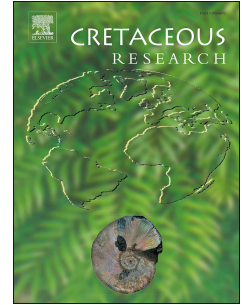


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Cricosaurus (Thalattosuchia, Metriorhynchidae) survival across the J/K boundary in the High Andes (Mendoza Province, Argentina)

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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.

Marta S. Fernández conceived and designed the experiments, contributed analysis tools, reviewed drafts of the paper, approved the final draft.

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.

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1 *Cricosaurus* (Thalattosuchia, Metriorhynchidae) survival across the J/K boundary in the
2 High Andes (Mendoza Province, Argentina)

3

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24 **Abstract**

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

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

38

39 **1. Introduction**

40 Metriorhynchidae, a clade of Mesozoic marine crocodylomorphs, are the only
41 Archosauria group adapted to a pelagic lifestyle as it is documented by several
42 morphological and physiological modifications such as laterally directed orbits, reduced
43 and paddle-like forelimbs, loss of osteoderms, regionalized caudal vertebral column with a
44 hypocercal tail, and hypertrophied nasal glands for salt excretion, among others (e.g. Fraas,
45 1902; Andrews, 1913; Fernández and Gasparini, 2008; Young et al., 2010; Herrera et al.,
46 2013a; Sachs et al., 2019). Also, they were probably bearing live young (Herrera et al.,
47 2017, and references therein).

48 Worldwide Jurassic records depict metriorhynchids as a diverse lineage, gathering
49 approximately 40 nominal species distributed in more than ten genera, being *Cricosaurus*
50 Wagner, 1858 one of the most speciose genera (e.g. Wagner, 1852, 1858; Fraas, 1902;
51 Gasparini and Dellapé, 1976; Young and Andrade, 2009; Herrera et al., 2013b; Sachs et al.,
52 2019). On the contrary, Cretaceous fossils are particularly sparse. Laurasian records are
53 mostly restricted to Germany and France. Two specimens were recovered from the
54 Valanginian of Germany: *Cricosaurus schroederi* (Kuhn, 1936), and the holotype of
55 *Enaliosuchus macrospondylus* Koken, 1883 (now referred as Metriorhynchidae indet., see
56 Sachs et al., 2020). French records include *Cricosaurus macrospondylus* (now referred as
57 cf. '*Cricosaurus*' *macrospondylus* see Sachs et al., 2020 and Young et al., 2020) from the
58 lower Valanginian (Hua et al., 2000), *Geosaurus lapparenti* (Debelmas and
59 Strannoloubsky, 1957) from the upper Valanginian to lower Hauterivian (Debelmas, 1952,
60 1958; Debelmas and Strannoloubsky, 1957), and the holotype of the nomen dubium
61 *Neustosaurus gigondarum* Raspail, 1842 from the lower Valanginian. Additionally, an
62 indeterminate Plesiosuchina specimen from the upper Valanginian (Young et al., 2014),
63 and an indeterminate metriorhynchid from the upper Valanginian–lower Hauterivian
64 (Debelmas and Demians D'Archimbaud, 1956) are also known from France (see Sachs et
65 al., 2020 for further information). To these finding, it must be added an isolated tooth from
66 the lowermost Aptian of Italy referred to cf. Plesiosuchina (Chiarenza et al., 2015).

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

70 In the Vaca Muerta Formation (Neuquén Basin), metriorhynchids are known from
71 the upper part of the lower Tithonian (*Aulacosphinctes proximus* Zone) to the upper

72 Tithonian–lower Berriasian (*Substeueroceras koeneni* Zone) (see e.g. Gasparini and
73 Dellapé, 1976; Vignaud and Gasparini, 1996; Pol and Gasparini, 2009; Herrera et al.,
74 2013b, 2015; Herrera, 2015; Fernández et al., 2019). The youngest specimens from this
75 basin (*Dakosaurus andiniensis* Vignaud and Gasparini, 1996, and *Purranisaurus potens*
76 Rusconi, 1948a) were recovered from upper Tithonian–lower Berriasian levels
77 (*Substeueroceras koeneni* ammonite Zone). Thus, up to date, no definitive Cretaceous
78 metriorhynchids have been found in the Neuquén Basin.

79

80 1.1. Metriorhynchids from southern Mendoza Province

81 The specimens of metriorhynchids discovered in Mendoza Province during the first
82 half of the XX Century were first described as an ichthyosaur and a plesiosaur (Rusconi,
83 1948a, b). Rusconi (1948b) nominated an "ichthyosaur" species as *Ichthyosaurus*
84 *inexpectatus* (from Cajón del Río Grande), however, this material likely corresponds to
85 *Dakosaurus* Quenstedt, 1856 (Vignaud and Gasparini, 1996). Also from Cajón del Río
86 Grande, Rusconi (1948a) described the metriorhynchid *Purranisaurus potens* as a
87 "plesiosaur" (see Gasparini, 1973; Herrera et al., 2015, Fernández et al., 2019 for detailed
88 information). Additionally, in two sites located near to the Mendoza-Neuquén provincial
89 boundary have been recovered three specimens of metriorhynchids. In Tithonian levels of
90 Sierra de Reyes two natural endocasts of the skull cavities referred to *Cricosaurus*
91 *araucanensis* (Gasparini and Dellapé, 1976) were found, and also from Tithonian levels but
92 from Cari-Lauquen comes the holotype of *Dakosaurus andiniensis* (Vignaud and
93 Gasparini, 1996). Except for the holotype (and the only specimen know) of *Purranisaurus*
94 *potens* for which an upper Tithonian–lower Berriasian age was determined based on an

95 associated ammonite shell (Herrera et al., 2015), the age of the other metriorhynchids
96 specimens from Mendoza Province is not accurately constrained.

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

103

104 **2. Geological context and biostratigraphic framework**

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

111 Upper Jurassic–Lower Cretaceous marine boundary beds are encompassed by the
112 Vaca Muerta Formation, Mendoza Group (Weaver, 1931; Groeber, 1946). The Vaca
113 Muerta Formation was deposited after a sudden transgression from the Pacific Ocean, and it
114 is composed of a rhythmic succession of organic-rich shales, marls and limestones
115 deposited within a carbonate ramp to platform setting (Mitchum and Uliana, 1985;
116 Legarreta and Uliana, 1991; Spalletti et al., 2000; Kietzmann et al., 2014). The remarkably
117 fossiliferous character of this lithostratigraphic unit has long enabled its relative dating
118 through age-diagnostic fossils, among which ammonites, calcareous nannofossils, and

119 calpionellids stand out (López-Martínez et al., 2017). In the last few years, the combination
120 of the ammonite biozonation scheme and nano- and microfossils bioevents, together with
121 the absolute age data obtained from the radio-isotopic geochronological analysis of detrital
122 and igneous zircons, resulted in interesting advances in the chrono-biostratigraphic
123 framework of the Andean Tithonian–Berriasian interval (Riccardi, 2015; Aguirre-Urreta et
124 al., 2019 and references therein).

