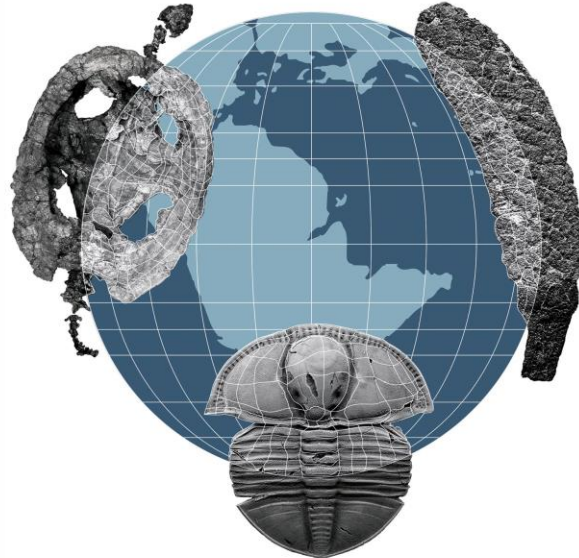




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1 **REDISCOVERED CRANIAL MATERIAL OF *VENATICOSUCHUS RUSCONII***
2 **ALLOWS THE FIRST JAW BIOMECHANICS IN ORNITHOSUCHIDAE**
3 **(ARCHOSAURIA: PSEUDOSUCHIA)**

4

5 M. BELÉN VON BACZKO^{1,2}

6 ¹División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n
7 (B1900FWA), La Plata, Argentina.

8 ² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Avenida
9 Rivadavia 1917 (C1033AAJ), Ciudad Autónoma de Buenos Aires, Argentina.

10 belen_vb13@yahoo.com.ar

11

12 28 pages (text+references); 3 figures, 3 tables

13

14 Running header: BACZKO: JAW BIOMECHANICS IN ORNITHOSUCHIDS

15 Corresponding autor: M. Belén von Baczko

16 **Abstract.** During the Triassic period, pseudosuchians had a wider variety of
17 feeding habits than those seen nowadays, including herbivorous, omnivorous, as well as
18 carnivorous diets. Ornithosuchids have been historically proposed as either hunters or
19 scavengers based on their general anatomy. The rediscovered cranial materials of the
20 ornithosuchid *Venaticosuchus* described here in detail which allowed the reconstruction
21 of its jaw musculature and a geometric biomechanic analysis was carried out to study
22 the possible feeding habits of ornithosuchids. The muscles were reconstructed based on
23 inferences of their osteological correlates seen in their closest living relatives such as
24 *Caiman*, *Alligator*, and *Iguana*. Consequently, the jaws were considered as a third class
25 lever system and the moment arms were calculated for the adductor and depressor
26 musculature. The study of the three species of ornithosuchids (*Ornithosuchus*,
27 *Venaticosuchus*, and *Riojasuchus*) revealed greater similarities between ornithosuchids
28 and aetosaurs, despite having different feeding habits, than between ornithosuchids and
29 crocodylians. The relative bite force of *Venaticosuchus* resulted higher than that of other
30 ornithosuchids, aetosaurs and *Alligator*. The elevated bite force identified for
31 ornithosuchids plus their low bite speed and the morphology of their constricted snouts
32 suggest features more compatible to scavenging feeding habits. Ornithosuchids were not
33 the apex predators of the Late Triassic continental communities but were more likely
34 regarded to scavenging or preyed on small animals such as procolophonids,
35 sphenodontians, juvenile aetosaurs, erpetosuchids, cinodonts, and dicynodonts that did
36 not exceed them in size.

37

38 **Keywords.** Triassic, skull, paleobiology, ornithosuchids, Ischigualasto Formation,
39 Argentina

40 **Resumen.** NUEVOS MATERIALES CRANEANOS DE *VENATICOSUCHUS*
41 *RUSCONII* PERMITEN EL PRIMER ANALISIS DE BIOMECÁNICA
42 MANDIBULAR EN ORNITHOSUCHIDAE (ARCHOSAURIA: PSEUDOSUCHIA).
43 Durante el período Triásico, los pseudosúquios presentaron una mayor variedad de
44 hábitos alimenticios que los que presentan hoy en día, incluyendo hábitos herbívoros,
45 omnívoros y carnívoros. Los ornitosúquidos han sido propuestos históricamente como
46 animales cazadores a carroñeros basados en su anatomía general. Los materiales
47 craneanos redescubiertos del ornitosúquido *Venaticosuchus* descritos aquí
48 detalladamente han permitido la reconstrucción de su musculatura mandibular y un
49 análisis biomecánico geométrico para evaluar su posibles hábitos alimenticios de los
50 ornitosúquidos. Los músculos fueron reconstruidos con base en inferencias sobre sus
51 correlatos óseos en sus parientes más cercanos como *Caiman*, *Alligator* e *Iguana*. . Las
52 mandíbulas se consideraron como un sistema de palancas de tercer grado y se
53 calcularon los brazos de palanca para cada músculo aductor y depresor. El estudio de las
54 tres especies de ornitosúquidos (*Ornithosuchus*, *Venaticosuchus* y *Riojasuchus*) reveló
55 mayores semejanzas entre estos y los aetosaurios, a pesar de sus diferentes hábitos
56 alimenticios, que entre los ornitosúquidos y los crocodylios. La fuerza relativa de
57 mordida de *Venaticosuchus* resultó ser mayor que las de los demás ornitosúquidos, los
58 aetosaurios y *Alligator*. Ésta elevada fuerza de mordida de los ornitosúquidos, sumada a
59 su baja velocidad de mordida, y asociado a la morfología de sus estrechos hocicos
60 aparentan ser características más compatibles con hábitos alimenticios carroñeros. Los
61 ornitosúquidos no habrían sido los mayores predadores de las comunidades
62 continentales del Triásico Tardío, sino que estarían relegados a roles carroñeros o
63 predarían sobre pequeñas presas que no los superaran en tamaño como procolofónidos,
64 esfenodontes, y juveniles de aetosaurios, erpetosúquidos, cinodontes y dicinodontes.

- 65 ***Palabras clave.*** Triásico, cráneo, paleobiología, ornitosúquidos, Formación
- 66 Ischigualasto, Argentina

67 DURING the Triassic, pseudosuchian archosaurs occupied a wide variety of
68 paleobiological roles because of their diversity in body sizes, shapes, and feeding habits
69 (Sereno, 1991; Brusatte *et al.*, 2010; Nesbitt, 2011). The variety of feeding habits of
70 Triassic pseudosuchians was much larger than those seen nowadays, being represented
71 by carnivorous forms like ornithosuchids, phytosaurs, gracilisuchids, rautisuchids, and
72 crocodylomorphs, as well as herbivorous and omnivorous forms such as aetosaurs, and
73 shuvosaurids (Desojo *et al.*, 2013; Irmis *et al.*, 2013; Nesbitt *et al.*, 2013; Stocker and
74 Butler, 2013). Ornithosuchids in particular have been historically proposed as
75 carnivorous forms, either hunters or scavengers, based on their general anatomy
76 (Walker, 1964; Benton, 1983). These are a group of pseudosuchian archosaurs known
77 from continental deposits of the Late Triassic and registered along with aetosaurs,
78 rautisuchians, poposaurids and crocodylomorphs (Nesbitt, 2011; Butler *et al.*, 2014).
79 They are carnivorous quadrupedal archosaurs with medium body sizes of about 2
80 metres long and have been registered only in present-day Argentina and Scotland. The
81 clade Ornithosuchidae currently comprises only three species: *Ornithosuchus*
82 *woodwardi* (Newton, 1894), *Riojasuchus tenuisiceps* (Bonaparte, 1967), and
83 *Venaticosuchus rusconii* (Bonaparte, 1970). The first one is known from the
84 Lossiemouth Sandstones Formation, Moray, Scotland and the latter two from the
85 Ischigualasto-Villa Union Basin, La Rioja province, Argentina. Ornithosuchids have
86 very distinctive cranial features such as a strongly downturned premaxilla, a two-tooth
87 diastema between the premaxilla and maxilla, the lower jaws shorter than the skull, and
88 the presence of a palatine-pterygoid fenestra, among others (Sereno, 1991; Baczko and
89 Desojo, 2016). They have been proposed as having either carnivorous or scavenger
90 habits based on their general morphology (*e.g.*, Walker, 1964, Benton, 1983), but only
91 the mechanical capabilities of *Riojasuchus tenuisiceps* have been quantitatively tested

