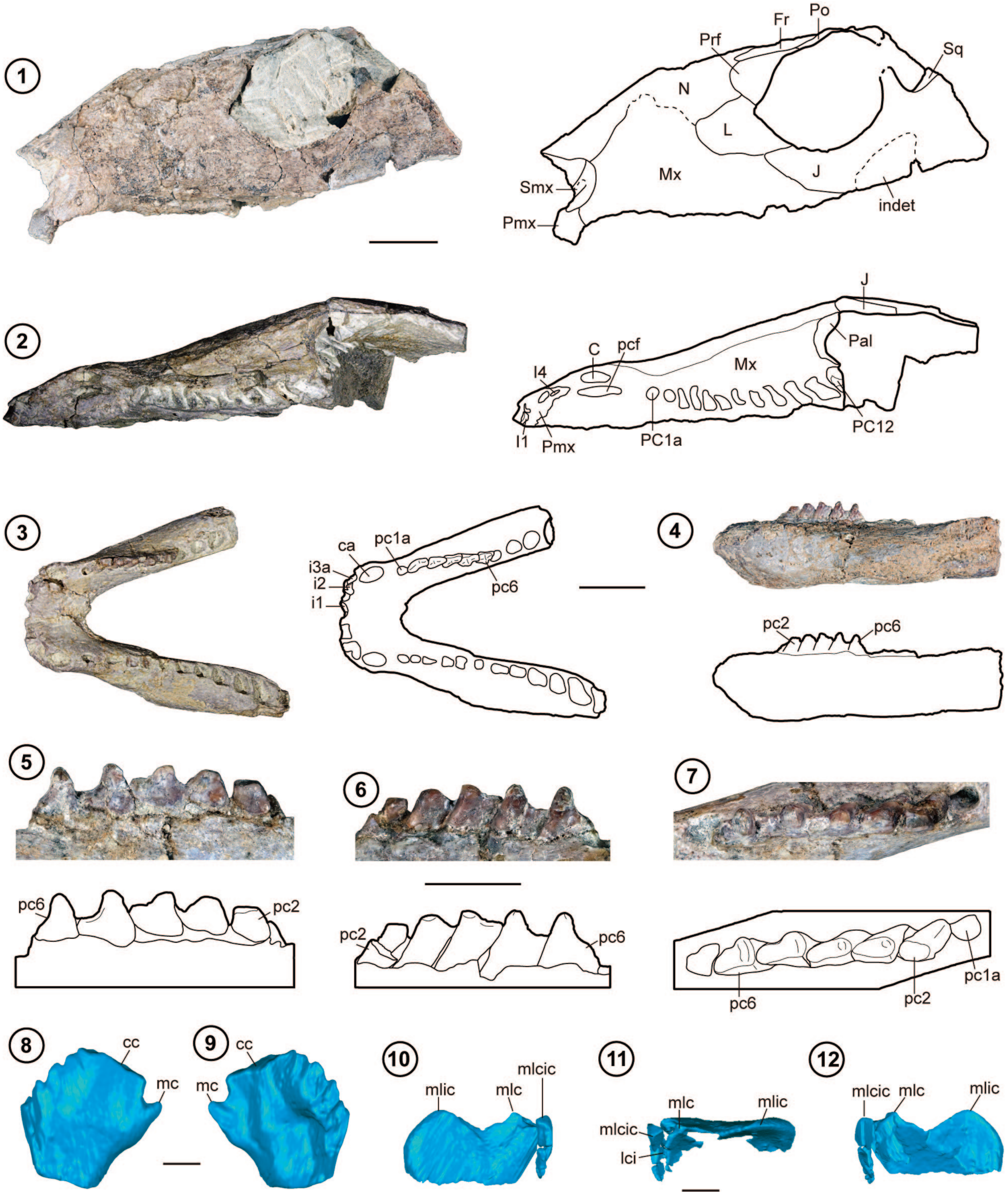

Figure 4. ***Massetognathus pascuali*** referred specimens. **1–2,** Partial skull (**PULR-V 288**); **1,** left lateral view; **2,** ventral view. **3–4,** Partial mandible (**PULR-V 289**); **3,** dorsal view; **4,** left lateral view. **5–7,** Detail of the preserved right lower postcanines; **5,** labial view; **6,** lingual view; **7,** occlusal view. **8–9,** Detail of the preserved right i2; **8,** labial view; **9,** lingual view. **10–12,** Detail of the postcanine preserved in the last left alveolus; **10,** mesial view; **11,** occlusal view; **12,** distal view. Abbreviations: **C,** upper canine; **ca,** lower canine alveolus; **cc,** central cusp; **Fr,** frontal; **i1,** first lower incisor; **I1,** first upper incisor; **i2,** second lower incisor; **i3a,** third lower incisor alveolus; **I4,** fourth upper incisor; **indet,** indeterminate bone fragment superimposed to the zygomatic arch; **J,** jugal; **L,** lacrimal; **lci,** labial cingulum; **mc,** mesial cusp; **mlc,** mesiolabial cusp; **mlcic,** mesiolabial cingular cusp; **mlic,** mesiolingual cusp; **Mx,** maxilla; **N,** nasal; **Pal,** palatine; **PC12;** twelfth upper postcanine; **pc1a,** first lower postcanine alveolus; **PC1a,** first upper postcanine alveolus; **pc2,** second lower postcanine; **pc6,** sixth lower postcanine; **pcf,** paracanine fossa; **Pmx,** premaxilla; **Po,** postorbital; **Prf,** prefrontal; **Smx,** septomaxilla; **Sq,** squamosal. Scale bar= 10 mm in 1–4; scale bar= 5 mm in 5–7; and scale bar= 1 mm in 8–12.

shape of the postcanine alveoli, and the medial projection of the zygomatic arch. The orbit length represents 62% of the snout length. The anterior portion features the incompletely preserved premaxilla being covered laterally by the maxilla, lacking preservation of the anteriormost margin of the bone, including the ascending process. The anterior portion of the septomaxilla covers the premaxilla dorsally on the anterior region of the