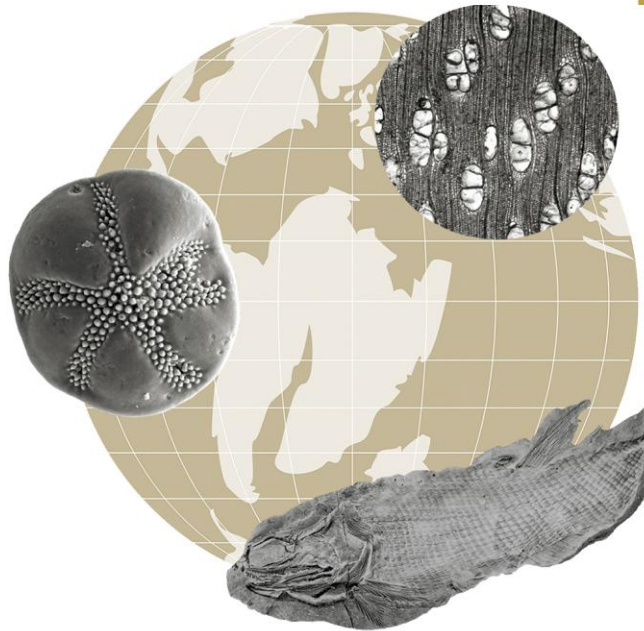




This file is an uncorrected accepted manuscript (i.e., postprint). Please be aware that this version will change during the production process. This postprint will be removed once the paper is officially published. All legal disclaimers that apply to the journal pertain.

Submitted: 19 June 2026 - **Accepted:** 21 August 2026 - **Posted online:** 24 September 2026

To link and cite this article:

doi: 10.5710/AMGH.21.08.2026.3703

PLEASE SCROLL DOWN FOR ARTICLE



The first rhynchocephalian from the Late Jurassic of South America (Cañadón Calcáreo Formation, Chubut, Argentina)

Victor Beccari¹; Oliver W. M. Rauhut^{1,2,3}

¹ SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, 80333 Munich, Germany

² GeoBio-Center, Ludwig-Maximilians-Universität München, 80333 Munich, Germany

³ Department of Earth and Environmental Sciences, Paleontology & Geobiology, Ludwig-Maximilians-Universität München, 80333 Munich, Germany

Total number of pages and figures: 14 pages; 2 figures

Header: First Late Jurassic rhynchocephalian from South America

Short description: Description of a rhynchocephalian specimen from the Late Jurassic of Chubut Province, Argentina, with implications for the distribution of South American rhynchocephalians.

Corresponding author: victor.beccari@gmail.com

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, of 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.

Keywords: Sphenodontia; Neosphenodontia; Oxfordian; paleobiogeography

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 (Martínez *et al.*, 2013). The youngest rhynchocephalian outside of New Zealand, i.e. *Kawasphenodon peligrensis* Apesteguía *et al.*, 2014, also comes from South America, from the Paleocene (Danian) Salamanca Formation, 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 the long geological extent, the rhynchocephalian fossil record in Argentina is highly incomplete, with no taxa described so far for 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 Egídio 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 Rio Negro into north-central Chubut Province, Argentina (Figari *et al.*, 2015). The formation consists of a basal lacustrine part with strongly varying thickness, often underlain by a basal breckzia or conglomerate, and a thick fluvial succession in the higher parts 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 (20-25 cm) sandstone layer that is part of an alternating series of sand- 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 part of the formation in this area, being placed in the lower part 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 Ferúglio, 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, the preserved part of the skeleton measuring about 46 x 44 mm. Pictures of the specimen were taken using the mirrorless camera OM-1 (OM Digital Solutions, Shinjuku, Tokyo, Japan) paired with the with an Olympus M.Zuiko Digital ED 60 mm F2.8 Macro lens. All measurements were taken in the physical specimen using an analogue Mitutoyo (Mitutoyo America Corporation, USA) calliper (error 0.02 mm).