92 with a finite elements analysis (Baczko *et al.*, 2014b). The information required for this
93 kind of study (*e.i.*, CTscans, virtual 3D models) was not currently available for the
94 ornithosuchids *Ornithosuchus woodwardi* and *Venaticosuchus rusconii*,
95 *Venaticosuchus rusconii* was erected by Bonaparte (1970) based on a partial skull
96 found in the Ischigualasto Formation (late Carnian–early Norian, Martinez *et al.* 2011)
97 of La Rioja. This specimen was very briefly described and assigned to Ornithosuchidae
98 for its general resemblance with *Riojasuchus tenuisiceps* and *Ornithosuchus woodwardi*.
99 Baczko *et al.* (2014a) carried out a detailed description of the holotype of
100 *Venaticosuchus rusconii* and supported its affinity to Ornithosuchidae within a
101 phylogenetic framework. In 2015, newly rediscovered skull elements of *Venaticosuchus*
102 *rusconii* were found in the palaeontology collection of the Instituto Miguel Lillo
103 (Tucuman, Argentina). These corresponded to the right side of the posterior region of
104 the skull and right mandible of the holotype, which were figured but not described by
105 Bonaparte (1970) and were also not described by Baczko *et al.* (2014a) because they
106 were thought to be lost.

107 These newly rediscovered materials corresponding to the holotype of
108 *Venaticosuchus rusconii* were here described in detail. The new anatomical information
109 allowed the first reconstruction of the muscles of the adductor chamber and the study of
110 the jaw biomechanics of ornithosuchids. The application of traditional biomechanic
111 models in extinct taxa is a good approach to test functional hypotheses, such as feeding
112 behaviour (Vizcaíno *et al.*, 1998). During feeding, in the closing movement of the jaws,
113 these act as a third class lever system in which the pivot is at the craniomandibular joint,
114 the input force is provided by the jaw muscles, and the output force is produced by the
115 teeth on food. This traditional biomechanical analysis is based on a first hand study of
116 the specimens and bibliographical references. Under this biomechanical model,

117 hypothesis about the feeding habits of Ornithosuchidae are put to test to try to
118 understand which role they occupied (scavenger or active predatory) in the continental
119 communities of the Late Triassic of Pangaea.

120 **MATERIAL AND METHODS**

121 This study was based on the holotype specimen of *Venaticosuchus rusconii* (PVL
122 2578) including the newly rediscovered cranial materials of the holotype found at
123 paleontology collection of the Instituto Miguel Lillo (Tucumán) that were described
124 here (quadrate, quadratojugal, surangular, articular, angular, prearticular). This
125 specimen was studied first hand and compared with the cranial material of the other
126 known ornithosuchids *Riojasuchus tenuisiceps* (PVL 3827, 3828) and *Ornithosuchus*
127 *woodwardi* (NHMUK PV R 2409–2410, 3142, 3143, 3149, 3562) as well as a variety of
128 archosauriforms (proterochampsids, erpetosuchids), pseudosuchians (aetosaurs,
129 gracilisuchids, erpetosuchids, loricatans, crocodylomorphs), and dinosaurs (theropods,
130 sauropodomorphs, ornithischians) studied first hand and through bibliographic
131 references.

132 The reconstruction of all the mandibular adductor and depressor muscles of
133 *Venaticosuchus rusconii* was inferred from direct observation of living reptiles using the
134 Extant Phylogenetic Bracket approach (Witmer, 1995), because there are no clear
135 muscular attachment scars on the skull of this species. Using this method, the
136 attachment scars of the adductor and depressor muscles of *Caiman yacare* (MACN HE
137 48841) and *Iguana iguana* (MACN HE 42334), some of the closest living relatives of
138 ornithosuchids, were directly observed through dissection and used to infer the same
139 attachment areas in the fossil taxa studied. . The seven main muscles present in living
140 crocodylians were identified in ornithosuchids as well as the six main muscles present

141 in *Iguana* (e.g., Bona and Desojo, 2011; Holliday and Witmer, 2007, Iordansky, 2000),
142 although the different parts that comprise each of these muscles cannot be differentiated
143 in ornithosuchids. The insertion area of the different parts of these muscles have subtle
144 variations within the extant taxa whose level of detail cannot be determined in
145 *Venaticosuchus* without the actual scars on the skull bones. All muscles were identified
146 with a Level I inference because they were present in both extant taxa, excepting the
147 intramandibular muscle which is present in *Caiman* but absent in *Iguana* and therefore
148 was reconstructed as a Level II inference (Witmer, 1995). Muscles were described by
149 comparison between *Venaticosuchus rusconii* and the other ornithosuchids, and the
150 correlation with their closest living relatives, crocodylians. The same muscular
151 reconstructions were made for *Riojasuchus tenuisiceps* and *Ornithosuchus woodwardi* to
152 carry out the biomechanical analysis.

153 Jaw biomechanics were analysed based on the moment arms of the jaw
154 musculature of the three known species of ornithosuchids (*Venaticosuchus rusconii*,
155 *Riojasuchus tenuisiceps*, and *Ornithosuchus woodwardi*). The moment arms of the lines
156 of action of the muscles can be estimated to analyse relationships between bite force and
157 bite velocity (Cassini and Vizcaíno, 2012). The moment arms of the reconstructed
158 musculature of ornithosuchids were estimated by the adaptation of the geometric model
159 carried out by Desojo and Vizcaíno (2009) for aetosaurs, which was based on the
160 models developed by Vizcaíno *et al.* (1998) for mammals. Desojo and Vizcaíno (2009)
161 reconstructed the jaw musculature of aetosaurs in detail comparing them with their
162 living relatives, crocodylians. In that study, the first quantitative biomechanical analysis
163 for pseudosuchians, the authors combined the moment arm of the external and posterior
164 adductor muscles (MAME + MAMP) because of their similar orientation, but in the
165 present study they were considered separately because the attachment areas could be

166 indicated separately in ornithosuchids. The pterygoid muscles were also considered by
167 Desojo and Vizcaíno (2009) as a unique element for aetosaurs (MAMIPT = MPtD +
168 MPtV) but here the pterygoid muscles are differentiated in their ventral and the dorsal
169 units for ornithosuchids, as in crocodylians and iguanas (Bona and Desojo, 2011;
170 Holliday and Witmer, 2007). The values of these pairs of muscles were combined later
171 only to allow comparing them with Desojo and Vizcaíno (2009) results for the
172 MAME+MAMP and MAMIPT. For the estimation of moment arms, total lengths of the
173 mandibles were standardized at the same length to remove the influence of size on the
174 comparisons between different species which had different sizes (Vizcaíno *et al.* 1998).
175 Therefore, measurements taken from the drawings of the skulls and the units are used
176 only in comparative terms independent of size of the species. The contribution of each
177 muscle was considered as its percentage over the sum of moment arm of the adductor
178 muscles ($X*100/AM$).

179 ***Institutional abbreviations.*** **MACN HE**, Colección Herpetología, Museo
180 Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;
181 **NHMUK PV R**, Natural History Museum, London, UK; **PULR**, Museo de
182 Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**,
183 Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; **SMNS**,
184 Staatliches Museum für Naturkunde, Stuttgart, Germany.

185 **SYSTEMATIC PALAEONTOLOGY**

186 ARCHOSAURIA Cope, 1869 *sensu* Gauthier and Padian, 1985

187 PSEUDOSUCHIA Zittel, 1887–1890 *sensu* Gauthier and Padian, 1985

188 ORNITHOSUCHIDAE Huene, 1908 *sensu* Sereno, 1991

189 ***Venaticosuchus*** Bonaparte, 1970

190 **Type species.** *Venaticosuchus rusconii* Bonaparte, 1970

191 (Fig. 1)

192 **Type material.** PVL 2578: Represented by an incomplete skull (lacking most of the
193 braincase and the skull roof) with both hemimandibles articulated. Bonaparte (1970)
194 reported an anterior limb and isolated osteoderms but these were neither described nor
195 figured and were later regarded as missing by Baczko and Ezcurra (2013). Recently, the
196 right side of the posterior region of the skull and lower jaw of the holotype were found
197 in the Vertebrate Palaeontology collection of the Instituto Miguel Lillo, Tucumán,
198 Argentina. This region corresponds to the right quadratojugal, quadrate, surangular,
199 angular, prearticular and articular, which had only been figured by Bonaparte (1970) but
200 not described. These elements have been regarded as missing until now and therefore
201 were not included in previous descriptions of *Venaticosuchus rusconii* (Baczko *et al.*,
202 2014a; Baczko, 2017).