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

133 Age assignation of the Arroyo Paulino section relies on bed-by-bed ammonite
134 sampling and the identification of all the Andean Assemblage Ammonoid Zones between
135 the *Windhausenicerias internispinosum* to the base of the *Argentinicerias noduliferum* Zones
136 –Microcanthum to Occitanica Standard Zones– (Vennari et al., 2014; Riccardi, 2015;
137 Aguirre-Urreta et al., 2019 and references therein). The specimen MCNAM-PV 5096 was
138 found *in-situ* in bed Py 38, a 0.65 m dark, massive, fine to medium calcareous sandstone
139 bounded by dark-grey laminated marls (Fig. 1B). That bed also retrieved some bivalve
140 fragments and an ammonite shell identified as *Groebericerias bifrons* Leanza, 1945
141 (MCNAM-PI 24878). Another representative of that species was collected from the
142 overlying Py 39 bed (MCNAM-PI 24858), and two additional specimens were found loose

143 closely around (MCNAM-PI 24879 and 24880). Presence of *G. bifrons* allows to
144 confidently constraint the bed bearing the metriorhynchid specimen (MCNAM-PV 5096)
145 to the base of the *A. noduliferum* Zone (i.e. to the lower Berriasian). Ammonite specific
146 assignation is supported by the compressed open-coiled shells, with rounded flanks and
147 rather acute venters (Fig. 2, Tab. 1). All specimens lack tubercles and bear narrow
148 prorsiradiate constrictions, and ribs that are more evident over the upper third of the flank.
149 Even though ornamentation-smoothing age tendency could not be properly evaluated given
150 the reduced diameter of the material (maximum diameter of *c.* 78 mm), the other characters
151 described are diagnostic of *G. bifrons* (Leanza, 1945; Aguirre-Urreta and Álvarez, 1999).

152 *Groebericeras bifrons* is interpreted as a lower Berriasian marker in the Neuquén
153 Basin and it is usually recorded at the very base of the *Argentincerases noduliferum* Zone
154 (Leanza, 1945; Aguirre-Urreta and Álvarez, 1999; Vennari et al., 2012; Parent et al., 2015;
155 Vennari and Aguirre-Urreta, 2017). The *A. noduliferum* Zone has in turn been tied up with
156 the Tethyan *Calpionella alpina* Subzone, the primary marker of the lower Berriasian
157 (López-Martínez et al., 2017; Wimbledon, 2017; Lena et al., 2019). In the Arroyo Paulino
158 section, *G. bifrons* has been recorded from two consecutive beds, located around 10 meters
159 below the first occurrence of *A. noduliferum*, and near 40 meters above the last beds with
160 ammonites typical of the *Substeuroceras koeneni* Zone. That 40 meters poorly fossiliferous
161 interval only yielded some dubious representatives of *Substeuroceras disputabile* and
162 "*Thurmanniceras duraznensis*". This drop in abundance and diversity could be related to
163 the development of a lowstand period in the basin coupled with a higher siliciclastic input
164 (Riccardi, 1991, 2008, 2015). Hence, it is feasible that *A. noduliferum* first occurrence in
165 Arroyo Paulino is lower in the section than Py 38 metriorhynchid-bearing bed.

166 The genus *Groebericeras* is recorded in the upper Berriasian of the Mediterranean
167 region (Hoedemaeker, 1982, 1987; Howarth, 1992; Aguado et al., 2000) and in the Lo
168 Valdez Formation in Chile according to Salazar Soto (2012). Notwithstanding, we agree
169 with Aguirre-Urreta and Álvarez (1999) that those records are not conspecific with *G.*
170 *bifrons* and that current lines of evidence suggest a younger early Berriasian age for that
171 species in Argentina and Chilean sections.

172

173 **3. Material**

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

177

178 **4. Institutional abbreviations**

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

189

190 **5. Systematic paleontology**

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

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

193 Metriorhynchoidea Fitzinger, 1843 (*sensu* Young and Andrade, 2009)

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

195 Rhacheosaurini Young et al., 2011

196 *Cricosaurus* Wagner, 1858

197 *Type species.* *Stenosaurus elegans* Wagner, 1852. Daiting, Mörsheim Formation,

198 Germany. *Hybonoticeras hybonotum* Standard Ammonite Zone, lower Tithonian, Upper

199 Jurassic. Now referred to as *Cricosaurus elegans* (Wagner, 1852) Wagner, 1858 [following

200 recommendation 67B of the International Commission on Zoological Nomenclature

201 (ICZN) code].

202 *Emended diagnosis.* Metriorhynchid crocodylomorph with the following unique

203 combination of characters: ornamentation of the external surface of the dermatocranium is

204 variable, with some species having a conspicuous to faint grooved, ridged or pitted patterns,

205 and others being largely smooth; external nares separated by a bony premaxillary septum,

206 with the nares terminating posterior to the second maxillary alveoli; acute angle formed by

207 the posterolateral and posteromedial processes of the frontal; orbits as large as the

208 supratemporal fenestrae (at least in morphologically mature individuals); lateral margin of

209 the prefrontal rounded; surangular and angular well-developed, anterolaterally exceeding

210 beyond the anterior margin of the orbits; symphyseal part of the mandible low; dentition has

211 variable labiolingual compression, with some species having teeth with a sub-circular

212 cross-section and others with a sub-rectangular one; dentition is bicarinate, but the carinae

213 are faint (i.e. a low carinal keel); deltopectoral crest reduced or absent; calcaneum tuber

214 absent or vestigial; proximal end of metatarsal I greatly enlarged (modified from Young
215 and Andrade, 2009; Herrera et al., 2013b; Sachs et al., 2019).

216

217 *Cricosaurus puelchorum* sp. nov.

218 Figures 3–6

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

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

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

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

227 *Stratigraphic horizon.* Vaca Muerta Formation, lower part of the *Argentiniceras*
228 *noduliferum* Andean Assemblage Zone, lower Berriasian, Lower Cretaceous (Leanza,
229 1945; López-Martínez et al., 2017).

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

237 with well-defined apicobasal aligned ridges; apicobasal parallel troughs on the middle facet
238 of the labial surface*.

239

240 **6. Description**

241 *6.1. General preservation*

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

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

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

259

260 *6.2. Cranial openings*

261 6.2.1. *Supratemporal fossa and fenestra*

262 The right supratemporal fossa is completely preserved, however, most of the bone's
263 surface that forms it was eroded by recent weathering, thus the contribution of the bones
264 cannot be determined. The supratemporal fossa is large, longer than wider, and triangle-
265 shaped, as in *Cricosaurus araucanensis*, *Cricosaurus vignaudi* (Frey et al., 2002), and
266 *Cricosaurus* sp. (SNSB-BSPG 1973 I 195); and the supratemporal fenestra is rounded (Fig.
267 3A).

268 6.2.2. *Suborbital fenestra*

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

272 6.2.3. *Secondary choana*

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

278 6.2.4. *Preorbital fossa*

279 Both preorbital fossae are partially preserved and crushed. The anterior-most
280 portion is not preserved. The preorbital fossa is very elongate, with the major axis
281 orientated obliquely (Fig. 4), as in all known metriorhynchids (e.g. *Cricosaurus*
282 *araucanensis*, MLP 72-IV-7-1; *D. andiniensis*, MOZ-PV 6146; *Maledictosuchus riclaensis*;
283 *Pu. potens*). The preorbital fossa excavates the maxilla and forms a sulcus that vanishes
284 anterodorsally, as in *C. araucanensis* (MLP 72-IV-7-1), but in MCNAM-PV 5096 this

285 sulcus is more prominent and high, and likely ends at the level of the anterior-most portion
286 of the nasals (Fig. 4). The dorsal margin of the preorbital fossa is formed by the nasal, and
287 the ventral one by the maxilla (we cannot rule out the participation of the jugal in the
288 ventral margin). The lacrimal contributes to the posterior margin (Fig. 4), as in all
289 metriorhynchids (Fernández and Herrera, 2009).