Systematic palaeontology

LEPIDOSAUIROMORPHA Gauthier, 1984

LEPIDOSAURIA Haeckel, 1866

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

RHYNCHOCEPHALIA indet.

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, missing the skull, cervical series, and caudal series. MPEF-PV 10457 would represent a small sized lepidosauromorph, with a total preserved dorsal vertebrae length of 30.3 mm (representing the presacral length, without the cervical series). The gastralia region measures about 21 mm in length, close to that of *Clevosaurus hudsoni* Swinton, 1939 NHMUK PV R36832 (O'Brien *et al.*, 2018), *Homoeosaurus parvipes* Cocude-Michel, 1963, and *Leptosaurus neptunius* Goldfuss, 1831 (Cocude-Michel, 1963). Thus, comparing with the average size of these taxa, MPEF-PV 10457 would represent an animal of about 50mm snout-vent length.

Three vertebrae are visible but poorly preserved in MPEF-PV 10457. The outlines of their centra resembles 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 & Posenato, 2003 (Renesto & Bernardi, 2014), the amphicoelous pleurocentra preserved the notochordal canal. This feature is synapomorphic of rhynchocephalians among lepidosauromorphs (Martínez *et al.*, 2021), albeit also being present in gekkotans and the stem squamate *Bellairsia gracillis* Evans, 1998 (Taňanda *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 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 pachyostosis* 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 range between 115° and 145°, with the posteriormost showing the lowest values. This range is similar to that of *Clevosaurus hudsoni* 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.*, 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 metatarsal (II-IV?) still preserve the bones. The outline of an elongated bone next to the vertebrae and ribs possibly pertains to a humerus, which cannot be described in detail due to the 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. What is possibly the distal end of a femur is still in articulation with two other long bones, here interpreted as the tibia and fibula. The shaft of these two bones is 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 velseae* 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 notochordal canal, and presence of gastralia with fused chevrons. Other Jurassic lepidosauromorphs, e.g., *Bellairsia* Evans, 1998, *Marmoretta* Evans, 1991, *Megachirella* Renesto & Posenato, 2003, show a combination of two, but never three of these characters. *Bellairsia* and crown squamates lacks gastralia (Simões *et al.*, 2016; 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 of MPEF-PV 10457, but their gastralia are pachyostotic and lack short medial chevrons (Diedrich, 2013; Li *et al.*, 2014). Furthermore, these reptiles are also substantially older than MPEF-PV 10457 and were fully marine animals. Thus, the combination of morphology and stratigraphy allow 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 their phylogenetic position 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 Argentinean taxa, even the oldest known representative, *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 be 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 more 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 persisting notochordal canal, and 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 difficult finer taxonomic attribution. Thus, new specimens are necessary to fully understand the presence and evolutionary history of Argentine rhynchocephalians.

Acknowledgements

The authors would like to thank Eduardo Ruigomez (MPEF) and Evangelos Vlachos (MPEF) for access to the specimens. This work is a contribution to the Deutsche Forschungsgemeinschaft (D.F.G) grants RA 1012/26 and 1012/28, awarded to OWMR. We would also like to thank the Province of Chubut for fieldwork permits, and Pablo Puerta for logistics of the fieldwork. We would like to thank the anonymous reviewer and Paulo Romo for their comments on the manuscript.