203 **Diagnosis.** Ornithosuchid archosaur that differs from the others by one local
204 autapomorphy: the absence of the surangular foramen. *Venaticosuchus rusconii* also
205 differs from other pseudosuchians by the following character state combination: (1)
206 basiptyergoid processes ventrally projected, (2) articular without a foramen on its
207 medial surface, and (3) dentary dorsally expanded on its anterior tip. (Baczko *et al.*,
208 2014a).

209 **Geographic and stratigraphic occurrence.** Hoyada del Cerro Las Lajas, La Rioja.
210 Middle section of the Ischigualasto Formation (late Carnian–early Norian, Late Triassic;
211 Martinez *et al.*, 2011). This locality has yielded two other archosaur specimens, the
212 holotype of the dinosaur *Pisanosaurus mertii* Casamiquela, 1967 (Casamiquela, 1967;
213 Bonaparte, 1976, Agnolín and Rozadilla, 2017), and the specimen PVL 3889 referred to
214 the crocodylomorph *Trialestes romeri* Reig, 1963 (Bonaparte, 1970, 1976, 1978,

215 Lecuona *et al.*, 2016). These outcrops have been regarded as equivalent to the middle
216 levels of the type section of the Ischigualasto Formation (Bonaparte, 1976, 1982). This
217 formation has been dated at its type locality by radioisotopic methods, yielding ages of
218 231 ± 0.3 Ma for its basal levels (Rogers *et al.*, 1993; Furin *et al.*, 2006) and 225.9 ± 0.9
219 Ma for its uppermost levels (Martinez *et al.*, 2011). Therefore, the age of the sediments
220 from which PVL 2578 was recovered is considered as bracketed by these two dates on
221 the absence of more specific information about the Cerro Las Lajas area. Nevertheless,
222 the lateral correlation between the outcrops of Cerro Las Lajas and the type locality of
223 the Ischigualasto Formation proposed by Bonaparte (1976) cannot be determined with
224 certainty because there are no shared faunal components to support it (Baczko *et al.*,
225 2014a).

226 **RESULTS**

227 **Comparative description of the newly rediscovered cranial material**

228 The **quadratojugal** of *Venaticosuchus ruconii* (PVL 2578) is a mediolaterally
229 compressed, L-shaped element (Fig. 1.1: ITF, qj). The quadratojugal forms the ventral
230 half of the posterior margin of the infratemporal fenestra, unlike that of some aetosaurs
231 (*e.g.*, *Neoaetosauroides engaeus*: PVL 5698, *Aetosaurus ferratus*: SMNS 5770),
232 loricatans (*e.g.*, *Batrachotomus kupferzellensis*: SMNS 52970, *Postosuchus kirkpatricki*:
233 Weinbaum, 2011), and crocodylomorphs (*e.g.*, *Hesperosuchus agilis*: Clark *et al.*, 2000)
234 in which the quadratojugal delimits the entire posterior margin of such fenestra. The
235 quadratojugal also delimits the medial margin of the quadrate foramen, located between
236 the quadratojugal and the quadrate, although the suture between these two elements is
237 not clear in *Venaticosuchus rusconii* (Fig. 1.3: q.f). The anterior ends of the anterior and
238 dorsal processes are broken, therefore the articular facets for the jugal and the

239 squamosal cannot be identified. The anterior process of the quadratojugal is
240 anteroposteriorly oriented and tapers anteriorly. The dorsal process is anterodorsally
241 directed with an inclination of 45° from the horizontal plane and keeps the same width
242 along its entire length. The shape of the quadratojugal of *Venaticosuchus rusconii* and
243 its inclination would grant a distinctive L-shape to the infratemporal fenestra as seen in
244 other ornithosuchids (*Riojasuchus tenuisiceps*: PVL 3827, 3828; *Ornithosuchus*
245 *woodwardi*: NHMUK PV R2409) (Fig. 1: ITF, qj). The infratemporal fenestra shape
246 seen in ornithosuchids resembles that of some proterochampsids (e.g., *Chanaresuchus*
247 *bonapartei*: PVL 4586 y *Gualosuchus reigi*: PULR 05) in which a concavity on the
248 posteroventral margin gives the fenestra a similar L-shape. The quadratojugal of
249 *Venaticosuchus rusconii* (PVL 2578) does not have an infratemporal fossa, as is also the
250 case of the other ornithosuchids *Ornithosuchus woodwardi* (NHMUK PV R2409) and
251 *Riojasuchus tenuisiceps* (PVL 3827, 3828). The external surface of the quadratojugal of
252 *Venaticosuchus rusconii* is poorly preserved but no crests can be recognized on it, it is
253 convex and smooth without any kind of ornamentation as that seen in *Ornithosuchus*
254 *woodwardi* (NHMUK PV R3143). The posterior region of the skull of *Venaticosuchus*
255 *rusconii* was preserved in articulation with the lower jaw, which allows to see that the
256 quadratojugal lies on the dorsal surface of the surangular shelf when the mandibles
257 occlude (Fig. 1.1–3: qj, sa, sa.sh) as can also be recognized in *Riojasuchus tenuisiceps*
258 (PVL 3827).

259 [Place here Figure 1]

260 The right **quadrate** of *Venaticosuchus rusconii* (PVL 2578) is complete and was
261 preserved in articulation with the quadratojugal and close to its natural articulation with
262 the mandible (Fig. 1.1–3: q, qj). The quadrate is posteroventrally directed like in most
263 archosaurs, excepting the aetosaurs (e.g., *Neoaetosauroides engaeus*: PVL 5698), the

264 shuvosaurid *Shuvosaurus inexpectatus*, spinosaurid and ornithomimid dinosaurs in
265 which the quadrate is anteroventrally directed. The posteroventral inclination of the
266 quadrate of *Venaticosuchus rusconii* (PVL 2578) almost reaches 45° above the
267 horizontal plane (Fig. 1.1, 2: q). This condition is quite rare within archosauriforms and
268 has only been registered in ornithosuchids (*e.g.*, *Riojasuchus tenuisiceps*, PVL 3827),
269 gracilisuchids (*e.g.*, *Gracilisuchus stipanicorum*: PULR 08, *Yonghesuchus*
270 *sangbiensis*: Wu *et al.*, 2001), erpetosuchids (*e.g.*, *Erpetosuchus granti*: Benton and
271 Walker, 2002, *Tarjadia ruthae*: CRILAR-Pv 478, 495), and some proterosuchids (*e.g.*,
272 *Proterosuchus fergusi*: Ezcurra y Butler, 2015). The quadrate of *Venaticosuchus*
273 *rusconi* (PVL 2578) delimits the medial half of the quadrate foramen which is round
274 and formed between the quadrate and the quadratojugal (Fig. 1.3: q.f). The suture
275 between these last two elements cannot be clearly recognized because of the poor
276 preservation of their external surface. The dorsal head of the quadrate is convex and
277 subtriangular in dorsal view and is slightly damaged on its lateral margin. The ventral
278 end of the quadrate has an anteromedially directed furrow on its distal surface that
279 divides this end into two condyles. The lateral condyle is twice as wide as the medial
280 condyle. The pterygoid process of the quadrate is fan-shaped, expanding anteroventrally
281 and forming a 90° angle with the quadratojugal (Fig. 1.1, 2: q, qj). The quadrate of
282 *Venaticosuchus rusconii* is smooth on its posterior surface and unlike the ornithosuchid
283 *Riojasuchus tenuisiceps* (PVL 3827) and some rauisuchids (*e.g.*, *Postosuchus*
284 *kirkpatricki*: Weinbaum, 2011; *Polonosuchus sileasicus*: ZPAL Ab III 563) it does not
285 have a crest on its posterior surface.

