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Author statement

Yanina Herrera conceived, designed, and performed the experiments, analyzed the data, contributed materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
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Verónica V. Vennari conceived and designed the experiments, contributed materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
Cricosaurus (Thalattosuchia, Metriorhynchidae) survival across the J/K boundary in the High Andes (Mendoza Province, Argentina)

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Abstract
Metriorhynchidae is an extinct group of Jurassic–Cretaceous crocodylomorphs that
developed a fully pelagic lifestyle. Its Jurassic record is outstanding (it includes around 40
nominal species), while the records that can be restricted to the Cretaceous are particularly
sparse. Here we describe a partial skull of a new species of *Cricosaurus*, *Cricosaurus*
*puelchorum* sp. nov., from the lower Berriasian of the Vaca Muerta Formation (Neuquén
Basin, Argentina). The description of the specimen reveals a series of autapomorphyes and
a unique combination of characters that justify the creation of a new species. Phylogenetic
analysis places *Cricosaurus puelchorum* sp. nov. closer to three upper Kimmeridgian–
lower Tithonian species of southern Germany. The new taxon was recovered in connection
with an accurate ammonoid-based biostratigraphic control and allows confirming the
survival of *Cricosaurus* across the J/K boundary at the southeastern Pacific.

**Keywords:** Crocodylomorpha, Ammonoidea, Lower Cretaceous, Vaca Muerta Formation,
Neuquén Basin.

### 1. Introduction

Metriorhynchidae, a clade of Mesozoic marine crocodylomorphs, are the only
Archosauria group adapted to a pelagic lifestyle as it is documented by several
morphological and physiological modifications such as laterally directed orbits, reduced
and paddle-like forelimbs, loss of osteoderms, regionalized caudal vertebral column with a
hypocercal tail, and hypertrophied nasal glands for salt excretion, among others (e.g. Fraas,
Andrews, 1913; Fernández and Gasparini, 2008; Young et al., 2010; Herrera et al.,
2013a; Sachs et al., 2019). Also, they were probably bearing live young (Herrera et al.,
2017, and references therein).
Worldwide Jurassic records depict metriorhynchids as a diverse lineage, gathering approximately 40 nominal species distributed in more than ten genera, being *Cricosaurus* Wagner, 1858 one of the most speciose genera (e.g. Wagner, 1852, 1858; Fraas, 1902; Gasparini and Dellapé, 1976; Young and Andrade, 2009; Herrera et al., 2013b; Sachs et al., 2019). On the contrary, Cretaceous fossils are particularly sparse. Laurasian records are mostly restricted to Germany and France. Two specimens were recovered from the Valanginian of Germany: *Cricosaurus schroederi* (Kuhn, 1936), and the holotype of *Enaliosuchus macrospondylus* Koken, 1883 (now referred as Metriorhynchidae indet., see Sachs et al., 2020). French records include *Cricosaurus macrospondylus* (now referred as *cf. 'Cricosaurus' macrospondylus* see Sachs et al., 2020 and Young et al., 2020) from the lower Valanginian (Hua et al., 2000), *Geosaurus lapparenti* (Debelmas and Strannoloubsky, 1957) from the upper Valanginian to lower Hauterivian (Debelmas, 1952, 1958; Debelmas and Strannoloubsky, 1957), and the holotype of the nomen dubium *Neustosaurus gigondarum* Raspail, 1842 from the lower Valanginian. Additionally, an indeterminate Plesiosuchina specimen from the upper Valanginian (Young et al., 2014), and an indeterminate metriorhynchid from the upper Valanginian–lower Hauterivian (Debelmas and Demians D'Archimbaud, 1956) are also known from France (see Sachs et al., 2020 for further information). To these finding, it must be added an isolated tooth from the lowermost Aptian of Italy referred to *cf. Plesiosuchina* (Chiarenza et al., 2015).

The Gondwanan Cretaceous records are even more scarce and restricted to a single metriorhynchid from Colombia (Rosa Blanco Formation, lower upper Valanginian) (Larsson et al., 2011).

In the Vaca Muerta Formation (Neuquén Basin), metriorhynchids are known from the upper part of the lower Tithonian (*Aulacosphinctes proximus* Zone) to the upper
Tithonian–lower Berriasian (*Substeueroceras koeneni* Zone) (see e.g. Gasparini and Dellapé, 1976; Vignaud and Gasparini, 1996; Pol and Gasparini, 2009; Herrera et al., 2013b, 2015; Herrera, 2015; Fernández et al., 2019). The youngest specimens from this basin (*Dakosaurus andiniensis* Vignaud and Gasparini, 1996, and *Purranisaurus potens* Rusconi, 1948a) were recovered from upper Tithonian–lower Berriasian levels (*Substeueroceras koeneni* ammonite Zone). Thus, up to date, no definitive Cretaceous metriorhynchids have been found in the Neuquén Basin.

### 1.1. Metriorhynchids from southern Mendoza Province

The specimens of metriorhynchids discovered in Mendoza Province during the first half of the XX Century were first described as an ichthyosaur and a plesiosaur (Rusconi, 1948a, b). Rusconi (1948b) nominated an "ichthyosaur" species as *Ichthyosaurus inexpectatus* (from Cajón del Río Grande), however, this material likely corresponds to *Dakosaurus* Quenstedt, 1856 (Vignaud and Gasparini, 1996). Also from Cajón del Río Grande, Rusconi (1948a) described the metriorhynchid *Purranisaurus potens* as a "plesiosaur" (see Gasparini, 1973; Herrera et al., 2015, Fernández et al., 2019 for detailed information). Additionally, in two sites located near to the Mendoza-Neuquén provincial boundary have been recovered three specimens of metriorhynchids. In Tithonian levels of Sierra de Reyes two natural endocasts of the skull cavities referred to *Cricosaurus araucanensis* (Gasparini and Dellapé, 1976) were found, and also from Tithonian levels but from Cari-Lauquen comes the holotype of *Dakosaurus andiniensis* (Vignaud and Gasparini, 1996). Except for the holotype (and the only specimen know) of *Purranisaurus potens* for which an upper Tithonian–lower Berriasian age was determined based on an
associated ammonite shell (Herrera et al., 2015), the age of the other metriorhynchids specimens from Mendoza Province is not accurately constrained.

Here we describe a new species which represents the first definitively Cretaceous metriorhynchid from the Vaca Muerta Formation (Neuquén Basin, Argentina), and showing the survival of *Cricosaurus* across the J/K boundary in the High Andes (Mendoza Province). The specimen here described (MCNAM-PV 5096) is the only metriorhynchid from Mendoza Province recovered in connection with an accurate ammonoid-based biostratigraphic control.