290

291 6.3. Cranium

292 6.3.1. Maxilla

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

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

308 6.3.2. Nasal

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

326 6.3.3. Lacrimal

327 Both lacrimals are incompletely preserved and due to postmortem deformation are
328 partially exposed. As in all metriorhynchids, they are oriented vertically, and face laterally
329 (e.g., Fraas, 1902; Andrews, 1913; Pol and Gasparini, 2009; Young et al., 2010) (Fig. 4A,
330 B). The lacrimal dorsally contacts the prefrontal, anteriorly the nasal, and forms the
331 posterior margin of the preorbital fossa (Fig. 4B). The lacrimal has a process that anteriorly
332 extends beyond the anterior margin of the prefrontal (Fig. 4A, B), which can be seen in

333 dorsal view (Fig. 3A). In *C. araucanensis* this process does not extend beyond the anterior
334 margin of the prefrontal.

335 6.3.4. Prefrontal

336 Only the left prefrontal is completely preserved, but there is a transverse fracture in
337 the dorsal surface of the bone, whereas the right element misses the posterior portion, the
338 external surface is damaged, and also a fracture extends across its dorsal surface. The
339 prefrontal is enlarged, teardrop-shaped in dorsal view and projects laterally, as in all
340 metriorhynchids (e.g. Andrews, 1913; Pol and Gasparini, 2009; Young and Andrade,
341 2009). The prefrontal has a rounded 'V'-shaped anterior margin with its apex directed
342 anteriorly. Its medial margin extensively contacts the posteromedial process of the nasal
343 through a straight suture. The lateral margin is sutured to the posterolateral process of the
344 nasal. The suture with the frontal is not clear (Fig. 3A). In dorsal view, the prefrontal is
345 about twice as long as broad and the posterolateral margin is rounded, as in e.g. *C.*
346 *araucanensis*, and *C. lithographicus*.

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

353 6.3.5. Frontal

354 The frontal is partially preserved with the interorbital region severely damaged. In
355 the sagittal plane, there seems to be a suture that might resemble the interfrontal suture. The
356 dorsal surface of the anterior process has a steep longitudinal depression almost continuous

357 with the one presents in the nasals. In dorsal view, the anterior process of the frontal
358 extends anteriorly between the posteromedial processes of the nasal, with a 'V'-shaped
359 suture pointing anteriorly. At the apex, the suture is strongly serrated (Fig. 3A). The
360 anterior process is short as it does not reach the level of the anterior margin of the
361 prefrontal, as in *C. lithographicus*, *Rhacheosaurus gracilis*, *Dakosaurus maximus*, among
362 others and unlike *C. araucanensis* (MLP 72-IV-7-1), *D. andiniensis* (MOZ-PV 6146), *Pu.*
363 *potens*, and *Torvoneustes coryphaeus* (Young et al., 2013).

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

372 6.3.6. Palatine

373 Both palatines are incomplete and badly preserved. They sutured each other in the
374 midline of the skull. They form the ventral boundary of the nasopharyngeal ducts. The
375 palatine has a "V"-shaped midline anterior process (Fig. 3B), as in *Ma. riclaensis* (Parrilla-
376 Bel et al., 2013), *Maledictosuchus nuyivijanan* (Barrientos-Lara et al., 2018), and *D.*
377 *andiniensis* (MHNSR PV 344; Vignaud and Gasparini, 1996: photos 2). Based on
378 preservation we cannot identify if the palatine has two non-midline anterior processes as in
379 other metriorhynchids (e.g. *Cricosaurus araucanensis*, MLP 72-IV-7-1; *D. andiniensis*,

380 MHNSR PV 344; *Maledictosuchus* spp.). The paired depressions described in the palatines
381 of *Cricosaurus bambergensis* Sachs et al., 2019, are not present in this specimen.

382 6.3.7. Pterygoid

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

386 6.3.8. Vomer

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

391

392 6.4. Mandible

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

395 6.4.1. Dentary

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

401 6.4.2. Splenial, surangular, and angular

402 Fragments of the three left elements were identified. However, based on
403 preservation a detailed description is not possible. The angular and surangular extend

404 anteriorly beyond the anterior margin of the orbit (Fig. 4A), a feature present in all
405 *Cricosaurus* spp., *Rhacheosaurus gracilis*, and ‘*Metriorhynchus*’ *casamiquelai*.

406

407 6.5. Dentition

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

414 As in most Metriorhynchinae, teeth are small (1.5–2 cm), single cusped, slightly
415 curved, and bicarinated with a macroscopic keeled and unserrated carina (Fig. 5A–G). All
416 tooth crowns are laminar, labiolingually compressed, with the labial surface almost flat and
417 the lingual one convex, as in Geosaurina (Andrade et al., 2010; Foffa et al., 2018). The
418 labial surface is divided into three apicobasal facets, with the posterior facet better defined
419 than the anterior one (Fig. 5). Tooth with three apicobasal facets on the labial surface is a
420 feature that has only been reported in the geosaurins *Geosaurus* Cuvier, 1824, and *Ieldraan*
421 *melkshamensis* Foffa et al., 2018 (Young and Andrade, 2009; Andrade et al., 2010; Foffa et
422 al., 2018). In *Cricosaurus puelchorum*, these facets are not strongly defined as in the
423 geosaurins mentioned above but can be easily identified. The medial facet is wider than the
424 lateral ones along the entire crown, and it diminishes towards the apex whereas the lateral
425 facets have a constant width along the crown, as was described for *Geosaurus* (Andrade et
426 al., 2010).

427 In *Cricosaurus puelchorum* teeth are bicarinated, as in most Metriorhynchidae. The
428 distal carina extends from the base to the apex of the crown, whereas the mesial carina is
429 more prominent in the apical-half of the tooth crown, and in some teeth, it is completely
430 absent in the basal-most region of the crown.

431 The enamel ornamentation of the labial and lingual surface is composed of scattered
432 apicobasal parallel ridges of low relief, that are restricted to the 3/4 basal region of the
433 crown (Fig. 5A–F). Tooth crowns with well-defined apicobasal aligned ridges also occur in
434 *Cricosaurus schroederi* (S. Sachs pers. com). In *C. puelchorum* the longitudinal ridges are
435 better defined and are more densely packed on the lingual surface (Fig. 5E, F), as in
436 *Cricosaurus lithographicus* (Herrera et al., 2013b). Additionally, in the labial surface, the
437 middle facet is sculpted by two well-developed troughs separated by broad continuous,
438 parallel, and well-developed ridges (Fig. 5), features present in all preserved teeth. A fluted
439 surface in the middle plane of the tooth crown was previously described in the geosaurins *I.*
440 *melkshamensis*, ‘*Metriorhynchus*’ *brachyrhynchus* (NHMUK PV R 3804) and an
441 undescribed geosaurin (see Foffa et al., 2018). In *I. melkshamensis* the five well-defined
442 troughs are more conspicuous than in MCNAM-PV 5096. In ‘*Me.*’ *brachyrhynchus* the
443 troughs are poorly defined, more than five, and are not present in all crowns (Foffa et al.,
444 2018).

445

446 6.6. Natural cast of *Cricosaurus puelchorum* (MCNAM-PV 5096)

447 Based on preservation, the natural casts of some soft structures are partially
448 exposed, mainly those from the preorbital region. We identified the infilling of the nasal
449 cavity proper, nasopharyngeal ducts, antorbital sinus, and the exocrine gland duct (Fig.
450 6A). The topographic relationships of the structures of the preorbital region fit well with the

451 pattern previously described in other metriorhynchids (e.g. Fernández and Gasparini, 2008;
452 Fernández and Herrera, 2009; Herrera et al., 2013a).