286 The right **surangular** of *Venaticosuchus rusconii* is better preserved than the left
287 one previously described by Baczko *et al.* (2014a). This element is anteroposteriorly
288 elongated, it delimits the posterodorsal margin of the external mandibular fenestra and

289 the dorsal margin of the posterior half of the lower jaw (Fig. 1.1, 2: EMF, sa). It
290 contacts the articular posteromedially and the angular ventrally at straight sutures. The
291 good preservation of the right surangular of *Venaticosuchus rusconii* (PVL 2578)
292 allowed the identification a well-developed surangular shelf that was not preserved on
293 the damaged left surangular. The surangular shelf is laterally projected forming a 90°
294 angle with the lateral surface of the bone (Fig. 1.1: sa.sh). This shelf would contact the
295 quadratojugal, as previously mentioned, when the mandibles occlude as can also be
296 seen other archosaurs (*e.g.*, *Riojasuchus tenuisiceps*: PVL 3827, 3828; *Gracilisuchus*
297 *stipaniticorum*: MCZ 4116, *Tarjadia ruthae*: CRILAR-Pv 478, 495). The surangular of
298 *Venaticosuchus rusconii* (PVL 2578) does not have a surangular foramen resembling
299 the condition of crocodylomorphs (*e.g.*, *Sphenosuchus acutus*: Walker, 1990,
300 *Dibothrosuchus elaphros*: Wu and Chatterjee 1993, *Caiman yacare*: MACN HE 43694)
301 but differing from all other archosauriforms in which the surangular foramen is present
302 (*e.g.*, *Chanaresuchus bonapartei*: PVL 4676, *Euparkeria capensis*: cast of SAM-PK
303 5867, *Riojasuchus tenuisiceps*: PVL 3827, *Aetosaurus ferratus*: SMNS 5770, *Effigia*
304 *okeeffeae*: Nesbitt, 2007).

305 The right **angular** and **prearticular** of *Venaticosuchus rusconii* are fragmentary,
306 poorly preserved and offer no novel information about the anatomy of these elements.
307 Only the posterior portion of these elements was preserved and they are sutured to the
308 articular posteriorly and to the surangular posterodorsally (Fig. 1.1, 2: an, pre). The
309 angular delimits the posteroventral margin of the external mandibular fenestra, whereas
310 the prearticular delimits the same margin of the internal mandibular fenestra. The suture
311 between the angular and the prearticular is straight and can be recognized on the ventral
312 margin of the hemimandible. Anterior to these bones, there is an internal mould that

313 corresponds to the filling of the intramandibular space delimited by the angular and the
314 prearticular.

315 The **articular** is a short element; it is equally wide as long and has a triangular
316 shape in dorsal view. It forms the posterior end of the mandibles, contacts the
317 surangular anteriorly and the prearticular anteromedially. The retroarticular process is
318 poorly developed reaching half the length of the glenoid fossa (Fig. 1.1, 2: ar, ra.p). This
319 fossa is mediolaterally wide and concave. It is located on the same plane as the dorsal
320 margin of the mandible, unlike that of aetosaurs (*e.g.*, *Neoaetosauroides engaeus*: PVL
321 4363), ornithischians (*Heterodontosaurus tucki*, Norman *et al.*, 2011), and
322 sauropodomorphs (*Plateosaurus erlenbergiensis*, Prieto-Márquez and Norell, 2011),
323 which have the glenoid fossa located below the plane of the dorsal margin of the
324 mandible.

325 **Reconstruction of the jaw musculature**

326 The *Musculus adductor mandibulae externus* (MAME) of *Venaticosuchus*
327 *rusconii* was attached on the ventral surface of the quadrate and inserted on the dorsal
328 surface of the surangular filling part of the infratemporal fenestra (Fig. 2.1). The
329 direction and shape of the MAME differs from that of crocodylians because of the
330 orientation of the quadrate. The MAME of *Venaticosuchus rusconii* was posterodorsally
331 to anteroventrally oriented resembling the condition of *Iguana iguana* but fan-shaped
332 because its dorsal attachment area is anteroposteriorly short, differing from *Caiman*
333 *latirostris* and *Alligator mississippiensis* in which that muscle is almost dorsoventrally
334 oriented, straight and anteroposteriorly long. In the case of *Venaticosuchus rusconii*, the
335 quadrate is anterodorsally directed at 45° from the horizontal plane, being more vertical
336 and not reaching the anterior extent of the surangular as in *Iguana iguana*, but unlike

337 crocodylians that have a quadrate oriented at 35° from the horizontal plane and therefore
338 projecting further anteriorly up to the same extent as the anterior end of the surangular
339 (Iordansky, 1973). In *Venaticosuchus rusconii*, the surface of the quadrate where this
340 muscle would attach is smooth and anteroposteriorly short, also differing from *Caiman*
341 *latirostris* and *Caiman yacare*, which have an anteroposteriorly larger area with a
342 longitudinal ridge on the ventral surface of this element for muscular attachment (Bona
343 and Desojo, 2011, fig. 4A–B).

344 [Place here Figure 2]

345 The *Musculus adductor mandibulae posterior* (MAMP) of *Venaticosuchus*
346 *rusconii* originated on the ventral surface of the quadrate, medial to the MAME, and
347 inserted on the dorsomedial surface of the angular and the medial surfaces of the
348 articular and surangular (Fig. 2.2). The medial surface of the surangular is gently
349 striated whereas no muscular attachment mark can be recognized on the surface of the
350 articular. This last insertion area is inferred using EPB approach, because of the
351 presence of the same structure in crocodylians and iguanas. The MAMP of
352 *Venaticosuchus rusconii* would fill the posterior half of the mandibular fenestra and,
353 together with the MAME, the infratemporal fenestra (Bona and Desojo, 2011). The
354 MAMP of *Venaticosuchus rusconii* was dorsoventrally oriented resembling the
355 condition of crocodylians and iguanids (*e.g.*, *Caiman latirostris*, *Caiman yacare*,
356 *Alligator mississippiensis*, and *Iguana iguana*).

357 The *Musculus pterygoideus dorsalis* (MPtD) was attached to the dorsal surface of
358 the palate and covered the posterior surface of the mandible inserting on the
359 posteromedial corner of the articular and angular. The *Musculus pterygoideus ventralis*
360 (MPtV) was attached on the posterodorsal region of the pterygoid and inserted on the

361 posterolateral side of the angular and articular covering the posterior region of the
362 mandible (Fig. 2.3, 4). Both these muscles would have an almost anteroposteriorly
363 orientation, which differs from the posterolateral direction seen in crocodylians. In
364 *Venaticosuchus* the MPtD and MPtV barely project laterally because its skull is higher
365 and laterally compressed compared to that the skull of crocodylians which is depressed
366 and wide (*Caiman latirostris*, *Caiman yacare*, *Alligator mississippiensis*).

367 The dorsal insertion area of the *Musculus pseudotemporalis* (MPst) was not
368 preserved in *Venaticosuchus rusconii* but was inferred by comparison with its sister taxa
369 *Riojasuchus tenuisiceps*. In crocodylians as *Caiman* and *Alligator* it attaches to the
370 lateral surface of the laterosphenoid although in iguanids it attaches to the ventrolateral
371 margin of the parietal because they do not have a laterosphenoid. As *Venaticosuchus*
372 has laterosphenoid it would be attached to that same element located anterodorsally to
373 the basal tubera (Fig. 2.5). The ventral insertion of the MPst was on the dorsolateral
374 buttress of the pterygoid as seen in crocodylians and differing from iguanids in which it
375 attaches to the coronoid process of the mandible. The MPst of *Venaticosuchus* would be
376 slightly posterodorsally oriented differing from the dorsoventral orientation that this
377 muscles has in crocodylians and iguanids.

378 The *Musculus intramandibularis* (MI) of *Venaticosuchus rusconii* was attached
379 on the pterygoid buttress. In iguanids this muscles is absent, but crocodylians it forms a
380 sesamoid element, the transiliens cartilage, where it contacts the *Musculus*
381 *pseudotemporalis* (Tsai and Holliday, 2011), but there is no evidence of this cartilage in
382 ornithosuchids. The MI of *Venaticosuchus* would insert on the medial surface of the
383 dentary and lateral surface of the splenial, filling the Meckelian canal and the anterior
384 half of the external mandibular fenestra (Fig. 2.6).