References

- Agassiz, L. (1833). *Recherches sur les Poissons fossiles: Neuchatel et Soleure* (Vol. 3). Société Neuchâteloise des Sciences Naturell.
- Agnolín, F., Aranciaga Rolando, M., Manabe, M., Tsuihiji, T., & Novas, F. E. (2025). Southernmost lepidosaur (Reptilia) assemblage from the Late Cretaceous of Patagonia. *Historical Biology*, 37(4), 888–902.
<https://doi.org/10.1080/08912963.2024.2341850>
- Agnolín, F. L., Aranciaga Rolando, A. M., Chimento, N. R., & Novas, F. E. (2024). New small reptile remains from the Late Cretaceous of Patagonia increase morphological diversity of spenodontids (Lepidosauria). *Proceedings of the Geologists' Association*, 135(1), 36–44. <https://doi.org/10.1016/j.pgeola.2023.09.007>
- Apesteguía, S. (2005). A Late Campanian spenodontid (Reptilia, Diapsida) from northern Patagonia. *Comptes Rendus Palevol*, 4(8), 663–669.
<https://doi.org/10.1016/j.crpv.2005.06.003>
- Apesteguía, S. (2016). Rhynchocephalians: The least known South American lepidosaurs. In F. L. Agnolín, G. Lio, F. Brissón Egli, N. R. Chimento, & F. E. Novas, *Historia Evolutiva y Paleobiogeográfica de los vertebrados de América del Sur* (pp. 7–19).

- Apesteguía, S., Garberoglio, F. F., & Gómez, R. O. (2021). Earliest tuatara relative (Lepidosauria: Sphenodontinae) from Southern Continents. *Ameghiniana*, 58(5).
<https://doi.org/10.5710/AMGH.13.07.2021.3442>
- Apesteguía, S., Gómez, R. O., & Rougier, G. W. (2012). A basal sphenodontian (Lepidosauria) from the Jurassic of Patagonia: New insights on the phylogeny and biogeography of Gondwanan rhynchocephalians. *Zoological Journal of the Linnean Society*, 166(2), 342–360. <https://doi.org/10.1111/j.1096-3642.2012.00837.x>
- Apesteguía, S., Gómez, R. O., & Rougier, G. W. (2014). The youngest South American rhynchocephalian, a survivor of the K/Pg extinction. *Proceedings of the Royal Society of London B*, 281(20140811).
- Apesteguía, S., & Novas, F. E. (2003). Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. *Nature*, 425(6958), 609–612.
<https://doi.org/10.1038/nature01995>
- Beccari, V., Guillaume, A. R. D., Jones, M. E. H., Villa, A., Cooper, N., Regnault, S., & Rauhut, O. W. M. (2025). An arboreal rhynchocephalian (Lepidosauria: Rhynchocephalia) from the Late Jurassic of Germany, and the importance of the appendicular skeleton for ecomorphology in lepidosaurs. *Zoological Journal of the Linnean Society*, 204(3), 39. <https://doi.org/10.1093/zoolinnea/zlaf073>
- Beccari, V., Jones, M. E. H., Villa, A., Martino, R., Regnault, S., Glaw, F., & Rauhut, O. W. M. (2026). The axial skeleton of the tuatara (Rhynchocephalia: Sphenodon): insights on intraspecific variability, ontogeny, sexual dimorphism, and remarks on fossil taxa. *Zoological Journal of the Linnean Society*, 206(4), zlaf135.
<https://doi.org/10.1093/zoolinnea/zlaf135>
- Beccari, V., & Rauhut, O. W. M. (in press). First occurrence of rhynchocephalians (Lepidosauria: Sphenodontidae) from the Middle Jurassic (Bathonian) of Grand