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

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

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

473

474 **7. Phylogenetic analysis**

475 *7.1. Taxon and character sampling*

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

487 *6.2. Method*

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

498

499 7.3. Phylogenetic results

500 The Most Parsimonious Trees (MPTs) recovered by our analysis are of 1798 steps
501 (CI =0.401, RI= 0.861, HI=0.599, RCI= 0.345261). The total number of MPTs is unknown
502 because the trees recovered in the second round of TBR exceeded the maximum space for
503 trees in memory. The strict consensus tree presented herein (Fig. S1 in Supplementary
504 Information 3) is consistent with the unweighted parsimony analysis performed by Young
505 et al. (2020, fig. 4A), except for the relationships among Rhacheosaurini. Within
506 Rhacheosaurini Young et al. (2020) recovered some minor clades, whereas our analysis
507 recovered most Rhacheosaurini forming a large polytomy except for *C. lithographicus*, *C.*
508 *araucanensis*, *C. vignaudi*, *C. schroederi*, and *Cricosaurus* sp. (SNSB-BSPG 1973 I 195)
509 which are clustered although their internal relationships are unresolved (Fig. S1 in
510 Supplementary Information 3). Focused on Metriorhynchinae, and to improve the
511 resolution of MPTs, a posteriori of the tree searches, we pruned unstable taxa (see
512 Supplementary Information 3) to build a reduced consensus tree (Fig. S2 in Supplementary
513 Information 3). After this procedure, the resolution of the internal relationships of the
514 Rhacheosaurini improved (Fig. 7). So, this tree will be used to describe the phylogenetic
515 relations of the new species. As in the most recent phylogenetic analyses of
516 Metriorhynchidae, '*Cricosaurus*' *saltillensis* (Buchy et al., 2006), and cf. '*Cricosaurus*'
517 *macrospondylus* are no longer being recovered in the same clade as other *Cricosaurus* (see
518 e.g. Ósi et al., 2018; Sachs et al., 2019; Young et al., 2020). *Cricosaurus sensu stricto* is
519 recovered as a clade supported by three synapomorphies: posterior margin of narial fossa
520 terminates approximately level to the M3 to the anterior margin of the M5 alveoli (Ch. 56,
521 5), convex supratemporal arch (Ch. 125, 1), and bifurcation of the parietal in dorsal view
522 (Ch. 159, 1) (see Supplementary Information 3). Within *Cricosaurus*, the OTUs are

523 clustered in two subclades although internal relationships among them are not resolved.
524 The first clade includes *C. araucanensis*, *C. lithographicus*, *C. vignaudi*, *C. schroederi*, and
525 *Cricosaurus* sp. (SNSB-BSPG 1973 I 195) supported by one synapomorphy: no
526 conspicuous ornamentation of the maxilla (Ch. 13, 0). The second subclade includes the
527 new taxon and three Late Jurassic (late Kimmeridgian–early Tithonian) taxa from southern
528 Germany: *C. puelchorum*, *C. suevicus*, *C. elegans*, and *Cricosaurus bambergensis*, and is
529 supported by three synapomorphies: frontal ornamented with shallow to deep elliptical pits
530 and shallow to deep grooves (Ch. 14, 0), maxillary teeth laterally compressed (Ch. 357, 0),
531 and dentary teeth laterally compressed (Ch. 358, 0). *Cricosaurus puelchorum* presents six
532 autapomorphies: lacrimal visible in dorsal and lateral views (Ch. 94, 0), supratemporal
533 fossae triangle-shaped (Ch. 118, 4), the anteromedial process of the frontal is noticeably
534 posterior to the prefrontals (Ch. 139, 1), presence of apicobasal facets on the labial surface
535 of the teeth (Ch. 359, 1), presence of laminar teeth (Ch. 360, 1), and tooth crowns with
536 well-defined apicobasal aligned ridges (Ch. 379, 2). Support measures are all low,
537 exhibiting Bremer values of one in most cases (Fig. S3 in Supplementary Information 3).

538

539 **8. Discussion**

540 *8.1. Comparative anatomy*

541 The unique combination of features present in MCNAM-PV 5096 including several
542 autapomorphies (see Diagnosis) differentiates it from any other taxon and justifies the
543 erection of a new species. *Cricosaurus puelchorum* is referred to as the genus *Cricosaurus*
544 based on the description and phylogenetic analysis. The new taxon shares the following
545 features with other *Cricosaurus*: acute angle formed by the posterolateral and
546 posteromedial processes of the frontal; convex supratemporal arch in dorsal view; lateral

547 margin of the prefrontal rounded; orbits as large as the supratemporal fossae; surangular
548 and angular well-developed, anterolaterally exceeding beyond the anterior margin of the
549 orbits; bicarinate dentition with a faint carina.

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

569 Also, the dental morphology of MCNAM-PV 5096 is unusual for a Rhacheosaurini.
570 The teeth are highly elliptical in cross-section and three-faceted on the labial surface with a

571 fluted middle facet features that contrast with all *Cricosaurus* species in which the teeth
572 vary from bearing sub-circular to elliptical cross-section with crowns largely unornamented
573 on the labial surface. In *Cricosaurus puelchorum* the crowns are labiolingually compressed,
574 with the mesial-distal axis approximately twice longer than the labial-lingual one, as in
575 Geosaurina (Foffa et al., 2018). Interestingly, three apicobasal faceted teeth are also
576 characteristic of Geosaurina (Andrade et al., 2010; Foffa et al., 2018). In *Cricosaurus*
577 *puelchorum* the middle facet is sculpted by two well-developed troughs separated by well-
578 developed ridges (Fig. 5). The presence of a fluted middle facet has only been reported in
579 the geosaurins *Ieldraan melkshamensis*, '*Metriorhynchus*' *brachyrhynchus* (NHMUK PV R
580 3804), and an undescribed specimen (see Foffa et al., 2018). The number, pattern, and
581 distribution of the troughs vary among these taxa. As such, in *Cricosaurus puelchorum* the
582 shape of the crown and the ornamentation of the enamel surface are convergent with
583 Geosaurina.

584 Herrera et al. (2013b) discussed the morphological diversity of metriorhynchids
585 from the Neuquén Basin and highlighted the tooth disparity between the dental morphology
586 present in *C. araucanensis* and *C. lithographicus*. The description of this new taxon and its
587 unusual dental morphology adds a new component to the diversity among the Neuquén
588 Basin *Cricosaurus*. *Cricosaurus araucanensis* (early late Tithonian) has smooth tooth
589 crowns, in *Cricosaurus lithographicus* (late early to early late Tithonian) the crowns have
590 fine apicobasal aligned ridges that vanish towards the smooth apex, and in *Cricosaurus*
591 *puelchorum* (early Berriasian), the crowns have apicobasal parallel ridges, restricted to the
592 3/4 basal region of the crown, and the labial surface is sculpted by troughs separated by
593 broad continuous, parallel and well-developed ridges (Fig. 5).

594 Based on their tooth morphologies, all *Cricosaurus* spp. found in the southeastern
595 Pacific fall into the pierce guild. However, differences as the one mentioned above indicate
596 that probably, within the general pierce guild, their prey preferences were different.
597 However, as they were collected from different beds (and ages) the differences cannot be
598 strictly linked with the co-occurrence of these species.

599

600 *8.2. Phylogenetic position of Cricosaurus puelchorum and its implication on the*
601 *metriorhynchid distribution across the J/ K boundary*

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

618 *Cricosaurus* sub-clades. Just for the discussion, we call sub-clade A to the group
619 containing: *C. puelchorum*, *C. suevicus*, *C. elegans*, and *C. bambergensis*, and sub-clade B
620 to the clade formed by *C. araucanensis*, *C. lithographicus*, *C. vignaudi*, *C. schroederi*, and
621 *Cricosaurus* sp. SNSB-BSPG 1973 I 195.