385 The *Musculus depressor mandibulae* (MDM) of the ornithosuchid *Venaticosuchus*
386 *rusconii* would have a different dorsal attachment area than that of crocodylians and
387 iguanids because the supraoccipital, parietal, and squamosal of ornithosuchids do not
388 have such exposure at the occipital table as that seen in the former (*e.g.*, *Alligator*
389 *mississippiensis* and *Caiman latirostris*, Baczko and Desojo, 2016: fig 5; Bona and
390 Desojo, 2011: fig. 2D; *Iguana iguana*: MACN HE 42334). Although the supraoccipital
391 and squamosal are not preserved in *Venaticosuchus rusconii*, in other ornithosuchids
392 (*e.i.*, *Riojasuchus tenuiscep*: PVL 3827, *Ornithosuchus woodwardi*: NHMUK PV
393 R2409) the supraoccipital is a flat anterodorsally directed element and the squamosals
394 do not have a posterior exposure, therefore there is no attachment surface available for
395 the MDM in these elements. The MDM would probably be dorsally attached to the
396 posterior surface of the exoccipital and the paroccipital process (Fig. 2.7), although
397 these elements were not preserved in *Venaticosuchus rusconii*, they can be seen in its
398 sister taxon *Riojasuchus tenuiscep* (PVL 3827) as reference. The posterodorsal surface
399 of the quadrate is also part of the attachment area for the MDM. The quadrate of
400 *Venaticosuchus rusconii* was preserved complete allowing a partial interpretation on the
401 MDM disposition. This muscle would insert on the dorsal surface of the retroarticular
402 process of the articular and is posteroventrally to anterodorsally oriented (Fig. 2.7). The
403 MDM of *Venaticosuchus rusconii* would be more dorsoventrally oriented (60°) than that
404 of *Caiman latirostris* and *Caiman yacare* (45°, Bona and Desojo, 2011) because in the
405 former the quadrate is more vertical and the retroarticular process is shorter. In occipital
406 view, the MDM of *Venaticosuchus rusconii* would be much more vertical compared to
407 crocodylians because the skull is higher and more laterally compressed than the
408 depressed and wide skulls of crocodylians.

409 **Jaw biomechanics**

410 The results of the biomechanical analysis are shown in Figure 3 and Tables 1–3.
411 The moment arms were calculated for the *Musculus adductor mandibulae externus*
412 (MAME); *Musculus adductor mandibulae posterior* (MAMP), *Musculus pterygoideus*
413 *dorsalis* (MPtD), *Musculus pterygoideus ventralis* (MPtV), *Musculus pseudotemporalis*
414 (MPst), *Musculus intramandibularis* (MI), *Musculus depressor mandibulae* (MDM) of
415 ornithosuchids and *Alligator* (Tab. 1). Even though the extant taxon *Iguana iguana* was
416 used for the EPB approach to reconstruct the muscular apparatus, it was not considered
417 for the biomechanical analysis. Iguanids have kinetic skulls and their feeding mechanics
418 are different to that of ornithosuchids which have akinetic skulls. From a biomechanical
419 point of view, the skull of crocodylians is best for comparative purposes because they
420 work the same way as that of ornithosuchids because they are both akinetic structures.

421 [Place here Figure 3]

422 In ornithosuchids, the MPst and MI represent the largest contribution to the total
423 adductor musculature (24–29%) whereas the MPtD and MPtV have the lowest
424 participation (7–11%) (Tab. 1). In *Venaticosuchus* the dominant muscle is the MPst,
425 differing from *Riojasuchus* and *Ornithosuchus* in which the main input is made by the
426 MI. The ratio of total arm moment to bite moment is remarkably highest in
427 *Venaticosuchus*, being approximately a 30% lower in *Riojasuchus* and *Ornithosuchus*
428 and a 70% lower in *Alligator*.

429 [Place here Table 1]

430 **DISCUSSION**

431 The sum of moment arms of the adductor muscles (AM) is similar within the
432 ornithosuchids, with *Venaticosuchus* representing the highest AM and *Ornithosuchus*
433 the lowest AM, 16% below *Venaticosuchus*. The difference of *Alligator* with

434 ornithosuchids is much higher, with the AM of *Alligator* being a 25% below the value
435 of *Venaticosuchus* (Tab. 1). The AM of ornithosuchids resembles that of aetosaurs
436 which according to Desojo and Vizcaíno (2009) are a 20% higher than *Alligator*. This
437 resemblance is probably a reflection of the skull shape of this terrestrial Triassic species
438 which is much higher and shorter than skull of living semiaquatic crocodylians. The
439 distribution of the adductor muscles in the high and short skulls of the fossil taxa is
440 more dorsoventrally oriented and generates higher moment arm than the more
441 anteroposteriorly inclined adductor muscles of the depressed and elongate skulls of
442 crocodylians (e.g., MAMP, MI). The elevated moment arm of the adductor muscles of
443 these terrestrial species is probably related to higher masticatory needs of these animals.
444 A resemblance to this condition can be seen within living crocodylians, in which the
445 long-snouted species (e.g., *Gavialis gangeticus*) have more reduced pterygoid muscles
446 compared to the short-snouted species (e.g., *Alligator mississippiensis*) which is
447 associated to a lower masticatory power in the long-snouted species that have more
448 specialized fish-eating diets (Endo *et al.*, 2002).

449 When comparing the input of each muscle among the three species of
450 ornithosuchids, it can be seen that the highest participation of both mandibular adductor
451 muscles (MAME: 18.5% and MAMP: 11.5%) is in *Riojasuchus* (Tab. 1). This could be
452 due to the anteroposterior distance between the craniomandibular articulation and the
453 posterior end of the skull roof, where these muscles are dorsally attached. This distance
454 is slightly larger in *Riojasuchus* than in other ornithosuchids, therefore the moment arm
455 is the highest in this species. On the contrary, when the distance between the
456 craniomandibular articulation and the posterior end of the skull roof is shorter, the
457 moment arm value decreases, as it can be seen in the ornithosuchids *Venaticosuchus*
458 (MAME+MAMP: 24.3%) and *Ornithosuchus* (23.2%) and the aetosaurs

459 *Desmotosuchus* (23.5%), *Neoaetosauroides* (20.7%), and *Stagonolepis* (21.8%) (Tab.
460 2). Aetosaurs particularly, have the posterior region of the skull almost anteroposteriorly
461 aligned with the craniomandibular joint and probably for that reason the values of
462 participation of the MAME and MAMP are the lowest among the pseudosuchians
463 analyzed (i.e., *Neoaetosauroides*, *Stagonolepis*).

464 [Place here Table 2]

465 The participation of the pterygoid muscles (MPtD and MPtV) to the total AM is
466 higher in *Ornithosuchus* (15.6% and 13.8% respectively) than in the other ornithosuchids
467 (7.7–10.5%) (Tab. 1). This difference could be given by the peculiar shape of the
468 surangular of *Ornithosuchus* which is oddly high compared to that of *Riojasuchus* and
469 *Venaticosuchus*. This high surangular increases the distance between the
470 craniomandibular joint and the ventral attachment of the pterygoid muscles and therefore
471 their arm moment. This condition resembles that of crocodylians like *Alligator* which has
472 proportionally high surangular, with MPtD and MPtV values (11% and 9% respectively)
473 slightly lower than *Ornithosuchus*. The results obtained for *Riojasuchus* and
474 *Venaticosuchus* (MPtD+MPtV: 17.7–20.2%) represented an intermediate value between
475 *Alligator* and aetosaurs (Tab. 2), which have lower participation of the pterygoid muscles
476 (MPtD+MPtV: 11–16%), and also have low surangulars.

477 The proportion of the pseudotemporal muscle (MPst) to the total adductor input is
478 slightly higher in *Venaticosuchus* and *Riojasuchus* (26.2% and 27.7%) than in
479 *Ornithosuchus* (24.1%) (Tab. 1). The values obtained for the former are closer to that of
480 *Alligator* (34%) but are lower than that presented for aetosaurs (30.9–34.1%). On the
481 other hand, the participation of the intramandibular muscle (MI) is higher in
482 *Venaticosuchus* (29.2%) than in other ornithosuchids (23.2–24.6%), but it is surpassed by

483 that of aetosaurs (30.9–34.1%) (Tab. 2). Considering the contribution of these last two
484 muscles (MPst and MI) to the total moment arm (AM) it is noticeable that in
485 *Venaticosuchus* the largest contribution to the AM is made by the MI, while in
486 *Riojasuchus* and *Ornithosuchus* it is made by the MPst (Tab. 1). This could be explained
487 by the robustness of the mandible of *Venaticosuchus* which is much higher than that of
488 other ornithosuchids. For instance, the mandible of the *Venaticosuchus* is 5.6 times longer
489 than high, contrasting with the other ornithosuchids which have more slender mandibles,
490 8 to 8.8 times longer than high. This difference in shape of the mandible would be
491 reflected in the distribution of the intramandibular musculature and consequently in the
492 moment arm of said muscles. The MI as a dominating input of the AM is also recognized
493 in the aetosaurs *Stagonolepis* and *Desmotosuchus* (Tab. 2) which also have high
494 mandibles with proportions similar to that of *Venaticosuchus*, 5 to 6 times longer than
495 high. In these species the MI represents the 31.7–34.9% of the AM, reaching a value even
496 higher than that of *Venaticosuchus rusconii*. On the other hand, in crocodylians such as
497 *Alligator mississippiensis*, the largest contribution to the AM is given by the MPst (34%)
498 as in the ornithosuchids *Riojasuchus tenuisiceps* and *Ornithosuchus woodwardi*.

