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THE FIRST RHYNCHOCEPHALIAN FROM THE LATE JURASSIC OF SOUTH AMERICA (CAÑADÓN CALCÁREO FORMATION, CHUBUT, ARGENTINA)

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Abstract. The fossil record of rhynchocephalian lepidosaurs in South America spans from the Late Triassic to the Paleocene, but remains sparse and elusive. Currently, there are many gaps in our understanding of the diversity and evolutionary history of South American taxa, due to the scarcity of specimens and often fragmentary remains. Here we describe the first Late Jurassic rhynchocephalian from the continent, from the probable Oxfordian Cañadón Calcáreo Formation of Chubut Province, Argentina. The specimen is poorly preserved and represented solely by postcranial elements. The presence of amphicoelous vertebrae with notochordal canal and gastralia allows the identification of this specimen as a rhynchocephalian of unclear affinities. The latest phylogenetic analyses suggest that only neosphenodontians were present in Argentina. Thus, it is likely that the specimen belongs to this derived clade of rhynchocephalians, but the lack of diagnostic features hampers secure referral.

Key words. Sphenodontia. Neosphenodontia. Oxfordian. Paleobiogeography.

Resumen. EL PRIMER RINCOCÉFALO DEL JURÁSICO SUPERIOR DE AMÉRICA DEL SUR (FORMACIÓN CAÑADÓN CALCÁREO, CHUBUT, ARGENTINA). El registro fósil de los lepidosaurios rincocéfalos en América del Sur abarca desde el Triásico Superior hasta el Paleoceno, aunque sigue siendo escaso y fragmentario. Actualmente, existen numerosos vacíos en el conocimiento sobre la diversidad y la historia evolutiva de los taxones sudamericanos, debido a la escasez de especímenes y a que los restos suelen estar incompletos. En este trabajo describimos el primer rincocéfalo del Jurásico Superior del continente, procedente de la Formación Cañadón Calcáreo (provincia del Chubut, Argentina), cuya antigüedad es probablemente oxfordiana. El espécimen está mal preservado y representado únicamente por elementos poscraneales. La presencia de vértebras anficélicas con canal notocordal y de gastralias permite identificar este ejemplar como un rincocéfalo de afinidades inciertas. Los análisis filogenéticos más recientes sugieren que en Argentina solo estaban presentes los neosfenodontes. Por tanto, es probable que el espécimen pertenezca a este clado derivado de rincocéfalos, aunque la ausencia de caracteres diagnósticos impide una asignación taxonómica definitiva.

Palabras clave. Sphenodontia. Neosphenodontia. Oxfordiano. Paleobiogeografía.

INTRODUCTION

Rhynchocephalia, a group of ancient reptiles closely related to lizards and snakes, is currently represented by a single species, *Sphenodon punctatus* (Gray, 1842), endemic to some islands off the coast of the North Island of New Zealand (Cree, 2014). During the Mesozoic, rhynchocephalians were taxonomically and ecologically diverse and cosmopolitan, being found on almost every continent up to the end of the Jurassic, when their diversity plummeted (Beccari *et al.*, 2025). South America is home to some of the oldest rhynchocephalians, *e.g.*, *Microsphenodon bonapartei* Chambi-Trowell *et al.*, 2021 and *Clevosaurus brasiliensis* Bonaparte & Sues, 2006, both from the Late Triassic (Norian) of the Caturrita Formation, Brazil (Chambi-Trowell *et al.*, 2021), and *Sphenotitan leyesi* Martínez *et al.*, 2013 from the Late Triassic (Norian) Quebrada del Barro Formation, San Juan province, Argentina (Martínez *et al.*, 2013). The youngest rhynchocephalian outside New Zealand, *i.e.*, *Kawasphenodon peligrensis* Apesteguía *et al.*, 2014, also comes from South America, from the Paleocene (Danian) Salamanca Formation, Chubut province, Argentina (Apesteguía *et al.*, 2014). Thus, Argentina holds the longest geological record of rhynchocephalians in South America and even globally, spanning from the Late Triassic to the Paleocene, some 150 Ma (Martínez *et al.*, 2013; Apesteguía *et al.*, 2014; Apesteguía, 2016). Despite its long geological extent, the rhynchocephalian fossil record in Argentina remains highly incomplete, with no taxa described so far

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from the Middle and Late Jurassic. Here we report the first rhynchocephalian from the Late Jurassic (Oxfordian) Cañadón Calcáreo Formation, north-central Chubut Province, Argentina.