- Causses, France. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 1–9. <https://doi.org/10.1017/S1755691026101182>
- Bonaparte, J. F., & Sues, H.-D. (2006). A new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Upper Triassic of Rio Grande do Sul, Brazil. *Palaeontology*, 49(4), 917–923. <https://doi.org/10.1111/j.1475-4983.2006.00568.x>
- Carroll, R. L. (1985). A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. *Palaeontographica. Abteilung A, Paläozoologie, Stratigraphie*, 189(1–3), 1–28.
- Chambi-Trowell, S. A. V., Martinelli, A. G., Whiteside, D. I., Vivar, P. R. R. de, Soares, M. B., Schultz, C. L., Gill, P. G., Benton, M. J., & Rayfield, E. J. (2021). The diversity of Triassic South American sphenodontians: A new basal form, clevosaurus, and a revision of rhynchocephalian phylogeny. *Journal of Systematic Palaeontology*, 19(11), 787–820. <https://doi.org/10.1080/14772019.2021.1976292>
- Cocude-Michel, M. (1963). Les rhynchocéphales et les sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Publications du musée des Confluences*, 7(1), 3–224. <https://doi.org/10.3406/mhnly.1963.992>
- Cree, A. (2014). *Tuatara – Biology and conservation of a venerable survivor* (Vol. 160). Canterbury University Press.
- Cúneo, R., Ramezani, J., Scasso, R., Pol, D., Escapa, I., Zavattieri, A. M., & Bowring, S. A. (2013). High-precision U–Pb geochronology and a new chronostratigraphy for the Cañadón Asfalto Basin, Chubut, central Patagonia: Implications for terrestrial faunal and floral evolution in Jurassic. *Gondwana Research*, 24(3–4), 1267–1275.
- DeMar, D. G., Jones, M. E. H., & Carrano, M. T. (2022). A nearly complete skeleton of a new eusphenodontian from the Upper Jurassic Morrison Formation, Wyoming, USA, provides insight into the evolution and diversity of Rhynchocephalia (Reptilia:

- Lepidosauria). *Journal of Systematic Palaeontology*, 20(1), 2093139.
<https://doi.org/10.1080/14772019.2022.2093139>
- Diedrich, C. G. (2013). Review of the Middle Triassic ‘sea cow’ *Placodus gigas* (Reptilia) in Pangea’s shallow marine macroalgae meadows of Europe. *New Mexico Museum of Natural History and Science, Bulletin*, 61, 104–131.
- Dussán Villanueva, M. G. (2019). Paleoenvironment and taphonomy of the fish-rich marls of the Cañadón Calcáreo Formation in Central Patagonia. *Unpublished M. Sc. Thesis*.
- Evans, S. E. (1991). A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society*, 103(4), 391–412. <https://doi.org/10.1111/j.1096-3642.1991.tb00910.x>
- Evans, S. E. (1998). Crown group lizards (Reptilia, Squamata) from the middle Jurassic of the British Isles. *Palaeontographica Abteilung A-Stuttgart-*, 250, 123–154.
- Evans, S. E., & Jones, M. E. H. (2010). The origin, early history and diversification of lepidosauromorph reptiles. In S. Bandyopadhyay, *New Aspects of Mesozoic Biodiversity* (Vol. 132, pp. 27–44). Springer Berlin Heidelberg.
https://doi.org/10.1007/978-3-642-10311-7_2
- Figari, E. G., Scasso, R. A., Cúneo, R. N., & Escapa, I. (2015). Estratigrafía y evolución geológica de la Cuenca de Cañadón Asfalto, Provincia del Chubut, Argentina. *Latin American journal of sedimentology and basin analysis*, 22(2), 135–169.
- Ford, D. P., Benson, R. B. J., Griffiths, E. F., & Evans, S. E. (2025). Evidence for clinging arboreality in a Middle Jurassic stem lepidosaur. *Proceedings of the Royal Society B: Biological Sciences*, 292(2045), 20250080. <https://doi.org/10.1098/rspb.2025.0080>
- Gauthier, J. A. (1984). *A cladistic analysis of the higher systematic categories of the Diapsida*. University of California, Berkeley.