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

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

634 This Metriorhynchinae phylogeny (Fig. 7) is interesting for two main reasons. First,
635 it depicts a *Cricosaurus* cluster split into two clades indicating close affinities between
636 species of two disparate paleobiogeographical units, as western Tethys Ocean and eastern
637 Pacific. The hypothesis of connection and interchange of herpetofauna and marine
638 invertebrates between these two biogeographic units, favored by the opening of seaways
639 like the Caribbean Corridor (or Hispanic Corridor), has been extensively cited (e.g.
640 Damborenea, 2000; Gasparini and Iturralde-Vinent, 2006 and references therein). Second,

641 time-calibrated phylogeny indicates the survival of both subclades of *Cricosaurus* but with
642 an evident diminishing of metriorhynchidae's diversity from the Tithonian onwards.

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

656

657 **9. Conclusions**

658 Here, we described a new Rhacheosaurini, *Cricosaurus puelchorum* from the lower
659 Berriasian (*Argentiniceras noduliferum* Zone) from southern Mendoza being the youngest
660 *Cricosaurus* record from the Vaca Muerta Formation (Argentina), and confirming the
661 survival of the genus in the Cretaceous of the southeastern Pacific. Time-calibrated
662 phylogenetic analysis shows a decrease in *Cricosaurus* species richness from the late
663 Tithonian onwards.

664 The new species is well defined by a unique combination of features and several
665 autapomorphies. Phylogenetic analysis indicates that *Cricosaurus puelchorum* is closer to
666 upper Kimmeridgian–lower Tithonian species of *Cricosaurus* from the Solnhofen
667 Archipelago than to the other two species from the Tithonian of the southeastern Pacific. It
668 is worthy to remark that the internal relationships of *Cricosaurus* spp, and the hypotheses
669 based on them like the biogeographical affinities, require further scrutiny to identify more
670 characters to improve branch supports of phylogenetic trees.

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

675

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1043 **Figure captions**

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1045 **Figure 1. A**, Location of the study section. Main geologic units were depicted after
1046 Dessanti (1978), Nullo et al. (2005), and Sruoga et al. (2005). **B**, Partial stratigraphic
1047 section of Arroyo Paulino showing *Cricosaurus puelchorum* (MCNAM-PV 5096) and
1048 *Groebericeras bifrons* occurrences.

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1050 **Figure 2. *Groebericeras bifrons*** Leanza, 1945. **1-2**, MCNAM-PI 24858. **1**, right lateral
1051 view, **2**, ventral view; **3-4**, MCNAM-PI 24879, **3**, left lateral view, **4**, ventral view. Scale
1052 bar: 1 cm. All specimens coated with Ammonium chloride.

1053

1054 **Figure 3. *Cricosaurus puelchorum***, MCNAM-PV 5096. **A**, Skull in dorsal view. **B**, Skull
1055 in ventral view. Abbreviations: an, angular; cnp, nasal cavity proper; cr, crest; d, dentary;
1056 dac, dorsal alveolar canal; fr, frontal; la, lacrimal; ls, laterosphenoid; mx, maxilla; na, nasal;
1057 pa, parietal; pl, palatine; po, postorbital; prf, prefrontal; pt, pterygoid; sch, secondary
1058 choana; sof, suborbital fenestra; sp, splenial; stf, supratemporal fenestra. The dash-dotted

1059 line indicates broken surfaces, dotted surface indicates matrix, striped surface indicates
1060 broken bone, grey surface shows the region preserved as natural endocast, arrows indicate
1061 the transversally broken plane. Scale bar: 5 cm.

1062

1063 **Figure 4.** *Cricosaurus puelchorum*, MCNAM-PV 5096. **A**, Skull in left lateral view. **B**,
1064 Skull in right lateral view. **C**, Right dentary partially preserved. Abbreviations: an, angular;
1065 asin, antorbital sinus; cnp, nasal cavity proper; d, dentary; dac, dorsal alveolar canal; fr,
1066 frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; or, orbit; po, postorbital; pref,
1067 preorbital fossa; pres, preorbital sulcus; prf, prefrontal; sp, splenial; sur, surangular; stf,
1068 supratemporal fossa. The dash-dotted line indicates broken surfaces, dotted surface
1069 indicates matrix, striped surface indicates broken bone, grey surface shows the region
1070 preserved as natural endocast, arrows indicate the transversally broken plane. Scale bars: 5
1071 cm.

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1073 **Figure 5.** *Cricosaurus puelchorum*, MCNAM-PV 5096. Dentition. **A**, Maxillary teeth. **B**,
1074 Dentary teeth. **C**, Close-up of a maxillary tooth in labial view. **D**, Close-up of a dentary
1075 tooth in labial view. **E**, Close-up of a maxillary tooth in lingual view. **F**, Microscopy image
1076 a maxillary tooth in lingual view. **G**, Microscopy image of the carina. **H**, Schematic labial
1077 view of a tooth. **I**, Schematic cross-section of a tooth. White arrows show the troughs.
1078 Abbreviations: f, facets; la.s; labial surface; li.s, lingual surface; r, ridges; t, troughs. Scale
1079 bars: 1 cm (A–E), 3 mm (F), 400 μ m (G).

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1081 **Figure 6.** *Cricosaurus puelchorum*, MCNAM-PV 5096. Natural cast. **A**, Preorbital region
1082 in anterolateral right view. **B**, Cranium in ventral view with detail of vascularization.

1083 Abbreviations: an, angular; asin, antorbital sinus; cnp, nasal cavity proper; fr, frontal; gd,
1084 salt gland duct; la, lacrimal; mx, maxilla; mx-na, maxillary-nasal suture; na, nasal; npdu,
1085 nasopharyngeal duct; pch, primary choana; pl, palatine; prf, prefrontal; vo, vomer. Arrows
1086 indicate anterior direction. Scale bars: 5 cm.

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1088 **Figure 7.** Time-calibrated reduced consensus tree of Metriorhynchidae.

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1090 SUPPORTING INFORMATION

1091 **Supporting Information 1.** Character list used in the phylogenetic analysis.

1092 **Supporting Information 2.** Applied changes of character codification from the original
1093 datasets.

1094 **Supporting Information 3.** Strict consensus cladogram, results from prunnelsen
1095 command, reduced consensus cladogram, list of synapomorphies of the reduced consensus,
1096 reduced consensus cladogram depicting the Bremer support values.

1097 **Supporting Information S4.** Character matrix, nexus file.

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

| Specimen | shell diameter | whorl height/shell diameter | whorl width/shell diameter | umbilical diameter/shell diameter |
|-----------------|----------------|-----------------------------|----------------------------|-----------------------------------|
| MCNAM-PI 24858 | 78.61 | 31.01 (0.39) | 22.32 (0.28) | 25.54 (0.32) |
| | 59.30 | 24.53 (0.41) | 17.98 (0.30) | 19.01 (0.32) |
| MCNAM-PI 24879 | 44.66 | 18.85 (0.42) | 13.98 (0.31) | 13.03 (0.29) |
| | 33.71 | 14.38 (0.43) | 12.01 (0.36) | 10.41 (0.31) |

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Table 2. List of taxa and specimens used for comparative purposes in the description.