Institutional abbreviations. MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina; **NKMUK PV R,** Natural History Museum, Collection of Palaeovertebrates, London, UK.

GEOLOGICAL SETTING

The specimen described here comes from the Cañadón Calcáreo Formation, a unit of lacustrine and fluvial deposits that forms part of the sedimentary infill of the Cañadón Asfalto basin, a large NNW-SSE trending hemigraben structure that extends from southern Río Negro Province into north-central Chubut Province, Argentina (Figari *et al.*, 2015). The formation consists of a basal lacustrine section with highly variable thickness, often underlain by a basal breccia or conglomerate, and a thick fluvial succession in its upper section that reaches several hundred to 1000 m in thickness (Proserpio, 1987; Figari *et al.*, 2015).

The specimen described here was collected by one of us (OR) during fieldwork in April 2019. It comes from a thin sandstone layer (20–25 cm) that is part of an alternating series of sandstones and siltstones in the area of Puesto Almada, close to the type locality of the crocodylomorph *Almadasuchus figarii* (Pol *et al.*, 2013), likely in the same layer. The layer is within the lower section of the formation in this area, being placed in the lower portion of the fluvial section, approximately 20–30 m above the main fish layer, an important marker horizon in the basal lacustrine part of the unit (Figari *et al.*, 2015; Dussán Villanueva, 2019). The Cañadón Calcáreo Formation has been radiometrically dated to the Oxfordian (157 Ma; Cúneo *et al.*, 2013).

MATERIAL AND METHODS

Specimen MPEF-PV 10457 (Museo Paleontológico Egidio Feruglio, Trelew, Argentina) consists of a highly weathered, partially articulated skeleton from the Late Jurassic of the Cañadón Calcáreo Formation. The specimen represents a small individual, with the preserved part of the skeleton measuring about 46 x 44 mm. Pictures of the specimen were taken using a mirrorless camera OM-1 (OM Digital Solutions, Shinjuku, Tokyo, Japan) paired with an Olympus M.Zuiko Digital ED 60 mm F2.8 Macro lens. All measurements were taken on the physical specimen using an analogue Mitutoyo calliper (error 0.02 mm; Mitutoyo America Corporation, USA).

SYSTEMATIC PALAEONTOLOGY

LEPIDOSAUROMORPHA Gauthier, 1984

LEPIDOSAURIA Haeckel, 1866

cf. Rhynchocephalia Günther, 1867 *sensu* DeMar *et al.*, 2022

Rhynchocephalia indet.

Figure 1

DESCRIPTION

The specimen comprises postcranial bones, most of which are preserved as impressions on the sediment (Fig. 1). All preserved bones represent the mid-region of the skeleton, with the skull, cervical series, and caudal series missing. MPEF-PV 10457 would represent a small-sized lepidosauromorph, with a total preserved length of 30.3 mm, comprising vertebrae, ribs, and gastralia, likely representing the presacral series length without cervical vertebrae. The gastralia region measures about 21 mm in length, close to that of *Clevosaurus hudsoni* Swinton, 1939 specimen NHMUK PV R36832 (O'Brien *et al.*, 2018), *Homoeosaurus parvipes* Cocude-Michel, 1963, and *Leptosaurus neptunius* Goldfuss, 1831 (Cocude-Michel, 1963). Thus, compared with the average size of these taxa, MPEF-PV 10457 would represent an animal of about 50 mm snout-vent length.

Three vertebrae are visible but poorly preserved in MPEF-PV 10457. The outlines of their centra resemble the typical amphicoelous, hourglass-shaped condition of non-squamatan lepidosauromorphs and most rhynchocephalians, *i.e.*, being laterally concave in dorsal and ventral views (Hoffstetter & Gasc, 1969; Beccari *et al.*, 2026). Different from the lepidosauromorphs *Marmoretta oxoniensis* Evans, 1991 (Ford *et al.*, 2025) and *Megachirella wachtleri* Renesto and Posenato, 2003 (Renesto & Bernardi, 2014), the amphicoelous pleurocentra preserved the notochordal canal (Fig. 1 C-D). This feature is synapomorphic of rhynchocephalians among lepidosauromorphs (Martínez *et al.*, 2021), albeit also being present in gekkotans and the stem

squamate *Bellairsia gracilis* Evans, 1998 (Tałanda *et al.*, 2022). The centra of MPEF-PV 10457 are almost as long as wide. If the proportions follow those of *Sphenodon* Gray, 1831, the cubic centra of MPEF-PV 10457 would represent anterior dorsal vertebrae (Beccari *et al.*, 2026).