499 The moment arm of the mandibular depressor muscle (MDM) is higher in
500 *Riojasuchus* than in other ornithosuchids, but that input is 1.6 times lower than that of
501 *Alligator* (Tab. 1). This difference is probably because the retroarticular process of
502 ornithosuchids, where the MDM inserts, is very short whereas that of *Alligator* is much
503 more posteriorly expanded. On the other hand, the moment arm of the MDM is even
504 larger in aetosaurs, reaching values that triple the MDM moment arm of ornithosuchids
505 (Tab. 2). Aetosaurs have a well-developed retroarticular process that, unlike in any
506 other pseudosuchian, is located below the dorsal level of the mandible, as in many

507 herbivorous animals, an important factor that possibly increases the moment arm of the
508 MDM.

509 The bite moment was analyzed on the first (Mb1) and last (Mb2) maxillary teeth
510 and on the first dentary tooth (Mb3). The dentary tooth position could not be considered
511 in *Venaticosuchus* because its dental configuration is different to that of the other
512 ornithosuchids. On one hand, the first two dentary teeth of *Venaticosuchus* are
513 hypertrophied and do not occlude with the premaxillary teeth because they fit into an
514 edentulous diastema. Then again, *Venaticosuchus* does not have a first small tooth that
515 occludes with the premaxilla, anterior to those hypertrophied ones, unlike that seen in
516 *Riojasuchus* and *Ornithosuchus* (Baczko *et al.*, 2014a; Baczko and Desojo, 2016). The
517 values here obtained for the bite moment of *Alligator* were slightly different to those
518 obtained by Desojo and Vizcaíno (2009). This difference might represent intraspecific
519 variation and therefore these values were combined to obtain an average value for the
520 taxon to be able to compare with their results.

521 The ratios (R) of total arm moments (AM) to bite moment (Mb) revealed much
522 higher values in ornithosuchids than in the crocodylian *Alligator*, resulting in a bite
523 force 31–74% stronger in ornithosuchids (Tab. 3). When comparing with the bite ratios
524 here estimated for the aetosaurs studied by Desojo and Vizcaíno (2009), it is remarkable
525 that *Desmotosuchus* reported a value between that of ornithosuchids and *Alligator* (Tab.
526 3), while *Stagonolepis* and *Neoaetosauroides* had values below *Alligator*. The high bite
527 ratio of *Desmotosuchus* was interpreted by Desojo and Vizcaíno (2009) as a strong
528 biting force which, according to their dental morphology, would be better for crushing
529 and chopping their food. But in the case of ornithosuchids, the strong bite ratios
530 obtained here combined with the laterally compressed and serrated teeth and their
531 laterally constricted snout would indicate better capacities of slicing and tearing their

532 food. The bite of ornithosuchids was probably slower than that of *Alligator*, as also
533 identified for herbivorous aetosaurs (Desojo and Vizcaíno, 2009), because the input
534 forces and the craniomandibular articulation of their mandibular lever system are more
535 distant from each other. Despite having a strong bite, the low speed inferred for
536 ornithosuchids would not support hunting abilities as those interpreted for the
537 animalivorous aetosaur *Neoaetosauroides* (Desojo and Vizcaíno, 2009), whose low bite
538 force was compensated by its velocity, as a fast bite is crucial for catching small preys.
539 Therefore, the relatively strong but slow bite of ornithosuchids seems more appropriate
540 for animals with scavenger habits, which do not require speed to catch a moving prey
541 and only need their strength for tearing flesh or crushing bones of a carcass.

542 [Place here Table 3]

543 The stronger adductor musculature of *Venaticosuchus* was accompanied by a slow
544 mandibular lever system resulting in relatively strong and slow bite movements.
545 Although this could be associated to an active predatory habit other factors need to be
546 considered. Particularly, the skull of ornithosuchids has a weak spot on their laterally
547 constricted snout (Baczko *et al.*, 2014b) that would not resist high lateral stresses like
548 those applied by living prey trying to escape. Moreover, the laterally compressed teeth
549 of ornithosuchids are useful for tearing the flesh of a prey in an anteroposterior direction
550 but structurally weak in lateral direction, unlike the conical caniniform teeth of
551 crocodylians (*e.g.*, *Caiman*, *Alligator*) that equally resist stresses in every direction and
552 hunt their living prey directly biting them. Considering this features, it is more likely that
553 ornithosuchids resorted to scavenging habits to avoid strong lateral stresses that may
554 occur while holding a prey that tries to escape and therefore prevent damaging
555 themselves.

556 **CONCLUSIONS**

557 The rediscovered cranial elements here described for *Venaticosuchus rusconii*
558 provided new information about some regions poorly known for this species and
559 supported the local autapomorphy proposed by Baczko *et al.* (2014a), the absence of a
560 surangular foramen.

561 The jaw biomechanics of ornithosuchids revealed more similarities between these
562 and herbivorous aetosaurs, despite having different feeding habits, than with
563 crocodylians who are also carnivorous as ornithosuchids. The overall resemblance in the
564 skull shape between ornithosuchids and aetosaurs probably emphasized the
565 phylogenetic distance that separates these basal pseudosuchians from their long-snouted
566 living relatives, crocodylians.

567 The skull of *Venaticosuchus* is larger and more robust than the other
568 ornithosuchids (*e.g.*, mandibles proportionally higher) and this was reflected its
569 muscular distribution. In this study, the intramandibular muscle (MI) represented the
570 dominating element of the adductor musculature of this species, whereas in
571 *Riojasuchus*, *Ornithosuchus* and crocodylians the main input is given by the
572 pseudotemporal muscle (MPst). The condition seen in *Venaticosuchus* is also shared by
573 the aetosaurs *Desmotosuchus* and *Stagonolepis*, and moreover, its robust mandibular
574 configuration resembles that of aetosaurs more than that of its nearest relatives
575 *Riojasuchus* and *Ornithosuchus*.

576 The highest bite force that distinguished *Venaticosuchus* from other
577 ornithosuchids resembles the situation of *Desmotosuchus* amongst aetosaurs. Despite
578 their different feeding habits, with the first being carnivorous and the second strictly
579 herbivorous, both presented elevated bite forces probably because their premaxillae do

580 not participate in the bite. In *Venaticosuchus* this condition is given because the
581 premaxillary teeth do not reach the mandibles when they occlude and the anterior-most
582 dentary teeth fit into a diastema, whereas in *Desmotosuchus* it is given by the complete
583 absence of premaxillary teeth. In both cases, their bite restricted to the maxillary region
584 and therefore is stronger than in others because the bite force is not dissipated up to the
585 premaxilla.

586 Both scavenger and active predator habits have been previously proposed for
587 ornithosuchids based on different sources of information. Benton (1983) reported bite-
588 marks on the middle-sized rhynchosaur *Hyperodapedon* (1.5 meters long) and assigned
589 *Ornithosuchus* as the scavenger that produce these marks because this was the largest
590 carnivore known for the Late Triassic of Scotland. On the other hand, Walker (1964)
591 interpreted that *Ornithosuchus* “fulfils the role of a large predatory form” based on its
592 morphology (*e.g.*, jaws with curved teeth, forelimbs shorter than hind limbs, possible
593 bipedalism), but mainly based on its large size. Nevertheless, it is important to note that,
594 at that time, *Ornithosuchus* was interpreted as a rather large carnivore of approximately
595 4 meters long, but considering the latest taxonomic revision of Baczko and Ezcurra
596 (2016), *Ornithosuchus* would have actually been much smaller, no longer than 2 meters.
597 Following this interpretation with *Ornithosuchus* being more even in size with its
598 putative prey *Hyperodapedon*, it is more likely that the former left bite marks on the
599 bones of the latter while scavenging. Actively hunting on a prey of its same size, as
600 proposed by Walker (1964), could have resulted harmful on the snout of an
601 ornithosuchid if lateral stresses were applied while said prey tried to escape, as
602 previously discussed. Alternatively, ornithosuchids might have resorted to different
603 hunting strategies such as overthrowing and holding medium to small-sized prey (*e.g.*,
604 procolophonids, sphenodontians, cynodonts or juvenile dicynodonts) with their

605 forelimbs before biting to prevent lateral stresses on their snout. However, this strategy
606 would have depended on their bipedal ability, and such locomotive capabilities are still
607 to be tested on ornithosuchids.