<https://search.proquest.com/openview/35bfca1ec17e44f6440d874ac7ae4c93/1?pq-origsite=gscholar&cbl=18750&diss=y>

- Gentil, A. R., Agnolin, F. L., Garcia Marsà, J. A., Motta, M. J., & Novas, F. E. (2019). Bridging the gap: Sphenodont remains from the Turonian (Upper Cretaceous) of Patagonia. Palaeobiological inferences. *Cretaceous Research*, 98, 72–83.
<https://doi.org/10.1016/j.cretres.2019.01.016>
- Goldfuss, G. A. (1831). Beiträge zur Kenntnis verschiedener Reptilien der Vorwelt. *Nova acta Academiae caesareae Leopoldino-Carolinae germanicae naturae curiosorum*, 15, 61–128.
- Gray, J. E. (1831). Note on a peculiar structure in the head of an *Agama*. *Zoological Miscellany*, 1, 13–14.
- Gray, J. E. (1842). Description of two hitherto unrecorded species of reptiles from New Zealand; presented to the British Museum by Dr. Dieffenbach. *London, Zoological Miscellany*, 1–72.
- Günther, A. (1867). Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). *Philosophical Transactions of the Royal Society of London*, 157, 595–629.
- Haeckel, E. (1866). *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von C. Darwin reformirte Descendenz-Theorie, etc* (Vol. 1). Verlag von Georg Reimer.
- Hoffstetter, R., & Gasc, J.-P. (1969). Vertebrae and ribs of modern reptiles. *Biology of the Reptilia*, 1(5), 201–310.
- Jones, M. E. H. (2006). The Early Jurassic clevosaurus from China (Diapsida: Lepidosauria). *New Mexico Museum of Natural History and Science Bulletin*, 37, 548–562.

- Klein, N., & Scheyer, T. M. (2017). Microanatomy and life history in *Palaeopleurosauros* (Rhynchocephalia: Pleuroosauridae) from the Early Jurassic of Germany. *The Science of Nature*, 104(1), 4. <https://doi.org/10.1007/s00114-016-1427-3>
- Li, C., Jiang, D.-Y., Cheng, L., Wu, X.-C., & Rieppel, O. (2014). A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. *Geological Magazine*, 151(1), 100–120. <https://doi.org/10.1017/S001675681300023X>
- Martínez, R. N., Apaldetti, C., Colombi, C. E., Praderio, A., Fernandez, E., Malnis, P. S., Correa, G. A., Abelin, D., & Alcober, O. (2013). A new sphenodontian (Lepidosauria: Rhynchocephalia) from the Late Triassic of Argentina and the early origin of the herbivore opisthodontians. *Proceedings of the Royal Society B: Biological Sciences*, 280(1772), 20132057. <https://doi.org/10.1098/rspb.2013.2057>
- Martínez, R. N., Simões, T. R., Sobral, G., & Apesteguía, S. (2021). A Triassic stem lepidosaur illuminates the origin of lizard-like reptiles. *Nature*, 597(7875), 235–238. <https://doi.org/10.1038/s41586-021-03834-3>
- O'Brien, A., Whiteside, D. I., & Marshall, J. E. A. (2018). Anatomical study of two previously undescribed specimens of *Clevosaurus hudsoni* (Lepidosauria: Rhynchocephalia) from Cromhall Quarry, UK, aided by computed tomography, yields additional information on the skeleton and hitherto undescribed bones. *Zoological Journal of the Linnean Society*, 183(1), 163–195. <https://doi.org/10.1093/zoolinnean/zlx087>
- Pol, D., Rauhut, O. W. M., Lecuona, A., Leardi, J. M., Xu, X., & Clark, J. M. (2013). A new fossil from the Jurassic of Patagonia reveals the early basicranial evolution and the origins of Crocodyliiformes. *Biological Reviews*, 88(4), 862–872. <https://doi.org/10.1111/brv.12030>