At least four ribs are preserved in MPEF-PV 10457. These are highly weathered and are seen through a longitudinal cut. The ribs are bowed and hollow. The size of these ribs increases posteriorly, with the last one being the longest. The smaller anterior ribs, which are associated with the preserved vertebrae, also suggest that those pertain to anterior dorsals (Beccari *et al.*, 2026). The internal walls of these ribs are thickened, but not to the same extent as in *Ankylosphenodon pachyostosus* Reynoso, 2000 and *Palaeopleurosaurus posidonae* Carroll, 1985 (Klein & Scheyer, 2017).

Many gastralia elements (between 18 and 19) are preserved, some of which preserve parts of the bones. These are divided into a pair of lateral and a median gastralia, the latter of which shows a short anterior chevron. The angle between the median gastralia arms ranges between 115° and 145°, with the posteriormost showing the lowest values. This range is similar to that of *Clevosaurus hudsoni* specimen NHMUK PV R36832 (O'Brien *et al.*, 2018), higher than that of *Megachirella wachtleri* (Renesto & Bernardi, 2014) and *Sphenodon* (between 90° to 120°), but lower than the Solnhofen rhynchocephalians *Kallimodon pulchellus* (Zittel, 1887–1890) and *Homoeosaurus maximiliani* von Meyer, 1847 (between 150° and 170°; Beccari *et al.*,