608 Considering the biomechanical information here obtained plus the anatomical and
609 structural data known for different ornithosuchids, they are here proposed as having
610 scavenger habits instead of being active predators because of their relatively strong and
611 slow bite and the structural weakness of their snout. Ornithosuchids did not occupy the
612 niche of apex predators of the Late Triassic continental communities but were more
613 likely regarded to scavenging the prey hunted by others or preyed on small animals such
614 as procolophonids, sphenodontians, juvenile aetosaurs, erpetosuchids, cinodonts, and
615 dicynodonts that did not exceed them in size.

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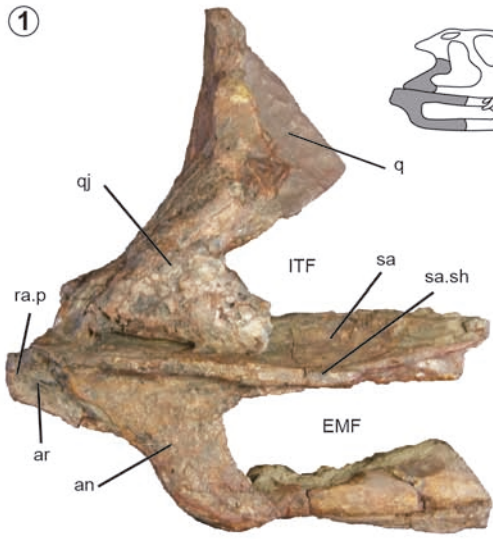
780 **Figure captions**

781 **Figure 1.** New cranial elements of *Venaticosuchus rusconii* in **1**, lateral view; **2**, medial
782 view; and **3**, posterior view. Abbreviations: **an**, angular; **ar**, articular; **EMF**,
783 external mandibular fenestra; **gl**, glenoid fossa; **ITF**, infratemporal fenestra; **pre**,
784 prearticular; **q**, quadrate; **q.f**, quadrate foramen; **qj**, quadratojugal; **ra.p**,
785 retroarticular process; **sa**, surangular; **sa.sh**, surangular shelf. Scale bar= 20 mm.

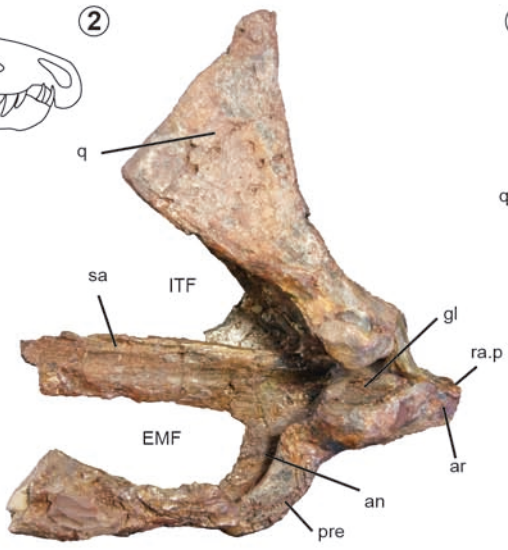
786 **Figure 2.** Dorsal (purple/dashed) and ventral (green/dotted) attachment areas of the
787 adductor and depressor muscles of *Venaticosuchus rusconii*. **1**, *Musculus*
788 *adductor mandibulae externus*; **2**, *Musculus adductor mandibulae posterior*; **3**,
789 *Musculus pterygoideus dorsalis*; **4**, *Musculus pterygoideus ventralis*; **5**, *Musculus*
790 *pseudotemporalis*; **6**, *Musculus intramandibularis*; and **7**, *Musculus depressor*
791 *mandibulae*. **Dash-lines** represent the reconstructed margins of incomplete
792 elements, reconstruction based on PVL 2578 and the complete skull of its sister
793 taxa *Riojasuchus tenuisiceps* (PVL 3827). Scale bar= 50 mm.

794 **Figure 3.** Moment arms and action lines of the adductor and depressor muscles of **1–7**,
795 *Venaticosuchus rusconii*; **8–14**, *Riojasuchus tenuisiceps*; **15–21**, *Ornithosuchus*
796 *woodwardi*; and **22–28**, *Alligator mississippiensis*. *Musculus adductor*
797 *mandibulae externus* (1,8,15,22); *Musculus adductor mandibulae posterior*
798 (2,9,16,23), *Musculus pterygoideus dorsalis* (3,10,17,24), *Musculus pterygoideus*
799 *ventralis* (4,11,18,25), *Musculus pseudotemporalis* (5,12,19,26), *Musculus*
800 *intramandibularis* (6,13,20,17), *Musculus depressor mandibulae* (7,14,21,28).
801 **Arrows** represent the line of action of each muscle. **Red lines** represent the
802 moment arm of each muscle. Not to scale.

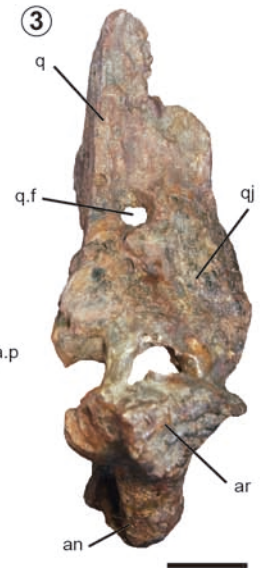
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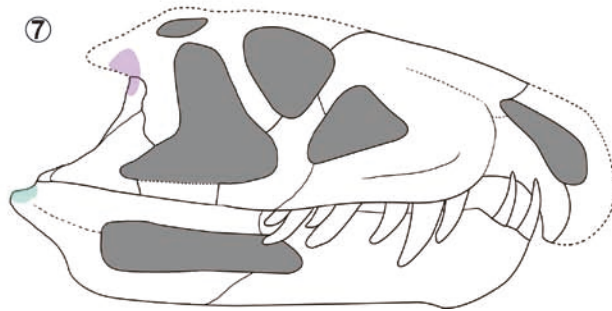
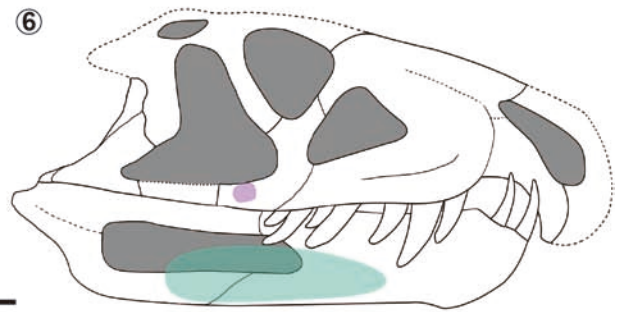
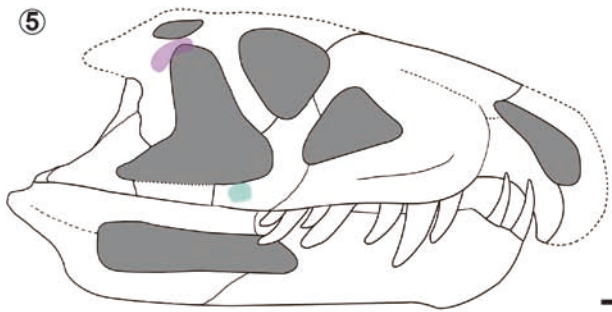
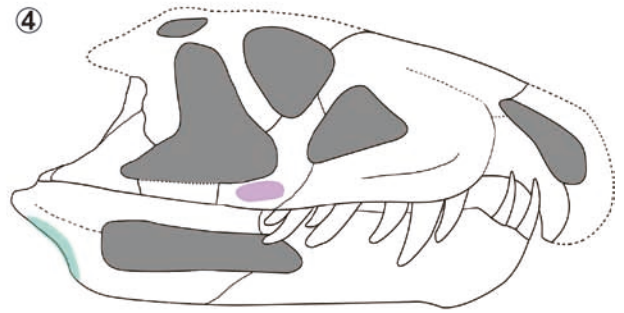
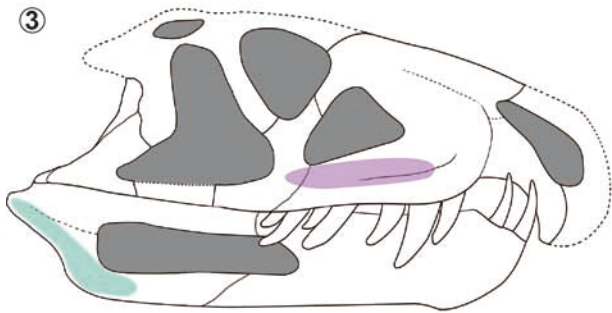
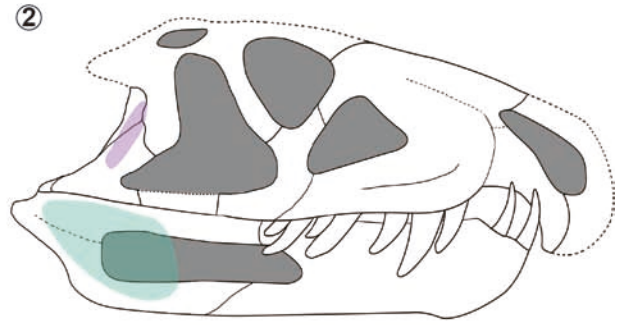
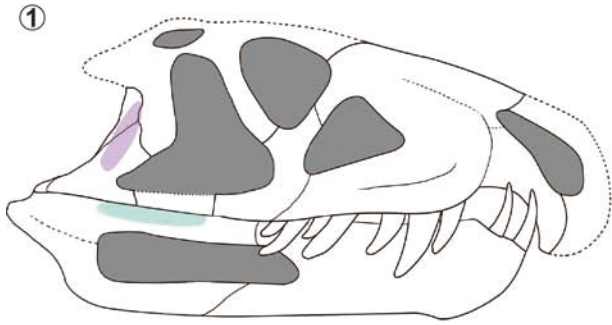