- Proserpio, C. A. (1987). *Descripción geológica de la hoja 44e, Valle General Racedo*.
<https://www.sidalc.net/search/Record/oai:https://repositorio.segemar.gov.ar:308849217-418/Description>
- Renesto, S., & Bernardi, M. (2014). Redescription and phylogenetic relationships of *Megachirella wachtleri* Renesto et Posenato, 2003 (Reptilia, Diapsida). *Paläontologische Zeitschrift*, 88(2), 197–210. <https://doi.org/10.1007/s12542-013-0194-0>
- Renesto, S., & Posenato, R. (2003). A new lepidosauromorph reptile from the Middle Triassic of the Dolomites (Northern Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 109(3). <https://riviste.unimi.it/index.php/RIPS/article/view/5517>
- Reynoso, V.-H. (2000). An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayua Formation (Albian), Central Mexico. *Journal of Paleontology*, 74(1), 133–148. [https://doi.org/10.1666/0022-3360\(2000\)074%3C0133:AUASRD%3E2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074%3C0133:AUASRD%3E2.0.CO;2)
- Russell, A. P., & Bauer, A. M. (2008). The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In C. Gans, A. Gaunt, & K. Adler, *Biology of the Reptilia. Vol. 21, Morphology I: The skull and appendicular locomotor apparatus of Lepidosauria* (pp. 1–468). Society for the Study of Amphibians and Reptiles.
- Simões, T. R., Caldwell, M. W., Nydam, R. L., & Jiménez-Huidobro, P. (2016). Osteology, phylogeny, and functional morphology of two Jurassic lizard species and the early evolution of scansoriality in geckoes. *Zoological Journal of the Linnean Society*. <https://doi.org/10.1111/zoj.12487>
- Simões, T. R., Caldwell, M. W., Tałanda, M., Bernardi, M., Palci, A., Vernygora, O., Bernardini, F., Mancini, L., & Nydam, R. L. (2018). The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature*, 557(7707), 706–709. <https://doi.org/10.1038/s41586-018-0093-3>

- Simões, T. R., Kinney-Broderick, G., & Pierce, S. E. (2022). An exceptionally preserved *Sphenodon*-like sphenodontian reveals deep time conservation of the tuatara skeleton and ontogeny. *Communications Biology*, 5(1), 1–19. <https://doi.org/10.1038/s42003-022-03144-y>
- Swinton, W. E. (1939). A new Triassic Rhynchocephalian from Gloucestershire. *Annals and Magazine of Natural History*, 4(24), 591–594. <https://doi.org/10.1080/00222933908655407>
- Talanda, M., Fernandez, V., Panciroli, E., Evans, S. E., & Benson, R. J. (2022). Synchrotron tomography of a stem lizard elucidates early squamate anatomy. *Nature*, 611(7934), 99–104. <https://doi.org/10.1038/s41586-022-05332-6>
- Villa, A., Montie, R., Röper, M., Rothgaenger, M., & Rauhut, O. W. M. (2021). *Sphenofontis velserae* gen. et sp. nov., a new rhynchocephalian from the Late Jurassic of Brunn (Solnhofen Archipelago, southern Germany). *PeerJ*, 9, e11363. <https://doi.org/10.7717/peerj.11363>
- von Meyer, H. (1847). *Homoeosaurus maximiliani und Rhamphorhynchus (Pterodactylus) longicaudus: Zwei Fossile Reptilien aus dem Kalkschiefer von Solenhofen*. S. Schmerber'schen Buchhandlung.
- Zittel, K. A. von. (1887–1890). *Handbuch der Paläontologie. Abteilung I. Paläozoologie Band III*.