external nares. Posteriorly, the septomaxilla is oriented dorsoposteriorly, contacting the maxilla and the nasal dorsally. The maxilla extends anteriorly well beyond the canine alveolus. As preserved, the maxilla is triangular in lateral view with the anterior margin ascending dorsoposteriorly, reaching its maximum height approximately at mid-length of the snout Fig. 4.1). Posteriorly, the dorsal margin of the maxilla cannot be clearly observed. The lacrimal presents a somewhat triangular outline and constitutes the anteroventral margin of the orbit. The prefrontal contacts the dorsoposterior portion of the lacrimal and reaches anteriorly until the middle length of the dorsal margin of the lacrimal. The prefrontal forms the anterior half of the dorsal margin of the orbit followed posteriorly by the postorbital, although it is not possible to observe a suture between these elements. The jugal extends anteriorly until the level of the anterior margin of the orbit and forms a deep suborbital bar and even deeper anterior root of the zygomatic arch. The maxillary platform lateral to the postcanine series is only slightly developed; it is a narrow triangular area that extends along the entire upper postcanine series (Fig. 4.2).

It is possible to observe three preserved incisors and a fourth one broken off at the level of the alveolar margin. The preserved and interpretable portion of these elements show that they were broad and leaf-shaped. The base of the crown of I1 shows a small mesial accessory cusp. The main cusp is symmetrically D-shaped in cross-section. One cuspule or tiny accessory cusp distal to the main cusp is observed in cross-section. This morphology is comparable to that described for other specimens of *Massetognathus pascuali* (Martinelli *et al.,* 2014a, 2014b). There is a large diastema between the last incisor and the canine. The canine appears to be a tiny tooth as judged by the size of the alveolus. A deep paracanine fossa is located medial to the upper canine (Fig. 4.2).