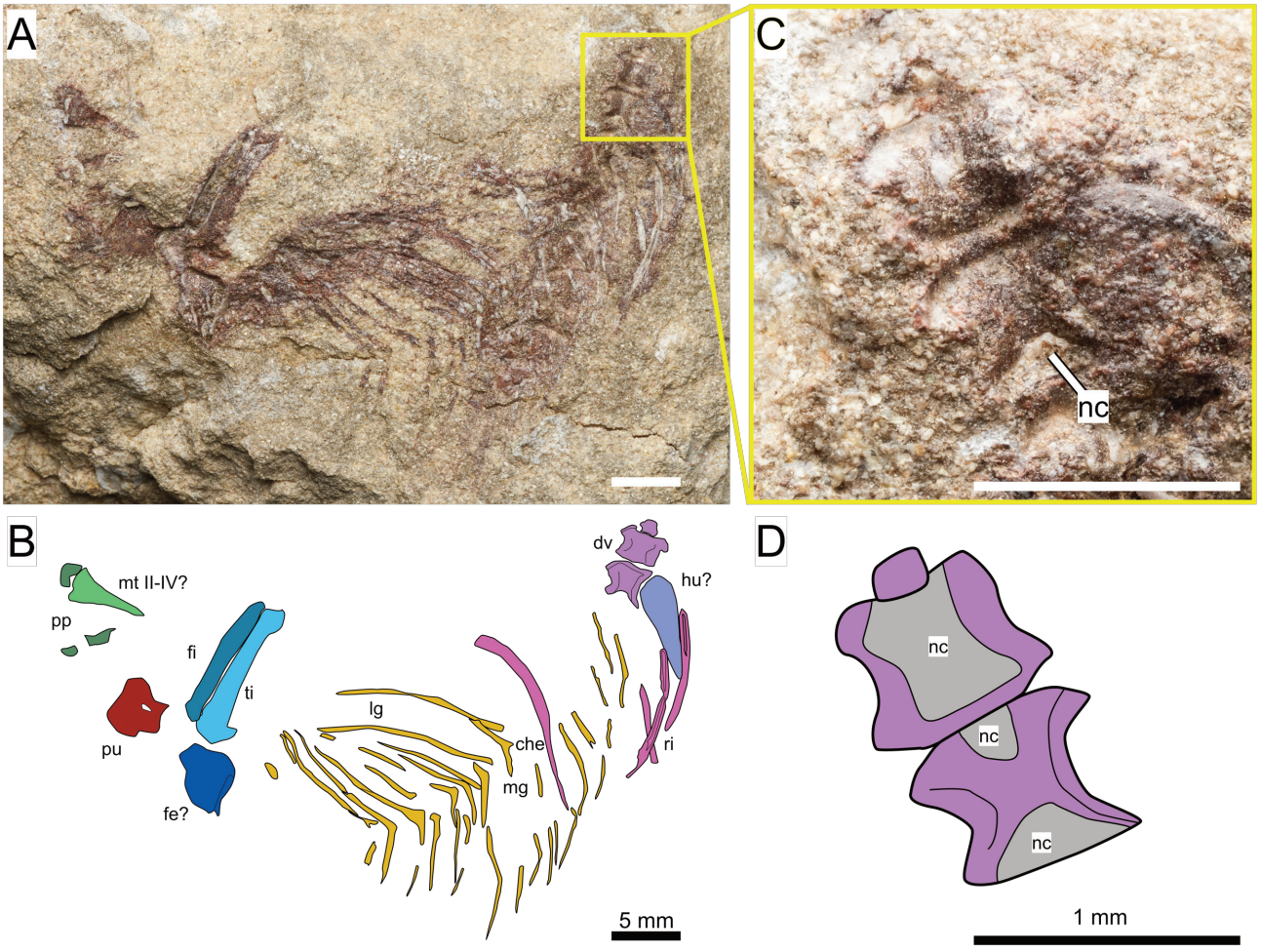


Figure 1. Rhynchocephalian specimen MPEF-PV 10457. **A,** photograph of the specimen; **B,** schematic drawing of the specimen; **C,** photograph of the anteriormost preserved (dorsal) vertebrae; **D,** schematic drawing of the dorsal vertebrae. Abbreviations: **che,** medial chevron; **dv,** dorsal vertebra; **fe?,** possible femur; **fi,** fibula; **hu?,** possible humerus; **lg,** lateral gastralium; **mg,** medial gastralium; **mt II–IV?,** metatarsal, possibly II to IV; **nc,** notochordal canal; **pp,** pedal phalanx; **pu,** pubis; **ri,** ribs; **ti,** tibia.

2026). Gastralia are absent in squamates (Russell & Bauer, 2008).

Some appendicular bones are preserved to varying degrees, most of which are only outlines, whereas the possible pubis and an undetermined metatarsal (II–IV?) still preserve the bone sections. The outline of an elongated bone next to the vertebrae and ribs can possibly be identified as a humerus, however, it cannot be described in detail due to its preservation. The pubis preserves only the proximal region, but the articular facets for the ilium and ischium cannot be observed. A lateromedially elongated obturator foramen is present. The possibly distal end of a femur is still in articulation with two other long bones, here interpreted as the tibia and fibula. The shafts of these two bones are relatively straight and robust, *i.e.*, midshaft width/length = 0.13 for both the tibia and fibula. These proportions are similar to those of *Sphenodon punctatus*, but lower than those of pleurosaurids, and higher than most other neosphenodontians, *e.g.*, *Homoeosaurus maximiliani*, *Navajosphenodon sani* Simões *et al.*, 2022, *Sphenodraco scandentis* Beccari *et al.*, 2025, and *Sphenofontis velserae* Villa *et al.*, 2021 (Beccari *et al.*, 2025, supplementary data 1 therein). Only the distal end of a metatarsal is preserved, in articulation with the proximal end of a pedal phalanx. This metatarsal is elongated, suggesting it is the second to fourth metatarsals (Russell & Bauer, 2008). The distal end is poorly preserved but is slightly expanded compared to the shaft.