2. Geological context and biostratigraphic framework

The Neuquén Basin, extending between 33° to 39° Southern Latitude over central-west Argentina and Chile, holds a thick marine and continental Meso-Cenozoic succession. Sedimentation within this retro-arc basin has a complex history, mainly controlled by successive tectonic regimes and the activity of the western arc, represented by the volcanogenic rocks that interbed the dominantly siliciclastic and carbonate column (Ramos and Folguera, 2005; Charrier et al., 2015).

Upper Jurassic–Lower Cretaceous marine boundary beds are encompassed by the Vaca Muerta Formation, Mendoza Group (Weaver, 1931; Groeber, 1946). The Vaca Muerta Formation was deposited after a sudden transgression from the Pacific Ocean, and it is composed of a rhythmic succession of organic-rich shales, marls and limestones deposited within a carbonate ramp to platform setting (Mitchum and Uliana, 1985; Legarreta and Uliana, 1991; Spalletti et al., 2000; Kietzmann et al., 2014). The remarkably fossiliferous character of this lithostratigraphic unit has long enabled its relative dating through age-diagnostic fossils, among which ammonites, calcareous nannofossils, and
Calpionellids stand out (López-Martínez et al., 2017). In the last few years, the combination of the ammonite biozonation scheme and nano- and microfossils bioevents, together with the absolute age data obtained from the radio-isotopic geochronological analysis of detrital and igneous zircons, resulted in interesting advances in the chrono-biostratigraphic framework of the Andean Tithonian–Berriasian interval (Riccardi, 2015; Aguirre-Urreta et al., 2019 and references therein).

The material here studied comes from the Arroyo Paulino section (34º 58' S; 69º 49' W), which is around 220 m thick and encompass upper Tithonian to lower Berriasian strata of the Vaca Muerta Formation cropping out on the right margin of the Paulino Creek, Malargüe, Mendoza. Arroyo Paulino can be reached following upstream a country-road that departs to the west from the 40 National Road and that parallels the course of the Atuel River and its tributaries (Fig. 1A). General geological features of the area have been published by Ugarte (1955), Dessanti (1978), Nullo et al. (2005), and Sruoga et al. (2005), and a detailed complete log of the section is available in Fernández et al. (2019).

Age assignation of the Arroyo Paulino section relies on bed-by-bed ammonite sampling and the identification of all the Andean Assemblage Ammonoid Zones between the *Windhauseniceras internispinosum* to the base of the *Argentiniceras noduliferum* Zones –Microcanthum to Occitanica Standard Zones– (Vennari et al., 2014; Riccardi, 2015; Aguirre-Urreta et al., 2019 and references therein). The specimen MCNAM-PV 5096 was found in-situ in bed Py 38, a 0.65 m dark, massive, fine to medium calcareous sandstone bounded by dark-grey laminated marls (Fig. 1B). That bed also retrieved some bivalve fragments and an ammonite shell identified as *Groebericeras bifrons* Leanza, 1945 (MCNAM-PI 24878). Another representative of that species was collected from the overlying Py 39 bed (MCNAM-PI 24858), and two additional specimens were found loose
closely around (MCNAM-PI 24879 and 24880). Presence of *G. bifrons* allows to
confidently constraint the bed bearing the metriorhynchid specimen (MCNAM-PV 5096)
to the base of the *A. noduliferum* Zone (i.e. to the lower Berriasian). Ammonite specific
assignation is supported by the compressed open-coiled shells, with rounded flanks and
rather acute venters (Fig. 2, Tab. 1). All specimens lack tubercles and bear narrow
prorsiradiate constrictions, and ribs that are more evident over the upper third of the flank.
Even though ornamentation-smoothing age tendency could not be properly evaluated given
the reduced diameter of the material (maximum diameter of c. 78 mm), the other characters
described are diagnostic of *G. bifrons* (Leanza, 1945; Aguirre-Urreta and Álvarez, 1999).

*Groebericeras bifrons* is interpreted as a lower Berriasian marker in the Neuquén
Basin and it is usually recorded at the very base of the *Argentiniceras noduliferum* Zone
(Leanza, 1945; Aguirre-Urreta and Álvarez, 1999; Vennari et al., 2012; Parent et al., 2015;
Vennari and Aguirre-Urreta, 2017). The *A. noduliferum* Zone has in turn been tied up with
the Tethyan *Calpionella alpina* Subzone, the primary marker of the lower Berriasian
(López-Martínez et al., 2017; Wimbledon, 2017; Lena et al., 2019). In the Arroyo Paulino
section, *G. bifrons* has been recorded from two consecutive beds, located around 10 meters
below the first occurrence of *A. noduliferum*, and near 40 meters above the last beds with
ammonites typical of the *Substeuroceras koeneni* Zone. That 40 meters poorly fossiliferous
interval only yielded some dubious representatives of *Substeuroceras disputabile* and
"*Thurmanniceras" duraznensis*. This drop in abundance and diversity could be related to
the development of a lowstand period in the basin coupled with a higher siliciclastic input
(Riccardi, 1991, 2008, 2015). Hence, it is feasible that *A. noduliferum* first occurrence in
Arroyo Paulino is lower in the section than Py 38 metriorhynchid-bearing bed.
The genus *Groebericeras* is recorded in the upper Berriasian of the Mediterranean region (Hoedemaeker, 1982, 1987; Howarth, 1992; Aguado et al., 2000) and in the Lo Valdez Formation in Chile according to Salazar Soto (2012). Notwithstanding, we agree with Aguirre-Urreta and Álvarez (1999) that those records are not conspecific with *G. bifrons* and that current lines of evidence suggest a younger early Berriasian age for that species in Argentina and Chilean sections.

3. Material

Materials of thalattosuchians used for comparisons were listed in Table 2, which include the collection number of the most informative specimen material. Unless noted otherwise, comparisons for the taxa mentioned in the description were based on these specimens.

4. Institutional abbreviations

MCNAM, Museo de Ciencias Naturales y Antropológicas J.C. Moyano, Mendoza, Argentina; MGHF, Museo Geológico H. Fuenzalida, Universidad Católica del Norte, Antofagasta, Chile; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MOZ, Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher”, Zapala, Argentina; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain; NHMUK R, Natural History Museum, London, United Kingdom; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns- Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.
5. Systematic paleontology

Crocodylomorpha Hay, 1930 (*sensu* Nesbitt, 2011)

Thalattosuchia Fraas, 1901 (*sensu* Young and Andrade, 2009)

Metriorhynchidea Fitzinger, 1843 (*sensu* Young and Andrade, 2009)

Metriorhynchinae Fitzinger, 1843 (*sensu* Young and Andrade, 2009)

Rhacheosaurini Young et al., 2011

*Cricosaurus* Wagner, 1858


*Emended diagnosis.* Metriorhynchid crocodylomorph with the following unique combination of characters: ornamentation of the external surface of the dermatocranium is variable, with some species having a conspicuous to faint grooved, ridged or pitted patterns, and others being largely smooth; external nares separated by a bony premaxillary septum, with the nares terminating posterior to the second maxillary alveoli; acute angle formed by the posterolateral and posteromedial processes of the frontal; orbits as large as the supratemporal fenestrae (at least in morphologically mature individuals); lateral margin of the prefrontal rounded; surangular and angular well-developed, anterolaterally exceeding beyond the anterior margin of the orbits; symphysial part of the mandible low; dentition has variable labiolingual compression, with some species having teeth with a sub-circular cross-section and others with a sub-rectangular one; dentition is bicarinate, but the carinae are faint (i.e. a low carinal keel); deltopectoral crest reduced or absent; calcaneum tuber...
absent or vestigial; proximal end of metatarsal I greatly enlarged (modified from Young and Andrade, 2009; Herrera et al., 2013b; Sachs et al., 2019).