Like other *Massetognathus pascuali* specimens of comparable size, PULR-V 488 presents 12 postcanine alveoli (Tab. 1). The anterior 11 upper postcanine alveoli are empty whereas the last postcanine is represented by a tooth fragment, only featuring a wall of the crown. The upper postcanine tooth row is medially convex. Considering the size of the alveoli, the postcanines appear to have been relatively labiolingually narrow when compared to other specimens of *Massetognathus pascuali*.

PULR-V 289 - lower jaw and dentition

PULR-V 289 is a fragmentary dentary (Fig. 4.3–7). It preserves the horizontal rami, showing a fused symphysis. The dentaries are robust and low. The lateral surface is somewhat flattened until the level of the sixth alveolus and then become convex. The ventral margin of the dentary is rounded and quite wide. In medial view, it is observed the splenial suture, which starts almost in the ventral margin at the symphysis and continues upward posteriorly in a way that the splenial is completely enclosed by the dentary.

There are three incisors oriented anteriorly and a canine alveolus that is only slightly larger than the third incisor and postcanines. The second right lower incisor is partially preserved inside its alveolus (Fig. 4.8–9). As oriented in life-position, the labial surface of the tooth faces anteriorly. The crown of i2 is compressed labiolingually and long mesiodistally. It has a central main cusp that is symmetrical D-shaped in cross-section, with a concave labial surface and a bulbous, convex lingual one. The tip of the main cusp is missing. Mesially, separated from the main cusp by a broad valley, there is a finger-like cusp. The distal margin of the tooth is a labiolingually compressed flange integrated by conspicuous, well-defined, relatively large cuspules. A conspicuous constriction marks the beginning of the root, which is circular in cross-section. The right i1 is also preserved inside its alveolus; what is preserved of its crown suggests that it was similar to the i2. PULR-V 289 lower incisors differ from those *Massetognathus pascuali* lower incisors previously described (Martinelli *et al.,* 2014a, 2014b). They lack the numerous cuspules adjacent to the main cusp, up to five cuspules mesially and up to six distally, reported for i1 (Martinelli *et al.,* 2014a, 2014b). They also differ from i2 and i3, which were described as lacking the numerous mesial and distal cuspules (Martinelli *et al.,* 2014a, 2014b).

Anteriorly, the lower postcanine tooth row is anteroposteriorly oriented, forming an oblique angle with respect to the long axis of the dentary. At the level of pc7, there is an inflection point, and the tooth row orientation becomes parallel to the long axis of the dentary. Between pc2 and approximately pc9, there is a platform on the dentary lateral to the teeth. There are 12 postcanine alveoli on the left dentary. However, X-rays images show that between the canine and the first alveolus, there is a small cylindrical structure representing a tiny tooth inside the left mandibular ramus in the region corresponding to the postcanine diastema. Considering the evidence of wear and the erupted teeth, this element could be interpreted as a resorbed postcanine. There is no evidence of lower postcanine tooth replacement. Alveoli become progressively larger posteriorly. The first nine alveoli are longer mesiodistally than labiolingually, broad and trapezoidal in outline, with a labiolingually broader anterior region and narrower posterior one. The posterior three preserved alveoli are broader labiolingually than long mesiodistally and present an ovoid outline, with a mesiodistally longer labial region and a shorter lingual one.

On the right side, there is no evidence of a hidden tooth anterior to the first observable postcanine alveolus, which is thus recognized as pc1. Right postcanines (pc2 to pc6) are preserved with the crowns complete but worn, followed by two empty alveoli. The preserved crowns are extremely small and even when their traversodontid nature is possible to ascertain, they are not labiolingually expanded (Fig. 4.7). In the first two preserved crowns (pc2 and pc3), the anterior crest (typically formed by two cusps in the majority of traversodontids) seems to be formed by a single mesial cusp Fig. 4.5–7). In the last two postcanines (pc5 and pc6), the anterior crest is a little more expanded labiolingually (not conical) and eventually, two small cusps could have been present in unworn teeth.