DISCUSSION

The specimen MPEF-PV 10457, although highly incomplete and poorly preserved, shows a combination of morphological features unique to rhynchocephalians: amphicoelous presacral vertebrae, persistence of the notochordal canal, and presence of gastralia with fused chevrons. Other Jurassic lepidosauromorphs, *e.g.*, *Bellairsia* Evans, 1998, *Marmoretta* Evans, 1991, *Megachirella* Renesto and Posenato, 2003, show a combination of two, but never three of these characters. *Bellairsia* and crown squamates lack gastralia (Simões *et al.*, 2017; Tałanda *et al.*, 2022), whereas the vertebral centra of both *Marmoretta* and *Megachirella* lack persistent notochordal canals (Simões *et al.*, 2018; Ford *et al.*, 2025). It is worth noting that the Triassic placodonts *Largocephalosaurus qianensis* Li *et al.*, 2014 and *Placodus gigas* Agassiz, 1833 show a similar combination of morphological characters to MPEF-PV 10457, but their gastralia are pachyostotic and lack short medial chevrons (Diedrich, 2013; Li *et al.*, 2014). Furthermore, these reptiles are substantially older than MPEF-PV 10457 and were fully marine. Thus, the combination of morphology and stratigraphy allows for a rather secure classification of the Calcáreo Formation specimen as an indeterminate rhynchocephalian.

A finer taxonomic assignment for MPEF-PV 10457 is currently not possible, owing especially to its poor preservation, but also to a general lack of detailed morphological descriptions of rhynchocephalian postcranial skeletons, although the latter has progressively changed in the past decade (Villa *et al.*, 2021; DeMar *et al.*, 2022; Beccari *et al.*, 2026). By the Late Jurassic, neosphenodontians (Neosphenodontia *sensu* DeMar *et al.*, 2022) were likely the sole survivors of this reptile group (Jones, 2006; Evans & Jones, 2010). Neosphenodontia has been divided into Sphenodontidae and Leptorhynchia (*sensu* DeMar *et al.*, 2022), with the latter currently known solely by Laurasian taxa (Europe and North America; Beccari *et al.*, 2026). Argentina has yielded 12 named rhynchocephalian species so far, but these are geographically and stratigraphically spread (Fig. 2), ranging from the Late Triassic (Norian; Martínez *et al.*, 2013) to the Paleocene (Danian; Apesteguía *et al.*, 2014). The majority of these taxa are known solely from fragmentary cranial elements (*e.g.*, *Alamitosphenos mineri* Agnolín *et al.*, 2024, *Kawasphenodon* Apesteguía, 2005, and *Sphenocondor gracilis* Apesteguía *et al.*, 2012). Even when the postcranium is preserved, it is either extremely fragmentary, as in the case of *Lamarquesaurus cabazai* Gentil *et al.*, 2019, or lacks formal description, as in the case of *Priosphenodon avelasi* Apesteguía & Novas, 2003. Thus, the phylogenetic relationships of Argentine rhynchocephalians have been underexplored, with taxa such as *Alamitosphenos* Agnolín *et al.*, 2024 and *Notosphenos finisterre* Agnolín *et al.*, 2025 never having had their phylogenetic positions tested, owing to their extremely fragmentary holotypes. However, most phylogenetic studies incorporating Argentine taxa (*e.g.*, Gentil *et al.*, 2019; Apesteguía *et al.*, 2021; Chambi-Trowell *et al.*, 2021; DeMar *et al.*, 2022; Beccari & Rauhut, in press) found that the Argentine taxa, even the oldest known representative,