*Cricosaurus puelchorum* sp. nov.

Figures 3–6

*LSID*. urn:lsid:zoobank.org:act:

Derivation of name. From *Puelches* (*pwelches* in Mapudungun, which means "people of the East"), a name given by the Spanish to the native people who inhabited the southeast of Mendoza. The name with which they defined themselves is unknown.

Holotype. MCNAM-PV 5096, incomplete cranium from the nasals to the posterior-most region of the right supratemporal fenestra, with part of the mandible and teeth.

Type locality. Arroyo Paulino (34° 58' S; 69° 49' W), cropping out on the right margin of the Paulino Creek, Mendoza Province, Argentina.

Stratigraphic horizon. Vaca Muerta Formation, lower part of the *Argentiniceras noduliferum* Andean Assemblage Zone, lower Berriasian, Lower Cretaceous (Leanza, 1945; López-Martínez et al., 2017).

Diagnosis. A member of *Cricosaurus* characterized by the following combination of characters (autapomorphic characters are indicated by an asterisk*): ornamentation of the external surface of the dermocranium consisting of small pits and shallow to deep grooves; palatal surface of the maxilla ornamented with ridges*; lacrimal visible in dorsal and lateral views*; anteroposteriorly oriented ridge in the posteromedial process of the nasal*; frontal anteromedial process noticeably posterior to the prefrontals; triangle-shaped supratemporal fossae; teeth with three apicobasal facets on the labial surface*; tooth crowns
with well-defined apicobasal aligned ridges; apicobasal parallel troughs on the middle facet of the labial surface.*

6. Description

6.1. General preservation

The skull of the holotype (MCNAM-PV 5096) and the only known specimen was diagenetically broken into six pieces that fit together (Figs. 3–6). There are four main pieces, three of them are transversally broken; the anterior one is a fragment of the snout, the middle piece is from the posterior-most region of the snout to the posterior-most region of the orbit, the posterior piece is from the supraorbital notch to the posterior margin of the right supratemporal fossa (Figs. 3–4). The extra piece is a bone region detached from the right lateral and ventral aspect of the cranium and includes part of the maxilla, lacrimal, and prefrontal. The small pieces include part of the maxilla and the mandible, and the other is a mandibular fragment. Most of the mandible is not preserved.

Maxilla, nasal, lacrimal, prefrontal, frontal, palatine, pterygoid, vomer, dentary, splenial, surangular, and angular can be confidently identified. A fragment of the postorbital was identified but not described. Several teeth are preserved, most of them still in life position in the left maxilla and right dentary. The infillings of the nasal cavity proper, antorbital sinus, salt gland duct, nasopharyngeal ducts, and brain can be observed.

The external surface of most of the dermal bones is ornamented with irregular, shallow ridges, grooves, and small pits. The sculpturing is pronounced on the maxilla, the posterior portion of the nasals, prefrontal, and anterior portion of the frontal.

6.2. Cranial openings
6.2.1. Supratemporal fossa and fenestra

The right supratemporal fossa is completely preserved, however, most of the bone's surface that forms it was eroded by recent weathering, thus the contribution of the bones cannot be determined. The supratemporal fossa is large, longer than wider, and triangle-shaped, as in *Cricosaurus araucanensis*, *Cricosaurus vignaudi* (Frey et al., 2002), and *Cricosaurus* sp. (SNSB-BSPG 1973 I 195); and the supratemporal fenestra is rounded (Fig. 3A).

6.2.2. Suborbital fenestra

The right suborbital fenestra is partially preserved. Its anterior margin is acute and extended anteriorly beyond the anterior margin of the orbit. The lateral margin is formed by the maxilla and the medial by the palatine, the posterior limit is not preserved (Fig. 3B).

6.2.3. Secondary choana

The secondary choana is partially preserved. The anterior margin is formed by the palatines, and the posterior by the pterygoids. Unfortunately, the lateral margins are not preserved. The region where the pterygoids are sutured is raised, and laterally there are two anteroposteriorly directed concavities, the presence of a septum could not be identified (Fig. 3B).

6.2.4. Preorbital fossa

Both preorbital fossae are partially preserved and crushed. The anterior-most portion is not preserved. The preorbital fossa is very elongate, with the major axis orientated obliquely (Fig. 4), as in all known metriorhynchids (e.g. *Cricosaurus araucanensis*, MLP 72-IV-7-1; *D. andiniensis*, MOZ-PV 6146; *Maledictosuchus riclaensis*; *Pu. potens*). The preorbital fossa excavates the maxilla and forms a sulcus that vanishes anterodorsally, as in *C. araucanensis* (MLP 72-IV-7-1), but in MCNAM-PV 5096 this
sulcus is more prominent and high, and likely ends at the level of the anterior-most portion
of the nasals (Fig. 4). The dorsal margin of the preorbital fossa is formed by the nasal, and
the ventral one by the maxilla (we cannot rule out the participation of the jugal in the
ventral margin). The lacrimal contributes to the posterior margin (Fig. 4), as in all
metriorhynchids (Fernández and Herrera, 2009).

6.3. Cranium

6.3.1. Maxilla

Both maxillae are incomplete; the lateral, alveolar, and ventral regions are partially
preserved (Figs. 3–4). Ornamentation of the external surface is composed of
anteroposteriorly oriented ridges, as in most metriorhynchines and geosaurines (e.g.
Rhaceosaurus gracilis, Cricosaurus elegans, 'Cricosaurus' medius, Cricosaurus suevicus,
Ma. ricaensis, Pu. potens, Plesiosuchus manselli).

A portion of the maxilla is exposed in ventral view. It contacts the palatine through
a serrated suture (see palatine description). The palatal region of the maxilla is ornamented
with deep grooves (Fig. 3B), a feature only shared with the Swiss rhaceosaurin (see
Young et al., 2020), and Pu. potens within Thalattosuchia. The left maxilla, in its middle
region, preserves six teeth included in a deep groove (Fig. 4A). In the right maxilla,
maxillary tooth row extends, at least, to the level of the anterior margin of the orbit, as in
other metriorhynchids (e.g. C. lithographicus, C. araucanensis, Metriorhynchus
superciliosus). The interalveolar spaces are shorter than the anteroposterior diameter of the
alveoli, as is common in metriorhynchids (e.g. Cricosaurus spp., Maledictosuchus
ricaensis).