The pc2 is broken and the crown slightly displaced in relation to the root (Fig. 4.5–7). The crown is worn away and it is quadrangular in occlusal view. With signs of strong wear, pc3 has a triangular outline in occlusal view. There is a large mesial cusp that gently slopes distally towards the end of the tooth. The pc3 fits in a mesial embayment on pc4, which is formed by the continuation of the mesial cusp lingually and the mesially projected labial margin of the crown (Fig. 4.5–7). The cusp in pc4 is almost in the centre of the tooth and is followed distally by a platform that, although partially covered by matrix, shows a higher lingual margin than the labial one. This tooth is in contact with the flat mesiolabial surface of pc5, but without interlocking. The anterior cusp in pc5 occupies the mesial half of the crown and is higher than in pc3 and pc4, showing less wear. Unlike more anterior postcanines, the cusp in pc5 is less conical and more labiolingually expanded as observed in occlusal view. The distal platform is not rimmed and inclined labially as in pc4. Unlike pc2 to pc4, which are placed obliquely regarding the long axis of the tooth row, pc5 and pc6 are aligned mesiodistally with the distal portion of pc5 in contact with the mesial surface of pc6. In this postcanine, the cusp is higher (as measured from the distal platform) than in pc5 and has a stepper mesial slope (Fig. 4.5–7). The cusp is not conical but somewhat spatulate, longer labiolingually than mesiodistally, convex mesially and straight to concave distally. The partially preserved distal platform appears to be similar to that of pc5.

A partial crown that differs notably from the above described postcanines is preserved inside the last left alveolus (Fig. 4.10–12). The morphological differences between this and the more anterior lower postcanines cannot be explained by any degree of wear. It is represented by the anterior crest of a labiolingually expanded tooth. The mesiolingual cusp is sharp, embodied by a leaf-shaped elevation of the anterior crest. It occupies approximately the lingual half of the crown. The mesiolabial cusp is missing at its tip. It is triangular in cross-section and interpreted as higher than the mesiolingual cusp. These cusps are separated by a broad V-shaped valley. Labial to the mesiolabial cusp, there is an accessory cusp which is as high as the mesiolingual cusp and is distally continuous with a cingulum rimmed by a sharp and well-defined crest (Fig. 4.10–12). There is no mesial cingulum. A deep and mesiodistally short basin is only partially preserved.

Considering the morphology of the preserved postcanine crowns and alveoli, it appears that the first nine alveoli corresponded to a postcanine morphology represented by the right pc2–pc6, whereas the last three alveoli were occupied by postcanines resembling the most posterior preserved left tooth. This suggests that lower postcanine crown morphology changed through life, with more labiolingually expanded teeth being added posteriorly. Notably, the most posterior tooth preserved in PULR-V 289 is relatively much wider labiolingually than long mesiodistally (Fig. 4.10–12) when compared to previously published specimens of *Massetognathus pascuali*, which also lack a large mesiolabial accessory cusp and a labial cingulum. It cannot be discarded that this tooth captures an incipient stage in tooth formation. It is also a possibility that the distal portion of the tooth has not yet developed.

DISCUSSION

Cynodonts are, by far, the most common fossils recovered from the traditional levels of the Chañares Formation, but the taxonomic diversity of cynodonts, as presently recognized, is less than that of non-archosaurian archosauriforms (Mancuso *et al.,* 2014, 2022; Ezcurra *et al.,* 2017; Ordoñez *et al.,* 2020). Based on Mancuso *et al.* (2014), approximately 150 traversodontid specimens have been collected up to that date, representing 46% of the total specimens recovered, a value well above any other group of tetrapods from the fauna. Nevertheless, only two traversodontid species, *Massetognathus pascuali* and, the here described *Pontognathus ignotus*, are currently considered valid. In addition, the lowermost levels of the formation yielded two fragmentary specimens of an indeterminate traversodontid similar to *Mandagomphodon* or *Scalenodon* (Ezcurra *et al.,* 2017). The presence of *Menadon* sp. in the upper levels of the Chañares Formation has been suggested (Martinelli *et al.,* 2023) but its proper publication still awaits.