Figure captions

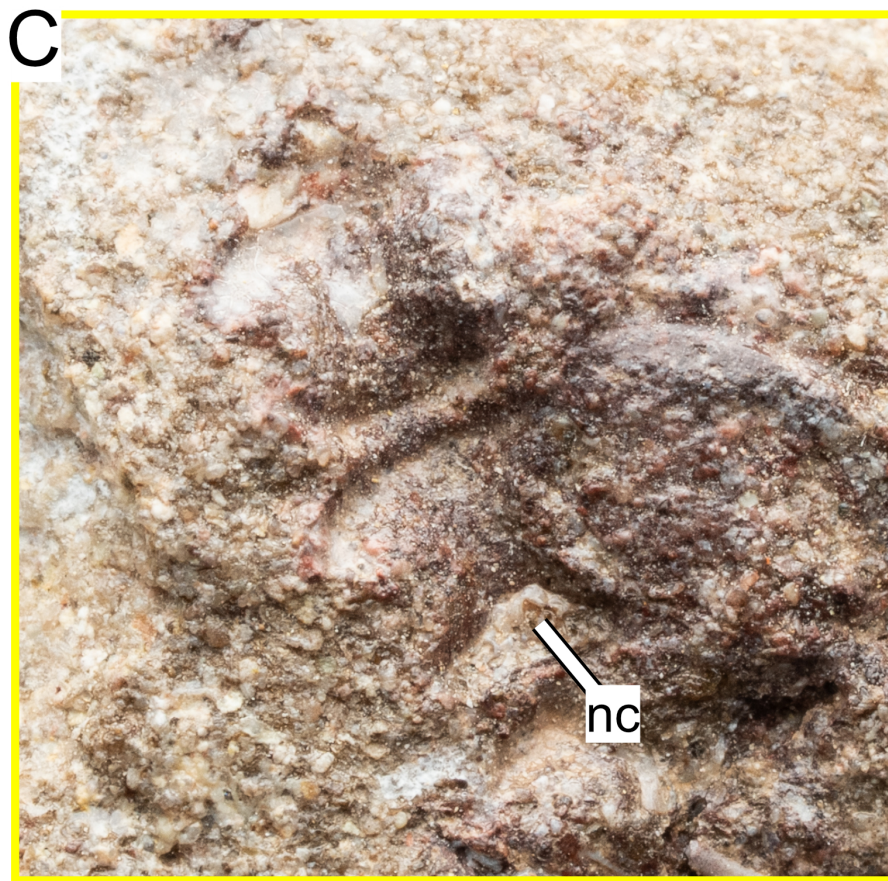
Figure 1. Rhynchocephalian specimen MPEF-PV 10457. A, photograph of the specimen; B, schematic drawing of the specimen; C, photograph of the anteriormost preserved (dorsal) vertebrae; D, schematic drawing of the dorsal vertebrae. Abbreviations: che, medial chevron; dv, dorsal vertebra; fe?, possible 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.

Figure 2. Distribution of Argentine rhynchocephalians. The colours on the silhouettes correspond to the fossil ages.