6.3.2. Nasal
The nasals are elongate and have the typical triangular outline in dorsal view of thalattosuchians (e.g. Andrews, 1913). Both nasals miss the anterior-most portion leaving exposed the infilling of the nasal cavity proper. Laterally the nasals are sutured to the maxilla. Along the midline, the dorsal surface has a steep longitudinal depression, as in most thalattosuchians (e.g. *Cricosaurus araucanensis*, MLP 72-IV-7-1; cf. *Dakosaurus*, MCNAM-PV 5091; *Opisuchus meieri*; ‘*Steneosaurus*’ bollensis). Laterally to this depression, the nasals bear an anteroposteriorly oriented ridge, which is developed on the posteromedial process (Fig. 3A). These ridges have not been observed before in any other thalattosuchian. The long posteromedial processes of the nasal contact the frontal medially and posteriorly, and the prefrontal laterally. The posterolateral process contributes to the anterodorsal margin of the preorbital fossa. This process is located between the prefrontal and the anterior process of the lacrimal (see lacrimal description), this feature is better preserved on the left side of the skull. The nasals are ornamented, faint grooves and ridges cover the anterior region of the nasal, as in *Ma. ricaensis*, *C. elegans*, and *Plesiosuchus manselii* (Young et al., 2013), among other metriorhynchids. The grooves become deeper and the ridges raise in the posteromedial processes and in the anterior (=nasal) process of the frontal (Fig. 3A).

6.3.3. Lacrimal

Both lacrimals are incompletely preserved and due to postmortem deformation are partially exposed. As in all metriorhynchids, they are oriented vertically, and face laterally (e.g., Fraas, 1902; Andrews, 1913; Pol and Gasparini, 2009; Young et al., 2010) (Fig. 4A, B). The lacrimal dorsally contacts the prefrontal, anteriorly the nasal, and forms the posterior margin of the preorbital fossa (Fig. 4B). The lacrimal has a process that anteriorly extends beyond the anterior margin of the prefrontal (Fig. 4A, B), which can be seen in
dorsal view (Fig. 3A). In *C. araucanensis* this process does not extend beyond the anterior margin of the prefrontal.

6.3.4. Prefrontal

Only the left prefrontal is completely preserved, but there is a transverse fracture in the dorsal surface of the bone, whereas the right element misses the posterior portion, the external surface is damaged, and also a fracture extends across its dorsal surface. The prefrontal is enlarged, teardrop-shaped in dorsal view and projects laterally, as in all metriorhynchids (e.g. Andrews, 1913; Pol and Gasparini, 2009; Young and Andrade, 2009). The prefrontal has a rounded ‘V’-shaped anterior margin with its apex directed anteriorly. Its medial margin extensively contacts the posteromedial process of the nasal through a straight suture. The lateral margin is sutured to the posterolateral process of the nasal. The suture with the frontal is not clear (Fig. 3A). In dorsal view, the prefrontal is about twice as long as broad and the posterolateral margin is rounded, as in e.g. *C. araucanensis*, and *C. lithographicus*.

The dorsal surface of the prefrontal is more exposed in lateral view (Fig. 4A), similar to *D. andiniensis* (MOZ-PV 6146), and unlike other metriorhynchids (e.g. *Cricosaurus* spp.; *Pu. potens*; *Tovrnoneustes coryphaeus* Young et al., 2013). Even if this feature in MCNAM-PV 5096 is exaggerated due to preservational effects, it seems that the prefrontals are less horizontally orientated than in most metriorhynchids. Some shallow pits and deep grooves ornament the dorsal surface of the prefrontal.

6.3.5. Frontal

The frontal is partially preserved with the interorbital region severely damaged. In the sagittal plane, there seems to be a suture that might resemble the interfrontal suture. The dorsal surface of the anterior process has a steep longitudinal depression almost continuous
with the one presents in the nasals. In dorsal view, the anterior process of the frontal
extends anteriorly between the posteromedial processes of the nasal, with a ‘V’-shaped
suture pointing anteriorly. At the apex, the suture is strongly serrated (Fig. 3A). The
anterior process is short as it does not reach the level of the anterior margin of the
prefrontal, as in C. lithographicus, Rhacheosaurus gracilis, Dakosaurus maximus, among
others and unlike C. araucanensis (MLP 72-IV-7-1), D. andiniensis (MOZ-PV 6146), Pu.
potens, and Torvoneustes coryphaeus (Young et al., 2013).

The lateral processes of the frontal are poorly preserved, however, the angle formed
by those processes and the midline of the skull can be estimated around 40–50º (Fig. 4A,
B), as in Cricosaurus and Dakosaurus. The frontal enters the supratemporal fossae taking
part in the frontoparietal fossa (sensu Holliday et al., 2019). The dorsal surface of the
intertemporal bar is eroded and the contact with the parietal cannot be identified. The
external surface of the frontal is mostly ornamented by shallow to deep grooves, as in C.
elegans, and C. suevicus, and contrasting with the unornamented frontal of cf. ‘C.’
macrospondylus, C. schroederi, C. araucanensis, and C. lithographicus.

6.3.6. Palatine

Both palatines are incomplete and badly preserved. They sutured each other in the
midline of the skull. They form the ventral boundary of the nasopharyngeal ducts. The
palatine has a “V”-shaped midline anterior process (Fig. 3B), as in Ma. riclaensis (Parrilla-
Bel et al., 2013), Maledictosuchus nuyivijanan (Barrientos-Lara et al., 2018), and D.
andiniensis (MHNSR PV 344; Vignaud and Gasparini, 1996: photos 2). Based on
preservation we cannot identify if the palatine has two non-midline anterior processes as in
other metriorhynchids (e.g. Cricosaurus araucanensis, MLP 72-IV-7-1; D. andiniensis,
MHNSR PV 344; *Maledictosuchus* spp.). The paired depressions described in the palatines of *Cricosaurus bambergensis* Sachs et al., 2019, are not present in this specimen.

6.3.7. Pterygoid

The pterygoids are partially preserved. Anteriorly, they contact the palatine and participate, at least, in the posterior margin of the secondary choana. Inside the secondary choana, the pterygoid-apterygoid suture is raised, but it does not form a septum (Fig. 3B).

6.3.8. Vomer

As the snout is transversally broken, the vomer is exposed. It is ventrally covered by the maxilla anteriorly and by the palatines posteriorly. As in *C. araucanensis*, the vomer is “U”-shaped with its base very thickened (Herrera, 2012) separating the nasal airway ventromedially.

6.4. Mandible

The mandible is incomplete and badly preserved and the boundaries of the bones that form it are not clear (Figs. 3B, 4A, C).