The low diversity of traversodontids from the Chañares Formation strongly contrasts with that of age-equivalent levels from Brazil, where a total of nine different traversodontid species have been reported from the *Dinodontosaurus* and *Santacruzodon* assemblage zones (Martinelli *et al.,* 2017; Abdala *et al.,* 2020). A similar scenario is also depicted true in relation to probainognathian diversity, with six nominated species from these Brazilian assemblage zones and only three or four species (*i.e.*, *Chiniquodon theotonicus, Probainognathus jenseni, Riojanodon nenoi*, and a specimen identifiable only as Aleodontinae indet.—possibly representing a more mature specimen of *R. nenoi*, a specimen of *Aleodon*, or a distinct aleodontine taxon) in the Chañares Formation (Martinelli *et al.,* 2017; Abdala *et al.,* 2020; Martinelli *et al.,* 2024). Considering the intensive prospection efforts in the Chañares Formation since the 1970s by different paleontological teams, the favourable taphonomic conditions for fossil preservation, especially of small- and medium-sized animals, and the very abundant fossil remains in the unit, it appears that the comparatively low taxonomic richness might be close to reflecting the actual ecological diversity (Mancuso *et al.,* 2014).

Three main factors could explain differences in cynodont taxonomic richness between the Chañares Formation and age-equivalent levels in Brazil, with paleoclimate and paleoenvironment being two of them. The currently accepted paleogeographic reconstructions suggest that fossiliferous localities of present-day La Rioja (Argentina) and Rio Grande do Sul (Brazil) shared similar latitudinal positions, with the Brazilian ones in a more inland setting relative to the Pangaean coastline, resulting in a relatively more pronounced seasonal climate (Mancuso *et al.,* 2021). These climatic variations led to contrasting paleoenvironments, with seasonally dry, open landscapes in southern Brazil, as opposed to the sub-humid forest prevailing in western Argentina (Ordoñez *et al.,* 2020; Mancuso *et al.*, 2021). Given the profuse fossil record, there is currently no evidence that the hypothesized seasonal semi-arid to sub-humid conditions for the Chañares Formation (Mancuso *et al.,* 2020, 2022; Benavente *et al.,* 2022) negatively impacted in the diversity of cynodonts. In addition, by extrapolation from the diversity represented in present-day ecosystems, a higher number of cynodont species would be expected to be registered in the Chañares Formation than in its Brazilian counterpart. Hence, the predominance of different biomes does not, at present, provide a feasible explanation for the dissimilar record of cynodonts species in the approximately coeval Chañares Formation faunal association and those from the *Dinodontosaurus* and *Santacruzodon* assemblage zones of the Santa Maria Supersequence.

The third factor that may influence taxonomic richness differences between the Argentinian and Brazilian faunal associations is the temporal range constraints. Nearly all vertebrate fossils in the Chañares Formation are derived from the lowermost 20 m of the unit (Mancuso *et al.,* 2014; Marsicano *et al.,* 2016; Ezcurra *et al.,* 2017), indicating a modelled age range of 237.9–235.0 Ma for this assemblage (Irmis *et al.,* 2022). According to this, the base of the Chañares Formation (and its fossils) may date to the latest Ladinian, whereas most of the formation, and its vertebrate assemblage, are likely earliest Carnian in age. In contrast, the age range of the *Dinodontosaurus* and *Santacruzodon* assemblage zones of the Santa Maria Supersequence is less precisely constrained. There is a single geochronological date of these levels, which yielded a maximum depositional age of 236.3 ± 7.0 Ma for the middle portion of the Santa Cruz Sequence (*Santacruzodon* Assemblage Zone) (Horn *et al*., 2014; Philipp *et al.,* 2018; Irmis *et al.,* 2022). According to preliminary age assessments, the *Dinodontosaurus* and *Santacruzodon* assemblage zones range from the Ladinian to the Carnian (*e.g.*, Martinelli *et al.,* 2017; Schmitt *et al.,* 2019; Schultz *et al.,* 2020; Irmis *et al.,* 2022). A putative longer temporal range of the Brazilian faunal associations could likely contribute to their apparent richness. The Santa Maria Supersequence might thus capture stages of faunal recovery, ecological succession, and shifts in taxonomic composition that are not represented in the ~3-million-year time span represented by the fossiliferous levels of the Chañares Formation. However, testing this hypothesis requires dating individual Brazilian fossil-bearing horizons with greater precision.