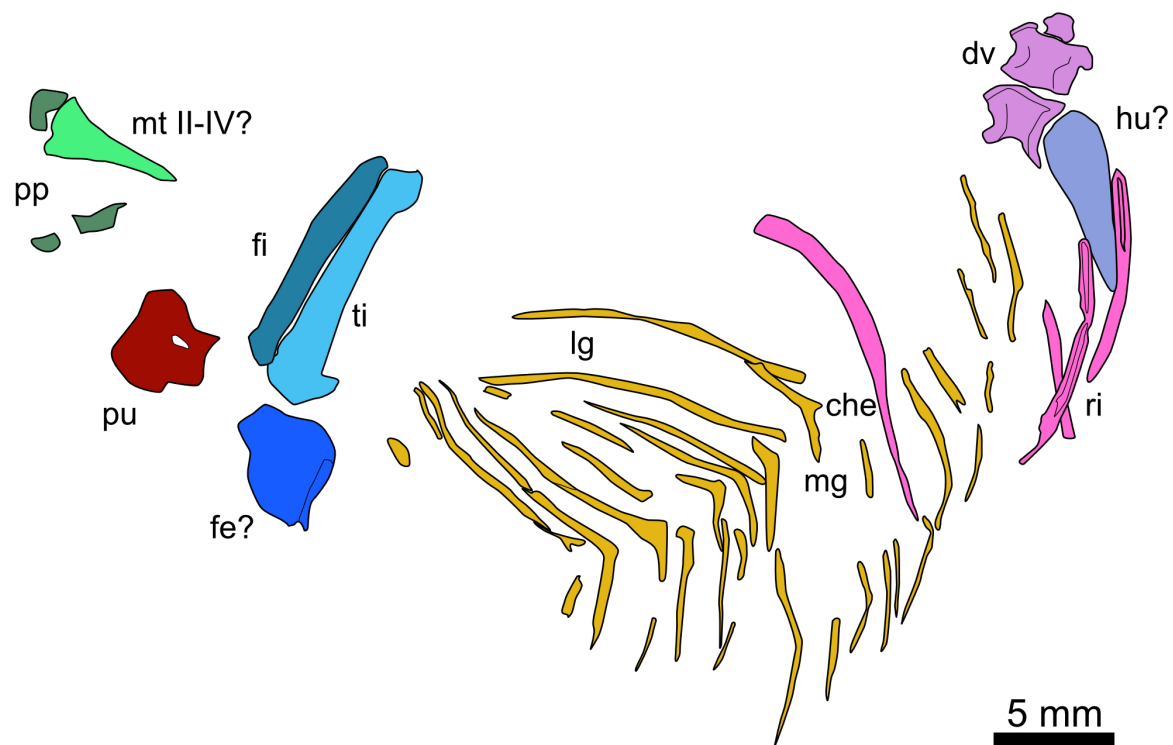
A



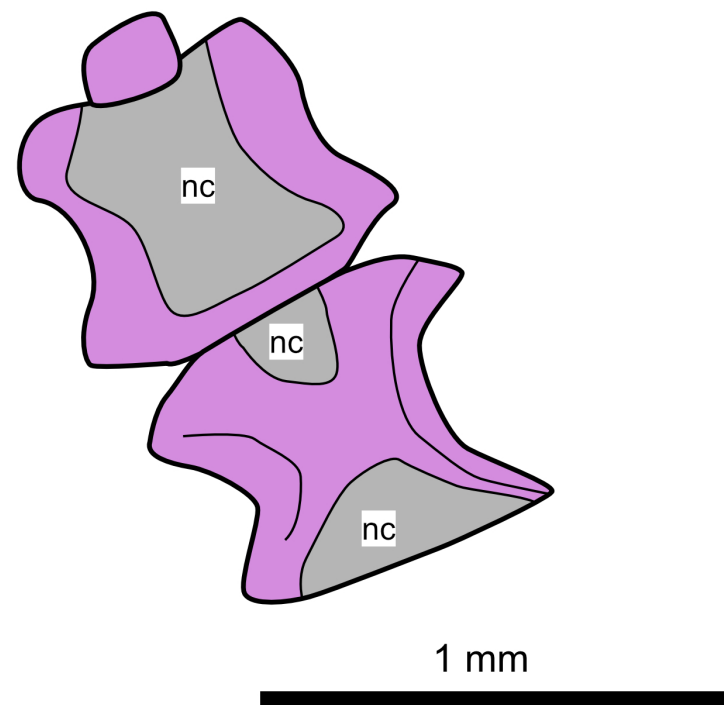
C



B



D



			Formation
Pg	Pe	Thanetian	Salamanca
		Selandian	
		Danian	
K	L	Maastrichtian	Los Alamos Chorillo
		Campanian	Allen
		Santonian	Huincul
		Coniacian	
		Turonian	
		Cenomanian	
	E	Albian	Cerro Barcino
		Aptian	Candeleros
		Barremian	
		Hauterivian	
		Valanginian	
J	L	Tithonian	Cañadón Calcáreo
		Kimmeridgian	
		Oxfordian	
	M	Callovian	
		Bathonian	Cañadón Asfalto
		Bajocian	
		Aalenian	
	E	Toarcian	Cañadón Asfalto
		Pliesbachian	
		Sinemurian	
		Hettangian	
Tr	L	Rhaetian	Quebrada del Barro
		Norian	
		Carnian	