6.4.1. Dentary

On the left side, a portion of the mandible is articulated with the maxilla (Fig. 4A). A small portion of the anterior-middle section of the right dentary with seven teeth is preserved (Fig. 4C). Posteriorly, the suture with the surangular is anteroventral to posterodorsal oriented. The dentary contacts the angular posteroventrally through a wedge-shaped suture (Fig. 4A). The contact with the splenial could not be identified.

6.4.2. Splenial, surangular, and angular

Fragments of the three left elements were identified. However, based on preservation a detailed description is not possible. The angular and surangular extend
anteriorly beyond the anterior margin of the orbit (Fig. 4A), a feature present in all Cricosaurus spp., Rhacheosaurus gracilis, and ‘Metriorhynchus’ casamiquelai.

6.5. Dentition

Maxillary and dentary teeth are preserved. Six teeth are emerging from the middle section of the left maxilla and seven from the anterior-middle section of the right dentary (Fig. 4A, C). The interalveolar spaces between them are variable, being some similar in length to the alveoli, while others are approximately half the anteroposterior length of the adjacent alveoli, as in most Metriorhynchidae (e.g. C. araucanensis, Maledictosuchus spp., Metriorhynchus superciliosus).

As in most Metriorhynchinae, teeth are small (1.5–2 cm), single cusped, slightly curved, and bicarinated with a macroscopic keeled and unserrated carina (Fig. 5A–G). All tooth crowns are laminar, labiolingually compressed, with the labial surface almost flat and the lingual one convex, as in Geosaurina (Andrade et al., 2010; Foffa et al., 2018). The labial surface is divided into three apicobasal facets, with the posterior facet better defined than the anterior one (Fig. 5). Tooth with three apicobasal facets on the labial surface is a feature that has only been reported in the geosaurins Geosaurus Cuvier, 1824, and Ieldraan melkshamensis Foffa et al., 2018 (Young and Andrade, 2009; Andrade et al., 2010; Foffa et al., 2018). In Cricosaurus puelchorum, these facets are not strongly defined as in the geosaurins mentioned above but can be easily identified. The medial facet is wider than the lateral ones along the entire crown, and it diminishes towards the apex whereas the lateral facets have a constant width along the crown, as was described for Geosaurus (Andrade et al., 2010).
In *Cricosaurus puelchorum* teeth are bicarinated, as in most Metriorhynchidae. The distal carina extends from the base to the apex of the crown, whereas the mesial carina is more prominent in the apical-half of the tooth crown, and in some teeth, it is completely absent in the basal-most region of the crown.

The enamel ornamentation of the labial and lingual surface is composed of scattered apicobasal parallel ridges of low relief, that are restricted to the 3/4 basal region of the crown (Fig. 5A–F). Tooth crowns with well-defined apicobasal aligned ridges also occur in *Cricosaurus schroederi* (S. Sachs pers. com). In *C. puelchorum* the longitudinal ridges are better defined and are more densely packed on the lingual surface (Fig. 5E, F), as in *Cricosaurus lithographicus* (Herrera et al., 2013b). Additionally, in the labial surface, the middle facet is sculpted by two well-developed troughs separated by broad continuous, parallel, and well-developed ridges (Fig. 5), features present in all preserved teeth. A fluted surface in the middle plane of the tooth crown was previously described in the geosaurins *I. melkshamensis*, ‘*Metriorhynchus*’ *brachyrhynchus* (NHMUK PV R 3804) and an undescribed geosaurin (see Foffa et al., 2018). In *I. melkshamensis* the five well-defined troughs are more conspicuous than in MCNAM-PV 5096. In ‘Me.’ *brachyrhynchus* the troughs are poorly defined, more than five, and are not present in all crowns (Foffa et al., 2018).

6.6. Natural cast of *Cricosaurus puelchorum* (*MCNAM-PV 5096*)

Based on preservation, the natural casts of some soft structures are partially exposed, mainly those from the preorbital region. We identified the infilling of the nasal cavity proper, nasopharyngeal ducts, antorbital sinus, and the exocrine gland duct (Fig. 6A). The topographic relationships of the structures of the preorbital region fit well with the
pattern previously described in other metriorhynchids (e.g. Fernández and Gasparini, 2008; Fernández and Herrera, 2009; Herrera et al., 2013a).

The snout is broken exposing a cross-section of the nasal cavity proper. It is roughly quadrate, with vertical lateral margins. The nasal airway is divided at the midline by the vomer (Fig. 6A). In ventral view, the nasopharyngeal ducts are partially exposed. They are long and arise anteriorly defining the primary choana, which is anterior to the internal antorbital fenestra and the preorbital opening (Fig. 6B). As in other described natural casts from the Vaca Muerta Formation, the infilling of blood vessels has been preserved on the external surface of the ducts suggesting an intensive blood supply (e.g. Fernández and Herrera, 2009; Herrera et al., 2013a).

In right lateral view, two subcircular structures can be observed, the dorsal one corresponds to the infilling of the salt gland duct whereas the ventral one is the infilling of the antorbital sinus, completely included within the maxilla. Both infillings are oval but the major axis of the infilling of the gland's duct is lateromedially oriented whereas for the antorbital sinus is dorsoventrally oriented (Fig. 6A). The same morphology was previously described in *Cricosaurus araucanensis* (Herrera et al., 2013a: fig. 2B–C).

In dorsal and lateral views a long subcircular structure is preserved from the posterior region to the preserved tip of the snout, positioned between the nasal cavity (medially), and the maxilla (laterally), and dorsal to the alveolar region (Figs. 3A, 4B). Based on CT scans of several metriorhynchoids, the same structure was identified and interpreted such as the dorsal alveolar canal (Bowman et al., submitted abstract), and also identified in *Pelagosaurus typus* Bronn, 1841 by Pierce et al. (2017).

7. Phylogenetic analysis
7.1. Taxon and character sampling

To evaluate the affinities of *Cricosaurus puelchorum*, we conducted a phylogenetic analysis using a dataset that is a combination of the slightly modified versions of the matrices of Aiglstorfer et al. (2020) and Young et al. (2020). Character descriptions are presented in Supplementary Information 1. Modifications consisted of the inclusion of MCNAM-PV 5096 and SNSB-BSPG 1973 I 195 as Operational Taxonomic Units (OTUs), and revision of scorings for other OTUs that were analyzed first-hand by one of the authors (YH) of this study (see Supplementary Information 2 for more information). As in previous analyses based on this dataset (e.g. Aiglstorfer et al., 2020; Young et al., 2020), *'Cricosaurus' medius*, *'Dakosaurus' lissocephalus* Seeley, 1869, and Geosaurinae indet. Argentina (MOZ-PV 6913) were consistently recovered as unstable taxa, thus they were excluded from the analysis. The new dataset consists of 176 taxa and 519 characters.