The *Massetognathus-Chanaresuchus* Assemblage Zone of the Chañares Formation is noteworthy by the relatively few specialized herbivorous species registered when compared to those that are interpreted to be mainly faunivorous (see for example Mancuso *et al.,* 2014). Considering all taxonomic groups reported from this assemblage zone, only synapsids show clear plant-eating specializations. Dicynodonts are represented by ~30 specimens of the large *Dinodontosaurus brevirostris* and a few postcranial remains of unidentified stahleckeriids (Mancuso & Irmis 2020; Kammerer & Ordoñez 2021; but see Escobar *et al.,* 2021). Among cynodonts, the very abundant *Massetognathus pascuali* dominates numerically the faunal association. Specimens of *Massetognathus pascuali* reportedly range from approximately 7 to 20 cm in basal skull length (Abdala & Giannini 2000; Mancuso *et al.,* 2014). Body mass estimates for *Massetognathus pascuali* suggest it was a medium-sized animal ranging from 20 to 40 kg (Mancuso *et al.,* 2014; Filippini *et al.,* 2022) and 10 to 30 kg (Filippini *et al*., 2025); although much lighter estimates have been proposed by Medina *et al*. (2025). The specialized, small-herbivore/omnivore ecological role that might have been occupied by *P. ignotus* in the community is otherwise shared by small, juvenile individuals of the traversodontid *Massetognathus pascuali. Riojanodon nenoi* and a potentially distinct indeterminate aleodontine (from the lowermost levels of the Chañares Formation; see Ezcurra *et al.,* 2017; Martinelli *et al.,* 2024) represent two probably herbivorous cynodonts comparable in size to *P. ignotus*.

In the *Dinodontosaurus* and *Santacruzodon* assemblage zones from Brazil, herbivorous taxa reach body-sizes comparable to those of *Massetognathus pascuali* and the dicynodonts from the Chañares Formation. Alternatively, small-sized specialized herbivorous cynodonts with expanded postcanine crowns are recognized among late Permian non-eucynodont cynodonts, the Middle Triassic trirachodontids, early-branching traversodontids, and the Late Triassic–Early Cretaceous tritylodontids. The aleodontine *Cromptodon mamiferoides* Bonaparte, 1972 (see Martinelli *et al.,* 2024, fig. 12) from the Middle Triassic Cerro de las Cabras Formation (Mendoza, Argentina) and the tiny, expanded allotherian-like postcanines described from the *Langbergia-Garjainia* subzone of the *Cynognathus* Assemblage Zone of South Africa (Abdala *et al.,* 2007; Gaetano *et al.,* 2012) are also interpreted as small herbivorous forms.

CONCLUSIONS

The new Carnian traversodontid *Pontognathus ignotus* presents a unique craniodental morphology. It is notable for the absence of the maxillary platform, which has not been previously observed among traversodontids. *P. ignotus* is among the smallest traversodontids reported to date and partially fills a gap in the Chañares Formation faunal association, in which small, specialized herbivorous/omnivorous taxa are underrepresented.

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AVAILABILITY OF MATERIALS AND DATA

All specimens presented in this contribution are catalogued and accessible in the fossil collection of the Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina. Digital surface models of specimens PULR-V 287 and PULR-V 289 are freely available in MorphoMuseuM (https://doi.org/10.18563/journal.m3.256).

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