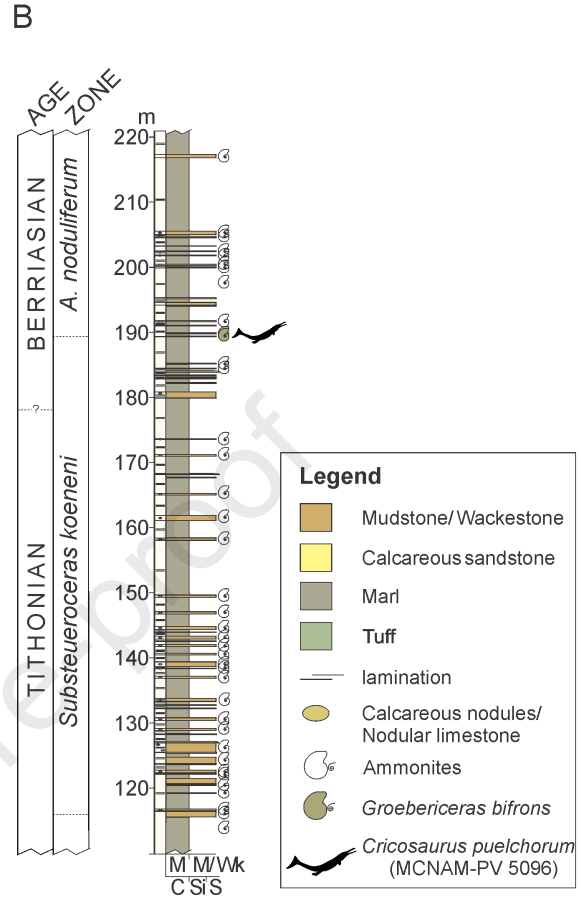
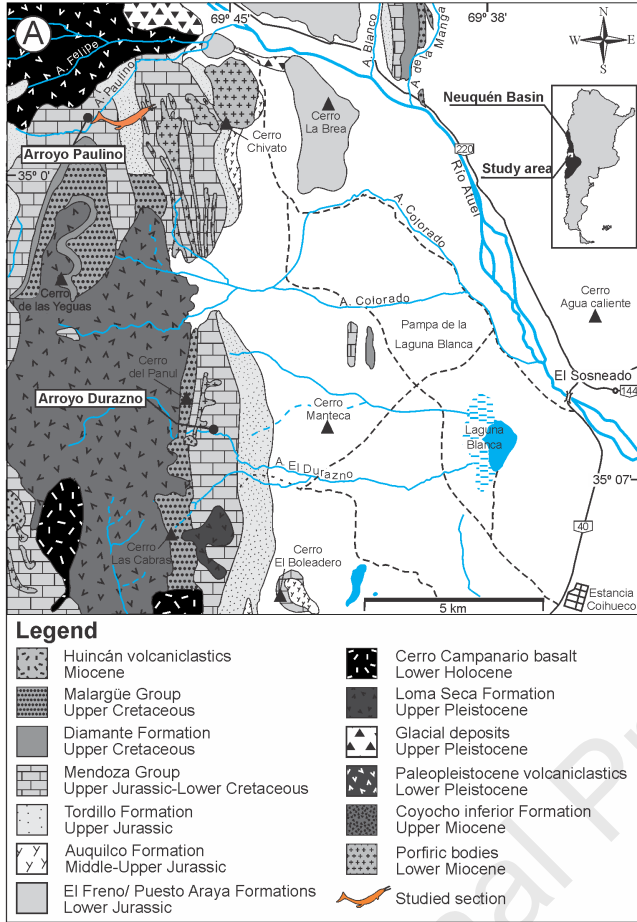
| Taxa | Specimens |
|--|---|
| ' <i>Steneosaurus</i> ' <i>bollensis</i> (Jäger, 1828) | SMNS 15391 |
| ' <i>Metriorhynchus</i> ' <i>brachyrhynchus</i> (Eudes-Deslongchamps, 1868) | NHMUK PV R 3700, NHMUK PV R 3804, NHMUK PV R 4763 |
| <i>Metriorhynchus superciliosus</i> (de Blainville, 1853) | SMNS 10115, SMNS 10116 |
| ' <i>Metriorhynchus</i> ' <i>casamiquelai</i> Gasparini and Chong Díaz, 1977 | MGHF 1-08573 |
| <i>Dakosaurus andiniensis</i> Vignaud and Gasparini, 1996 | MHNSR PV 344, MOZ-PV 6146 |
| <i>Dakosaurus maximus</i> (Plieninger, 1846) | SMNS 8203 |
| <i>Purranisaurus potens</i> Rusconi, 1948a | MCNAM-PV 2060 |
| <i>Rhacheosaurus gracilis</i> von Meyer, 1831 | NHMUK PV R 3948 |
| <i>Cricosaurus elegans</i> (Wagner, 1852) Wagner, 1858 | SNSB-BSPG AS I 504 |
| <i>Cricosaurus suevicus</i> (Fraas, 1901) | SMNS 9808 |
| ' <i>Cricosaurus</i> ' <i>medius</i> Wagner, 1858 | SNSB-BSPG AS VI 2 |
| <i>Cricosaurus araucanensis</i> Gasparini and Dellapé, 1976 | MLP 72-IV-7-1, MLP 72-IV-7-4 |
| <i>Cricosaurus lithographicus</i> Herrera et al., 2013b | MOZ-PV 5787 |
| <i>Maledictosuchus riclaensis</i> Parrilla-Bel et al., 2013 | MPZ 2001/130a |
| <i>Plesiosuchus manselii</i> (Hulke, 1870) | NHMUK PV OR40103 |

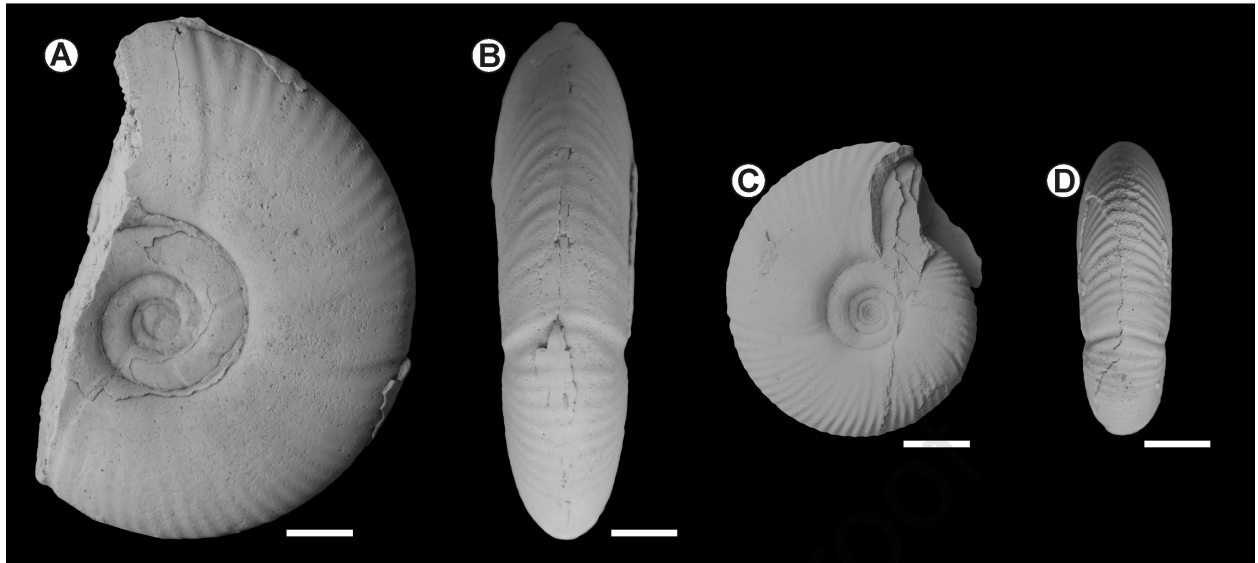
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| MCNAM-PI 24879 | 44.66 | 18.85 (0.42) | 13.98 (0.31) | 13.03 (0.29) |
| | 33.71 | 14.38 (0.43) | 12.01 (0.36) | 10.41 (0.31) |