6.2. Method

The resulting dataset was analyzed using TNT v 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016). A heuristic tree search strategy with 650,000 Max trees set in memory, and 1000 replications of Wagner trees (using random addition sequences) was conducted, followed by tree-bisection-reconnection (TBR) branch swapping (holding 10 trees per replicate). The most parsimonious trees recovered in this first search were subjected to a second round of TBR. To identify unstable taxa and generate a reduced consensus tree we used the prunnelsen command of TNT (Goloboff and Szumik, 2015). Nodal support was evaluated using Bremer support (Bremer, 1994). The time-calibrated reduced strict consensus tree of Metriorhynchidae was produced using the R packages APE (Paradis et al., 2004) and strap (Bell and Lloyd, 2015) in R (R Core Team, 2013).
7.3. Phylogenetic results

The Most Parsimonious Trees (MPTs) recovered by our analysis are of 1798 steps (CI = 0.401, RI = 0.861, HI = 0.599, RCl = 0.345261). The total number of MPTs is unknown because the trees recovered in the second round of TBR exceeded the maximum space for trees in memory. The strict consensus tree presented herein (Fig. S1 in Supplementary Information 3) is consistent with the unweighted parsimony analysis performed by Young et al. (2020, fig. 4A), except for the relationships among Rhacheosaurini. Within Rhacheosaurini Young et al. (2020) recovered some minor clades, whereas our analysis recovered most Rhacheosaurini forming a large polytomy except for *C. lithographicus*, *C. araucanensis*, *C. vignaudi*, *C. schroederi*, and *Cricosaurus* sp. (SNSB-BSPG 1973 I 195) which are clustered although their internal relationships are unresolved (Fig. S1 in Supplementary Information 3). Focused on Metriorhynchinae, and to improve the resolution of MPTs, a posteriori of the tree searches, we pruned unstable taxa (see Supplementary Information 3) to build a reduced consensus tree (Fig. S2 in Supplementary Information 3). After this procedure, the resolution of the internal relationships of the Rhacheosaurini improved (Fig. 7). So, this tree will be used to describe the phylogenetic relations of the new species. As in the most recent phylogenetic analyses of Metriorhynchidae, *'Cricosaurus' saltillensis* (Buchy et al., 2006), and cf. *'Cricosaurus' macrospondylus* are no longer being recovered in the same clade as other *Cricosaurus* (see e.g. Ősi et al., 2018; Sachs et al., 2019; Young et al., 2020). *Cricosaurus sensu stricto* is recovered as a clade supported by three synapomorphies: posterior margin of narial fossa terminates approximately level to the M3 to the anterior margin of the M5 alveoli (Ch. 56, 5), convex supratemporal arch (Ch. 125, 1), and bifurcation of the parietal in dorsal view (Ch. 159, 1) (see Supplementary Information 3). Within *Cricosaurus*, the OTUs are
clustered in two subclades although internal relationships among them are not resolved.

The first clade includes *C. araucanensis*, *C. lithographicus*, *C. vignaudi*, *C. schroederi*, and *Cricosaurus* sp. (SNSB-BSPG 1973 I 195) supported by one synapomorphy: no conspicuous ornamentation of the maxilla (Ch. 13, 0). The second subclade includes the new taxon and three Late Jurassic (late Kimmeridgian–early Tithonian) taxa from southern Germany: *C. puelchorum*, *C. suevicus*, *C. elegans*, and *Cricosaurus bambergensis*, and is supported by three synapomorphies: frontal ornamented with shallow to deep elliptical pits and shallow to deep grooves (Ch. 14, 0), maxillary teeth laterally compressed (Ch. 357, 0), and dentary teeth laterally compressed (Ch. 358, 0). *Cricosaurus puelchorum* presents six autapomorphies: lacrimal visible in dorsal and lateral views (Ch. 94, 0), supratemporal fossae triangle-shaped (Ch. 118, 4), the anteromedial process of the frontal is noticeably posterior to the prefrontals (Ch. 139, 1), presence of apicobasal facets on the labial surface of the teeth (Ch. 359, 1), presence of laminar teeth (Ch. 360, 1), and tooth crowns with well-defined apicobasal aligned ridges (Ch. 379, 2). Support measures are all low, exhibiting Bremer values of one in most cases (Fig. S3 in Supplementary Information 3).

8. Discussion

8.1. Comparative anatomy

The unique combination of features present in MCNAM-PV 5096 including several autapomorphies (see Diagnosis) differentiates it from any other taxon and justifies the erection of a new species. *Cricosaurus puelchorum* is referred to as the genus *Cricosaurus* based on the description and phylogenetic analysis. The new taxon shares the following features with other *Cricosaurus*: acute angle formed by the posterolateral and posteromedial processes of the frontal; convex supratemporal arch in dorsal view; lateral
margin of the prefrontal rounded; orbits as large as the supratemporal fossae; surangular
and angular well-developed, anterolaterally exceeding beyond the anterior margin of the
orbits; bicarinate dentition with a faint carina.

From the set of features that characterized *Cricosaurus puelchorum*, two of them
particularly stand out: the dermal bone ornamentation and the dental morphology. In
*Cricosaurus puelchorum* the ornamentation of the dermatocranium is more evident than in
all known *Cricosaurus*, having even the palatal surface of the maxilla ornamented (Fig. 3).
Among *Cricosaurus* spp., upper Kimmeridgian and lower Tithonian species have
ornamented premaxillae, maxillae, nasals, and frontal with grooves and pits, whereas lower
and lower upper Tithonian (*C. araucanensis*, and *C. lithographicus* respectively) and upper
Valanginian (*C. Schroederi*) species have unornamented and quite smooth dermal bones. In
*C. puelchorum* the ornamentation is comparable to that present in *C. suevicus*, and *C.
elegans* from southern Germany, but it is also more evident than in those species. A
common trend among all Metriorhynchidae clades is the reduction of dermal bone
ornamentation. Late Jurassic and Late Jurassic–Early Cretaceous forms are generally
specimens that have less ornamented dermatocranium than Middle Jurassic specimens
(Young et al., 2013). This condition (not ornamented or weakly ornamented skull roof) has
been linked with a pelagic lifestyle (Clarac et al., 2017). The other Late Jurassic–Early
Cretaceous metriorhynchids from the Vaca Muerta Formation: *C. araucanensis*, and *C.
lithographicus*, and the Geosaurini *D. andiniensis* also, shared the dermal bones
unornamented whereas *Cricosaurus puelchorum* disrupts the trend observed in
Rhacheosaurini, being Early Cretaceous in age and having an ornamented dermatocranium.