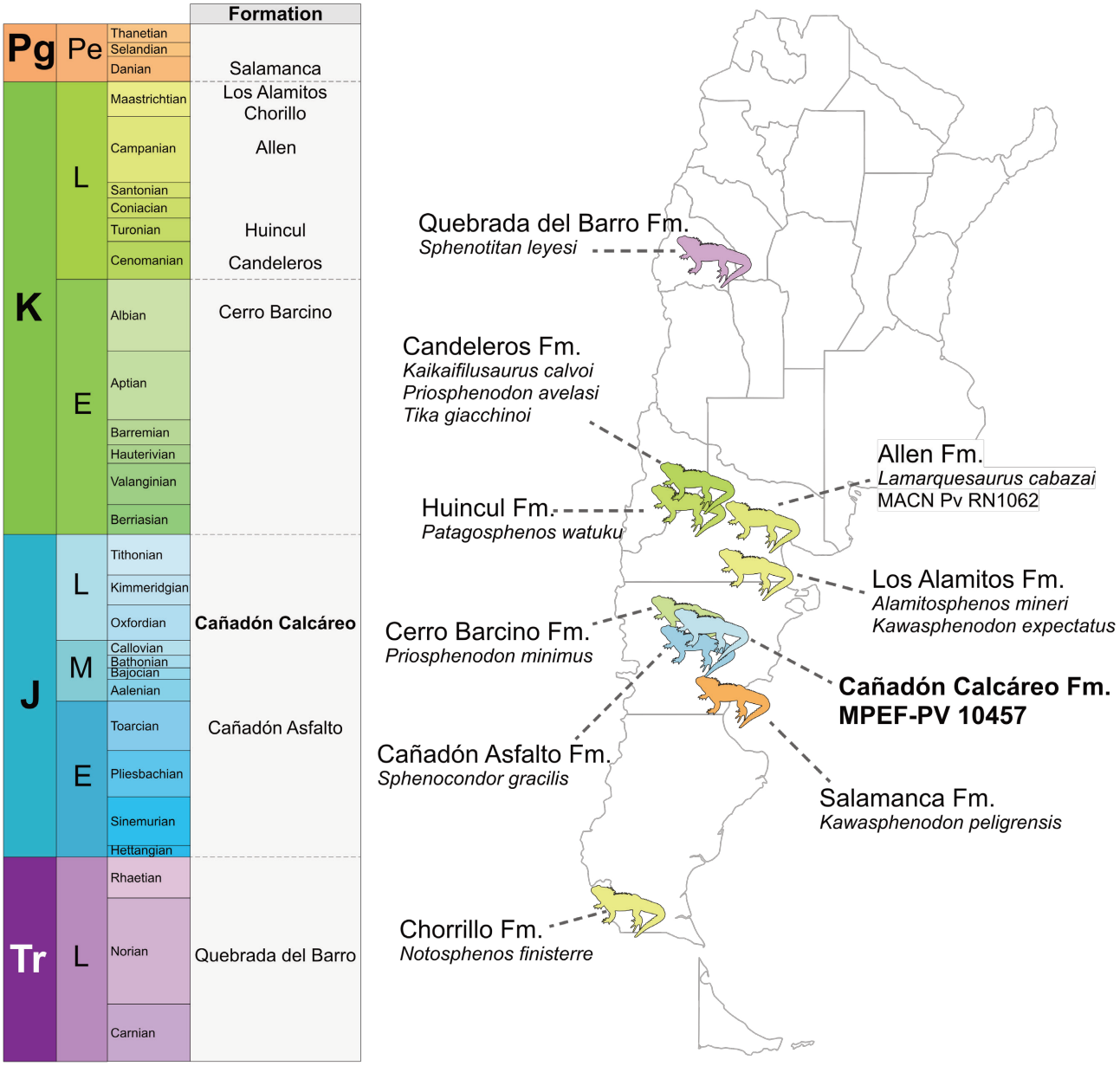


Figure 2. Distribution of Argentine rhynchocephalians. The colours on the silhouettes correspond to the fossil ages. Silhouette representing *Sphenodon punctatus* found in the public domain in PhyloPic (https://www.phylopic.org/).

Sphenotitan leyesi from the Norian Quebrada del Barro Formation of San Juan (Martínez *et al.*, 2013), represent neosphenodontians, and probably even sphenodontids. The only possible exception might be *Sphenocondor gracilis* from the Toarcian Cañadón Asfalto Formation of Chubut, which was argued to lie outside of Eusphenodontia by Apesteguía *et al.* (2012) and Gentil *et al.* (2019). However, other recent analyses, which improve on the previous phylogenetic dataset with the inclusion of taxa and morphological characters, recovered *Sphenocondor gracilis* within Neosphenodontia (*e.g.*, Chambi-Trowell *et al.*, 2021) or even the Sphenodontidae (Beccari & Rauhut, in press). Therefore, it is likely that MPEF-PV 10457 would pertain to a neosphenodontian, but without additional skeletal material, this assignment is tentative at most.

CONCLUSION

The record of Argentine and South American rhynchocephalians in general is here extended with the description of a new specimen. This specimen comes from the Cañadón

Calcáreo Formation, Late Jurassic of Argentina, and can be recognized as a rhynchocephalian by the combination of amphicoelous vertebrae with a persisting notochordal canal and the presence of gastralia. The specimen is the first for the Late Jurassic of South America and partially fills a temporal gap in the rhynchocephalian record in the continent. The poor preservation of the new specimen, as well as the lack of data for the postcranial skeleton of rhynchocephalians, makes finer taxonomic attribution difficult. Thus, new specimens are necessary to fully understand the presence and evolutionary history of Argentine rhynchocephalians.

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