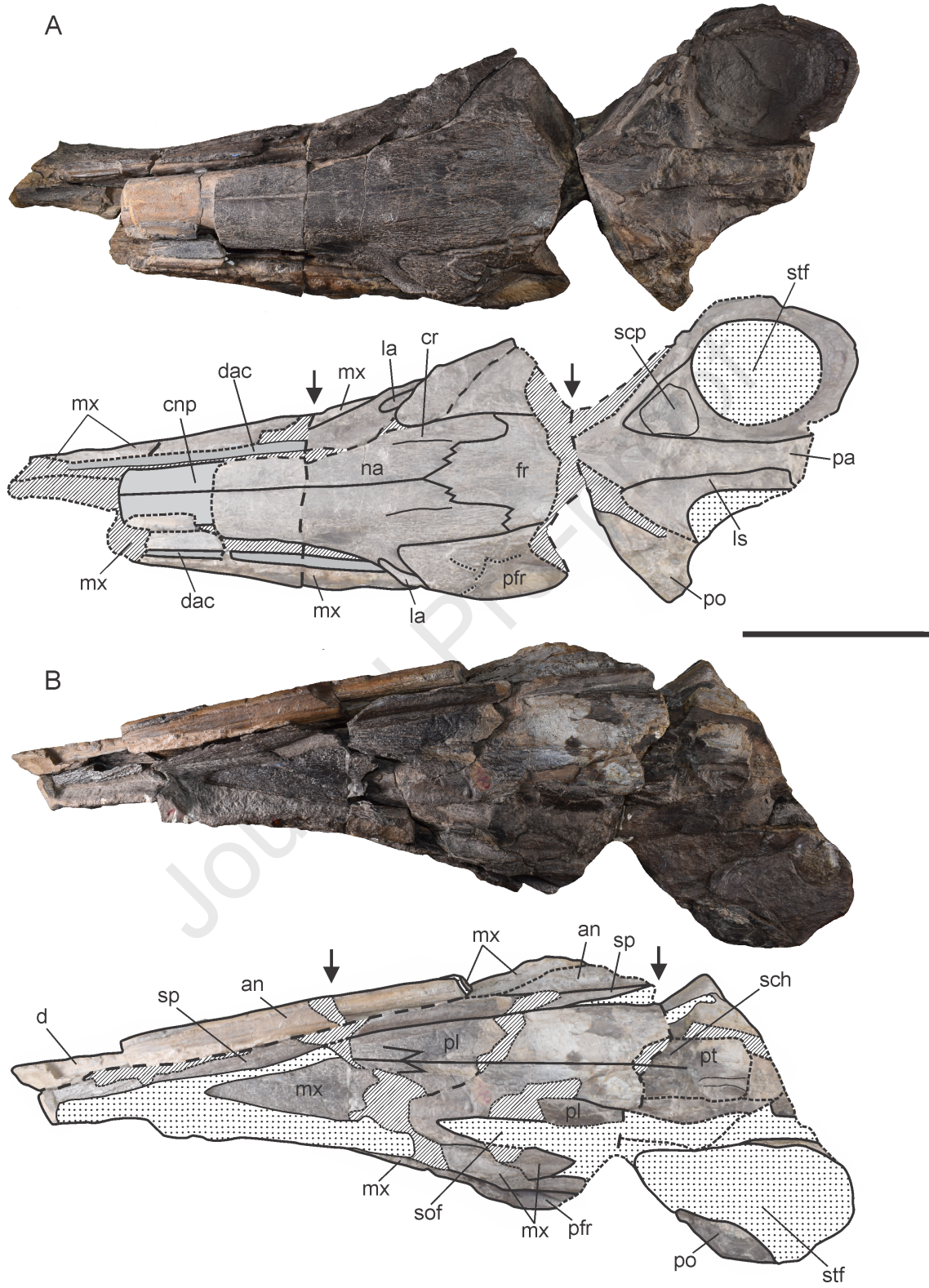
Table 2. List of taxa and specimens used for comparative purposes in the description.

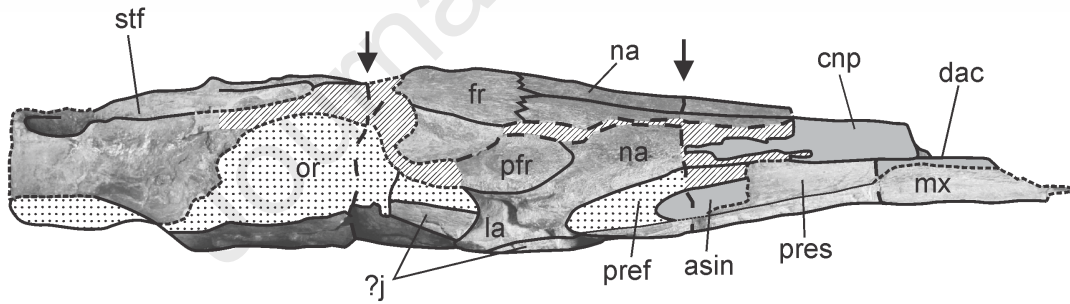
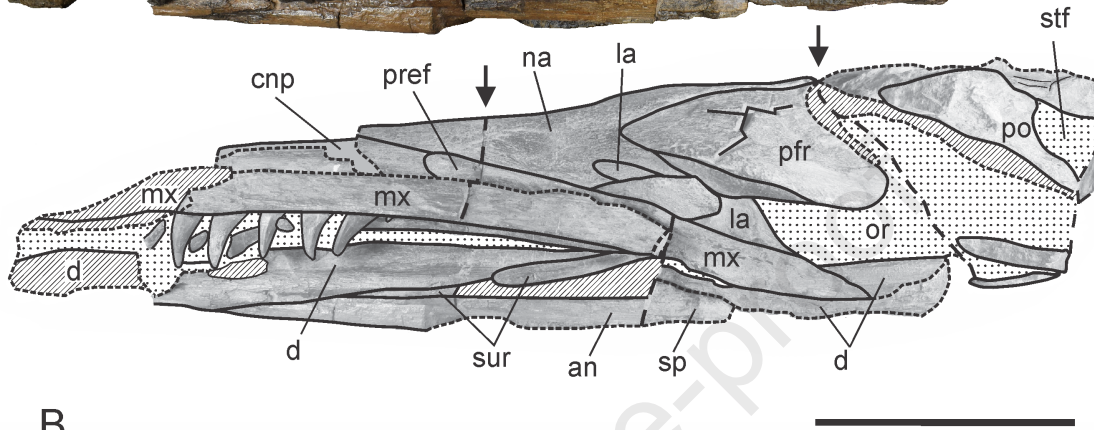
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| <i>Metriorhynchus superciliosus</i> (de Blainville, 1853) | SMNS 10115, SMNS 10116 |
| ' <i>Metriorhynchus</i> ' <i>casamiquelai</i> Gasparini and Chong Díaz, 1977 | MGHF 1-08573 |
| <i>Dakosaurus andiniensis</i> Vignaud and Gasparini, 1996 | MHNSR PV 344, MOZ-PV 6146 |
| <i>Dakosaurus maximus</i> (Plieninger, 1846) | SMNS 8203 |
| <i>Purranisaurus potens</i> Rusconi, 1948a | MCNAM-PV 2060 |
| <i>Rhacheosaurus gracilis</i> von Meyer, 1831 | NHMUK PV R 3948 |
| <i>Cricosaurus elegans</i> (Wagner, 1852) Wagner, 1858 | SNSB-BSPG AS I 504 |
| <i>Cricosaurus suevicus</i> (Fraas, 1901) | SMNS 9808 |
| ' <i>Cricosaurus</i> ' <i>medius</i> Wagner, 1858 | SNSB-BSPG AS VI 2 |
| <i>Cricosaurus araucanensis</i> Gasparini and Dellapé, 1976 | MLP 72-IV-7-1, MLP 72-IV-7-4 |
| <i>Cricosaurus lithographicus</i> Herrera et al., 2013b | MOZ-PV 5787 |
| <i>Maledictosuchus riclaensis</i> Parrilla-Bel et al., 2013 | MPZ 2001/130a |
| <i>Plesiosuchus manselii</i> (Hulke, 1870) | NHMUK PV OR40103 |