Also, the dental morphology of MCNAM-PV 5096 is unusual for a Rhacheosaurini.
The teeth are highly elliptical in cross-section and three-faceted on the labial surface with a
fluted middle facet features that contrast with all *Cricosaurus* species in which the teeth vary from bearing sub-circular to elliptical cross-section with crowns largely unornamented on the labial surface. In *Cricosaurus puelchorum* the crows are labiolingually compressed, with the mesial-distal axis approximately twice longer than the labial-lingual one, as in Geosaurina (Foffa et al., 2018). Interestingly, three apicobasal faceted teeth are also characteristic of Geosaurina (Andrade et al., 2010; Foffa et al., 2018). In *Cricosaurus puelchorum* the middle facet is sculpted by two well-developed troughs separated by well-developed ridges (Fig. 5). The presence of a fluted middle facet has only been reported in the geosaurins *Ieldraan melkshamensis*, *Metriorhynchus* *brachyrhynchus* (NHMUK PV R 3804), and an undescribed specimen (see Foffa et al., 2018). The number, pattern, and distribution of the troughs vary among these taxa. As such, in *Cricosaurus puelchorum* the shape of the crown and the ornamentation of the enamel surface are convergent with Geosaurina.

Herrera et al. (2013b) discussed the morphological diversity of metriorhynchids from the Neuquén Basin and highlighted the tooth disparity between the dental morphology present in *C. araucanensis* and *C. lithographicus*. The description of this new taxon and its unusual dental morphology adds a new component to the diversity among the Neuquén Basin *Cricosaurus*. *Cricosaurus araucanensis* (early late Tithonian) has smooth tooth crowns, in *Cricosaurus lithographicus* (late early to early late Tithonian) the crowns have fine apicobasal aligned ridges that vanish towards the smooth apex, and in *Cricosaurus puelchorum* (early Berriasian), the crows have apicobasal parallel ridges, restricted to the 3/4 basal region of the crown, and the labial surface is sculpted by troughs separated by broad continuous, parallel and well-developed ridges (Fig. 5).
Based on their tooth morphologies, all *Cricosaurus* spp. found in the southeastern Pacific fall into the pierce guild. However, differences as the one mentioned above indicate that probably, within the general pierce guild, their prey preferences were different. However, as they were collected from different beds (and ages) the differences cannot be strictly linked with the co-occurrence of these species.

8.2. Phylogenetic position of *Cricosaurus puelchorum* and its implication on the metriorhynchid distribution across the J/K boundary

One of the main unresolved issues of Metriorhynchoid phylogeny is the phylogenetic relationships within the species referred to *Cricosaurus*. The species-richness of this genus is one of the highest among Metriorhynchoida and, despite that their fossils are particularly abundant in Jurassic deposits of the Solnhofen Archipelago (the northern rim of the Tethys Ocean, see e.g. Rauhut et al., 2017) and the southeastern Pacific, the relationships among its species are still controversial (e.g. Young and Andrade, 2009; Herrera et al., 2013b; Parrilla-Bel et al., 2013; Foffa et al., 2018; Ósi et al., 2018). Sachs et al. (2019) described the new species *Cricosaurus bambergensis* and analyzed its phylogenetic position. As result, they recovered a *Cricosaurus* clade divided into two unresolved subclades, one formed by all of the upper Kimmeridgian–lower Tithonian *Cricosaurus* species from Germany (i.e. *C. suevicus*, *C. elegans*, and *C. bambergensis*), and the other containing *C. araucanensis*, *C. lithographicus*, *C. vignaudi*, and *C. Schroederi*. Noteworthy, despite the low branch supports of the phylogenetic tree of Sachs et al. (2019), the increase of the taxon sampling (i.e. the inclusion of MCNAM-PV 5096 and SNSB-BSPG 1973 I 195 to the data set) did not affect the results nor produced the collapse of *Cricosaurus* clade. Thus, after pruning the unstable taxa we recovered two unresolved
Cricosaurus sub-clades. Just for the discussion, we call sub-clade A to the group containing: C. puelchorum, C. suevicus, C. elegans, and C. bambergensis, and sub-clade B to the clade formed by C. araucanensis, C. lithographicus, C. vignaudi, C. schoeideri, and Cricosaurus sp. SNSB-BSPG 1973 I 195.

Interestingly, Cricosaurus puelchorum is recovered nested within the species from the sub-clade A –formed by the upper Kimmeridgian–lower Tithonian Cricosaurus species from southern Germany–, whereas Cricosaurus sp. (SNSB-BSPG 1973 I 195), a taxon from the lower Tithonian also from southern Germany, is nested within the sub-clade B that mainly contains American forms. However, the topology of sub-clade B should be treated with caution, as it is supported by a single synapomorphy, and the incorporation of new material or more characters might alter the topology.

Cricosaurus sensu stricto has a broad paleobiogeographical distribution (Germany, Mexico, and Argentina) with a long stratigraphic range (~ 27 ma) comprised between the late Kimmeridgian (Cricosaurus bambergensis) and the lower Valanginian (Cricosaurus schoeideri), and it is one of the few taxa of Metriorhynchidae that certainly crossed the J/K boundary.

This Metriorhynchinae phylogeny (Fig. 7) is interesting for two main reasons. First, it depicts a Cricosaurus cluster split into two clades indicating close affinities between species of two disparate paleobiogeographical units, as western Tethys Ocean and eastern Pacific. The hypothesis of connection and interchange of herpetofauna and marine invertebrates between these two biogeographic units, favored by the opening of seaways like the Caribbean Corridor (or Hispanic Corridor), has been extensively cited (e.g. Damborenea, 2000; Gasparini and Iturralde-Vinent, 2006 and references therein). Second,
time-calibrated phylogeny indicates the survival of both subclades of *Cricosaurus* but with
an evident diminishing of metriorhynchidae’s diversity from the Tithonian onwards.

Previous work in two localities from southern Mendoza (Vaca Muerta Fm., Neuquén Basin) showed that the findings of marine reptiles decline towards the J/K boundary, being common to abundant in the upper Tithonian *Corongoceras alternans Zone*, rare to common in the upper Tithonian–lower Berriasian *Substeueroeroceras koeneni* Zone, and with a single specimen—the one here described— recovered from the lower Berriasian *Argentiniceras noduliferum* Zone (Fernández et al., 2019). These authors suggested that this trend can be related to the occurrence of a shallower environment upward in the stratigraphic column and not to an extinction event. Taking into account that in the sections explored up to date J/K boundary beds are included within a shallowing-upwards ramp system (e.g. Legarreta and Gulisano, 1989), and that deeper sections of the Vaca Muerta Formation have not yet been explored, we still cannot confidently relate the decline of marine reptile findings towards the boundary to an extinction event, however, we also cannot discard it.