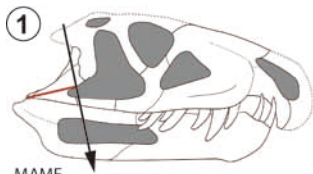
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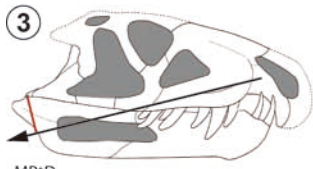




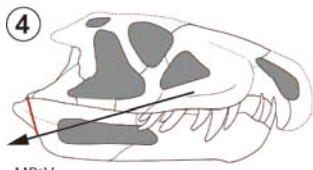
MAME



MAMP



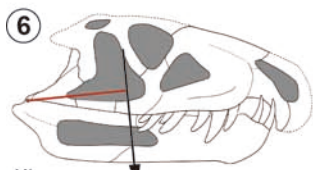
MPtD



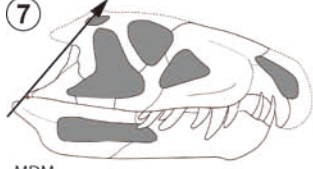
MPtV



MPst



MI



MDM

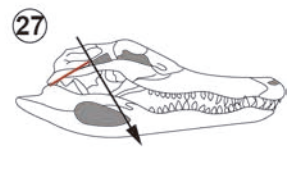
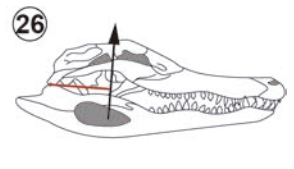
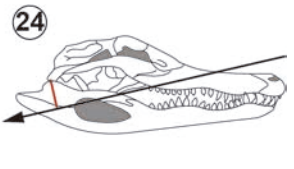
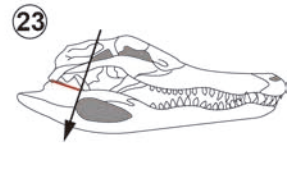
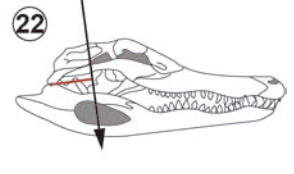
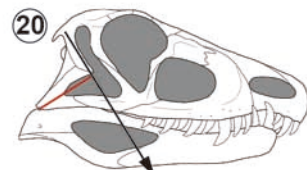
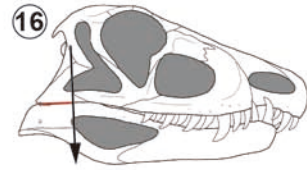
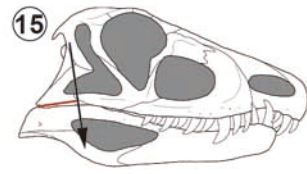


TABLE 1. Moment arm of the adductor and depressor muscles

Taxon	MAME	MAMP	MPtD	MPtV	MPst	MI	AM	MDM
Venaticosuchus	19.5 (14.6%)	13.0 (9.7%)	14.0 (10.5%)	13.0 (9.7%)	35.0 (26.2%)	39.0 (29.2%)	133.5	1.5
Riojasuchus	24,0 (18.5%)	15,0 (11.5%)	13,0 (10%)	10,0 (7.7%)	36,0 (27.7%)	32,0 (24.6%)	130,0	3.0
Ornithosuchus	14,0 (12.5%)	12,0 (10.7%)	17,5 (15.6%)	15,5 (13.8%)	27,0 (24.1%)	26,0 (23.2%)	112.0	2.0
Alligator	16,0 (16%)	11,0 (11%)	11,0 (11%)	9,0 (9%)	34,0 (34%)	19,0 (19%)	100.0	3.5

Musculus adductor mandibulae externus (MAME), *Musculus adductor mandibulae posterior* (MAMP), *Musculus pterygoideus dorsalis* (MPtD), *Musculus pterygoideus ventralis* (MPtV), *Musculus pseudotemporalis* (MPst), *Musculus intramandibularis* (MI), total adductor muscles (AM), and *Musculus depressor mandibulae* (MDM) of ornithosuchids and *Alligator*. Contribution to the total adductor moment arm in parenthesis.

TABLE 2. Moment arm of the adductor chamber muscles.

Taxon	MAME+MAMP	MPtD+MPtV	MPst	MI	AM	MDM
Venaticosuchus	32,5 (24,3%)	27 (20,2%)	35 (26,2%)	39 (29,2%)	133,5	1,5
Riojasuchus	39 (30%)	23 (17,7%)	36 (27,7%)	32 (26%)	130,0	3,0
Ornithosuchus	26 (23,2%)	33 (29,5%)	27 (24,1%)	26 (23,2%)	112,0	2,0
Alligator	27,0 (27%)	20,0 (20%)	34,0 (34%)	19,0 (19%)	100,0	3,5
Neoaetosauroides	17 (20,7%)	9 (11%)	28 (34,1%)	28 (34,1%)	82,0	8,5
Stagonolepis	17 (21,8%)	10 (12,8%)	25 (32,1%)	26 (33,3%)	78,0	7,0
Desmotosuchus	19 (23,5%)	13 (16%)	24 (29,6%)	25 (30,9%)	81,0	9,0

Values of MAME and MAMP, MPtD and MPtV were added to be able to compare with the results of Desojo and Vizcaíno (2009). Contribution to the total adductor moment arm in parenthesis.

TABLE 3. Moment arms of bite calculated at the posterior (Mb1) and anterior (Mb2) maxillary teeth, and the posterior premaxillary teeth (Mb3).

Taxon	Mb1	Mb2	Mb3	R1	R2	R3	X	AM
Venaticosuchus	44	79	N/A	3,03	1,69	N/A	2,36	133,5
Riojasuchus	54	82,5	92	2,41	1,58	1,41	1,8	130,0
Ornithosuchus	40,5	81	95	2,77	1,38	1,18	1,78	112,0
Alligator combined	40	81	90,5	2,11	1,04	0,94	1,36	84,5
Neoaetosauroides	46	76	89,5	1,78	1,08	0,92	1,26	82,0
Stagonolepis	47	76	89	1,66	1,03	0,88	1,19	78,0
Desmotosuchus	39	71	N/A	2,08	1,14	N/A	1,61	81,0

Bite ratios ($R=AM/Mb$) and average bite ratio (X). N/A= not applicable.