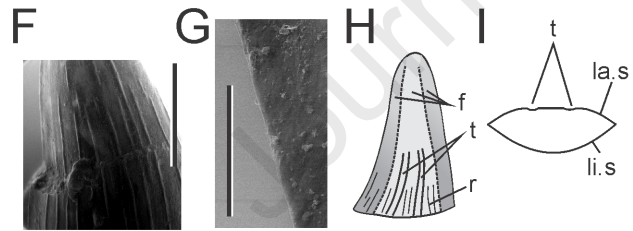
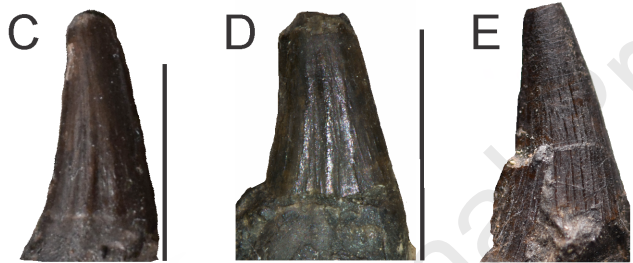


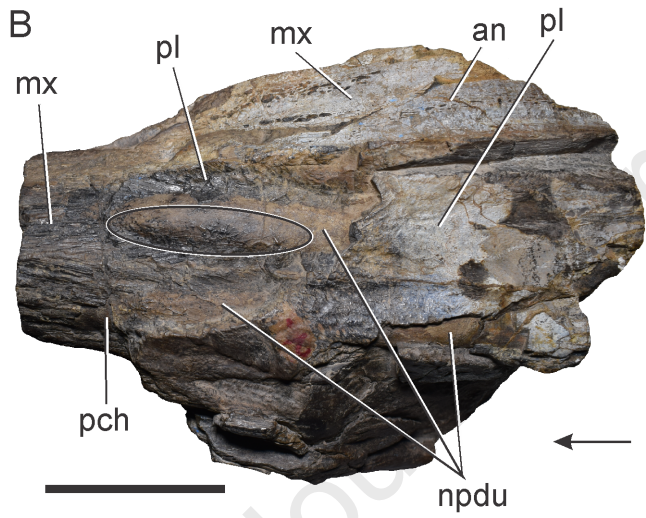
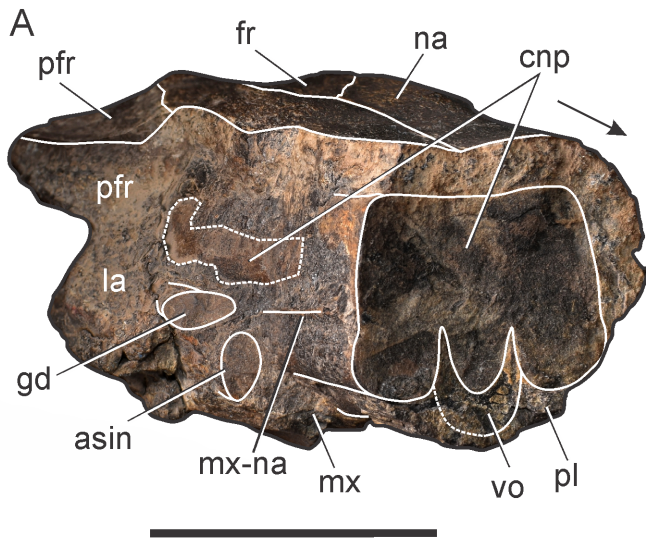


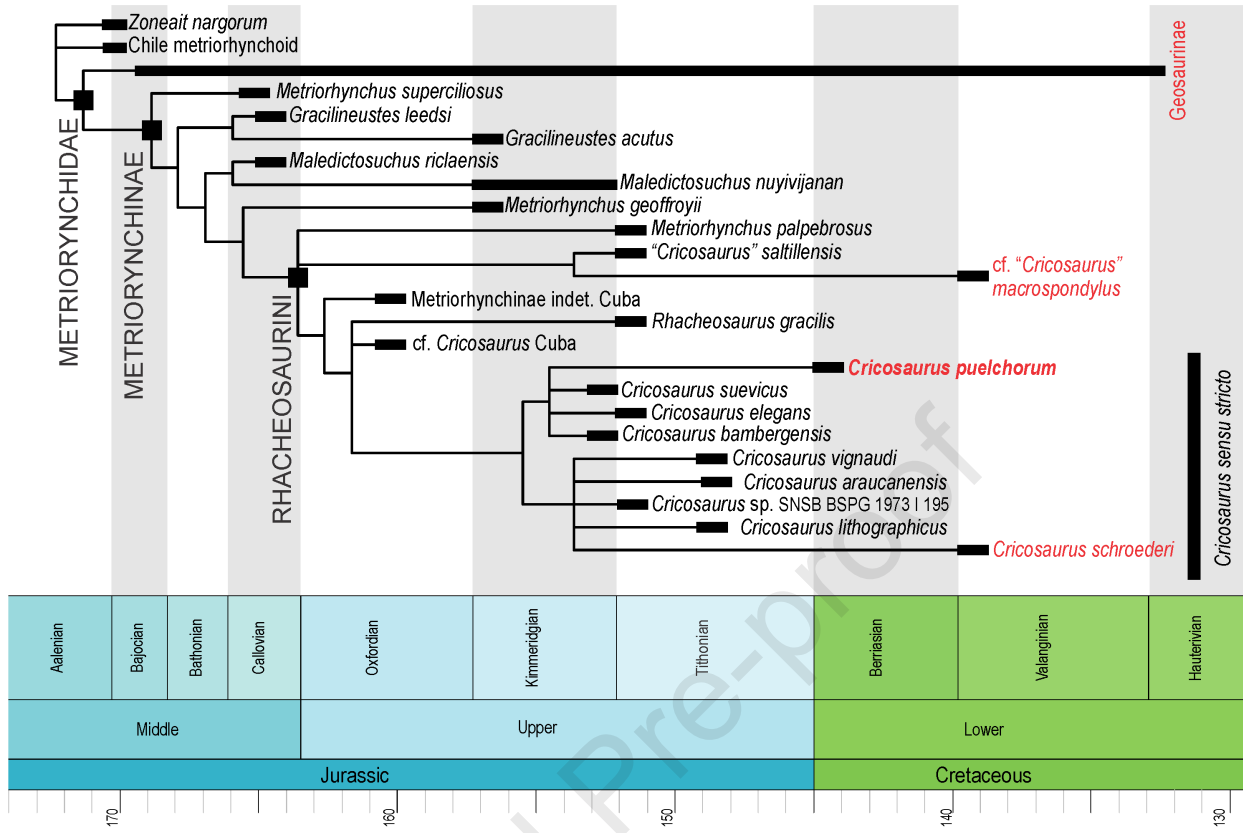
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Highlights

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.

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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:

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