9. Conclusions

Here, we described a new Rhacheosaurini, *Cricosaurus puelchorum* from the lower Berriasian (*Argentiniceras noduliferum* Zone) from southern Mendoza being the youngest *Cricosaurus* record from the Vaca Muerta Formation (Argentina), and confirming the survival of the genus in the Cretaceous of the southeastern Pacific. Time-calibrated phylogenetic analysis shows a decrease in *Cricosaurus* species richness from the late Tithonian onwards.
The new species is well defined by a unique combination of features and several autapomorphies. Phylogenetic analysis indicates that *Cricosaurus puelchorum* is closer to upper Kimmeridgian–lower Tithonian species of *Cricosaurus* from the Solnhofen Archipelago than to the other two species from the Tithonian of the southeastern Pacific. It is worthy to remark that the internal relationships of *Cricosaurus* spp, and the hypotheses based on them like the biogeographical affinities, require further scrutiny to identify more characters to improve branch supports of phylogenetic trees.

Whether the decrease of *Cricosaurus* records from upper Tithonian levels of the Vaca Muerta onwards is an artifact of uneven collecting efforts, or if it can be linked to a real drop of the metriorhynchid diversity towards the Cretaceous, requires further field explorations especially in younger geological units within the Neuquén Basin.

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Figure captions

**Figure 1.** A, Location of the study section. Main geologic units were depicted after Dessanti (1978), Nullo et al. (2005), and Sruoga et al. (2005). B, Partial stratigraphic section of Arroyo Paulino showing *Cricosaurus puelchorum* (MCNAM-PV 5096) and *Groebiceras bifrons* occurrences.

**Figure 2.** *Groebiceras bifrons* Leanza, 1945. 1-2, MCNAM-PI 24858. 1, right lateral view, 2, ventral view; 3-4, MCNAM-PI 24879, 3, left lateral view, 4, ventral view. Scale bar: 1 cm. All specimens coated with Ammonium chloride.

**Figure 3.** *Cricosaurus puelchorum*, MCNAM-PV 5096. A, Skull in dorsal view. B, Skull in ventral view. Abbreviations: an, angular; cnp, nasal cavity proper; cr, crest; d, dentary; dac, dorsal alveolar canal; fr, frontal; la, lacrimal; ls, laterosphenoid; mx, maxilla; na, nasal; pa, parietal; pl, palatine; po, postorbital; prf, prefrontal; pt, pterygoid; sch, secondary choana; sof, suborbital fenestra; sp, splenial; stf, supratemporal fenestra. The dash-dotted
line indicates broken surfaces, dotted surface indicates matrix, striped surface indicates broken bone, grey surface shows the region preserved as natural endocast, arrows indicate the transversally broken plane. Scale bar: 5 cm.

**Figure 4.** *Cricosaurus puelchorum*, MCNAM-PV 5096. **A,** Skull in left lateral view. **B,** Skull in right lateral view. **C,** Right dentary partially preserved. Abbreviations: an, angular; asin, antorbital sinus; cnp, nasal cavity proper; d, dentary; dac, dorsal alveolar canal; fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; or, orbit; po, postorbital; pref, preorbital fossa; pres, preorbital sulcus; prf, prefrontal; sp, splenial; sur, surangular; stf, supratemporal fossa. The dash-dotted line indicates broken surfaces, dotted surface indicates matrix, striped surface indicates broken bone, grey surface shows the region preserved as natural endocast, arrows indicate the transversally broken plane. Scale bars: 5 cm.

**Figure 5.** *Cricosaurus puelchorum*, MCNAM-PV 5096. Dentition. **A,** Maxillary teeth. **B,** Dentary teeth. **C,** Close-up of a maxillary tooth in labial view. **D,** Close-up of a dentary tooth in labial view. **E,** Close-up of a maxillary tooth in lingual view. **F,** Microscopy image of a maxillary tooth in lingual view. **G,** Microscopy image of the carina. **H,** Schematic labial view of a tooth. **I,** Schematic cross-section of a tooth. White arrows show the troughs. Abbreviations: f, facets; la.s, labial surface; li.s, lingual surface; r, ridges; t, troughs. Scale bars: 1 cm (A–E), 3 mm (F), 400 µm (G).

**Figure 6.** *Cricosaurus puelchorum*, MCNAM-PV 5096. Natural cast. **A,** Preorbital region in anterolateral right view. **B,** Cranium in ventral view with detail of vascularization.
Abbreviations: an, angular; asin, antorbital sinus; cnp, nasal cavity proper; fr, frontal; gd, salt gland duct; la, lacrimal; mx, maxilla; mx-na, maxillary-nasal suture; na, nasal; npdu, nasopharyngeal duct; pch, primary choana; pl, palatine; prf, prefrontal; vo, vomer. Arrows indicate anterior direction. Scale bars: 5 cm.

Figure 7. Time-calibrated reduced consensus tree of Metriorhynchidae.

SUPPORTING INFORMATION

Supporting Information 1. Character list used in the phylogenetic analysis.

Supporting Information 2. Applied changes of character codification from the original datasets.

Supporting Information 3. Strict consensus cladogram, results from prunnelsen command, reduced consensus cladogram, list of synapomorphies of the reduced consensus, reduced consensus cladogram depicting the Bremer support values.

Table 1. Measurements (in mm) of best-preserved *Groebbericeras bifrons* Leanza, 1945 specimens.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Shell diameter</th>
<th>Whorl height/shell diameter</th>
<th>Whorl width/shell diameter</th>
<th>Umbilical diameter/shell diameter</th>
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<tbody>
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<td>MCNAM-PI 24858</td>
<td>78.61</td>
<td>31.01 (0.39)</td>
<td>22.32 (0.28)</td>
<td>25.54 (0.32)</td>
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<td>59.30</td>
<td>24.53 (0.41)</td>
<td>17.98 (0.30)</td>
<td>19.01 (0.32)</td>
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<tr>
<td>MCNAM-PI 24879</td>
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<td>18.85 (0.42)</td>
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</tr>
</tbody>
</table>
Table 2. List of taxa and specimens used for comparative purposes in the description.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Steneosaurus' bollensis (Jäger, 1828)</td>
<td>SMNS 15391</td>
</tr>
<tr>
<td>'Metriorhynchus' brachyrhynchus (Eudes-Deslongchamps, 1868)</td>
<td>NHMUK PV R 3700, NHMUK PV R 3804, NHMUK PV R 4763</td>
</tr>
<tr>
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<td>MGHF 1-08573</td>
</tr>
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<td>MHNSR PV 344, MOZ-PV 6146</td>
</tr>
<tr>
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<td>SMNS 8203</td>
</tr>
<tr>
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<td>SMNS 9808</td>
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<tr>
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<tr>
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Table 1. Measurements (in mm) of best-preserved *Groebericeras bifrons* Leanza, 1945 specimens.

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<tr>
<th>Specimen</th>
<th>shell diameter</th>
<th>whorl height/shell diameter</th>
<th>whorl width/shell diameter</th>
<th>umbilical diameter/shell diameter</th>
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<tr>
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Highlights

*Cricosaurus puelchorum* a new species of Metriorhynchidae from Mendoza (Argentina).

It is the first definitively Cretaceous metriorhynchid from the Neuquén Basin.

*Cricosaurus* survives across the J/K boundary at the southeastern Pacific.
Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: