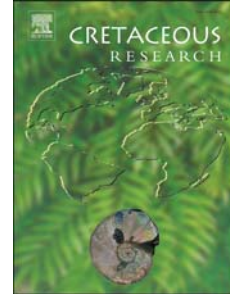


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1 **A new ornithopod dinosaur from the Santonian of Northern Patagonia (Rincón de**
2 **los Sauces, Argentina)**

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19 Key words: Gondwana, Elasmaria, intercostal plates, Upper Cretaceous, Neuquén Basin
20

21 ABSTRACT

22 In recent decades, the Argentinian ornithopod record – which includes eight species that
23 have been described – has increased as a result of the discovery of diverse new bone
24 remains from the Upper Cretaceous. The area near the town of Rincón de los Sauces
25 (Neuquén Province) presents rich fossiliferous outcrops that have provided new
26 ornithopod remains. These bones are from two units: the Plottier and Bajo de la Carpa
27 formations. In the latter, several isolated postcranial bones and a partial articulated
28 skeleton (MAU-Pv-CO-596) have been found. The holotype of *Mahuidacursor*
29 *lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) comes from the Cerro Overo site
30 (Santonian, Upper Cretaceous). The skeleton preserves elements from the cervical and
31 dorsal series, the pectoral girdle and the right forelimb. It corresponds to a medium-
32 bodied ornithopod with a gracile general appearance. Histological analysis suggests that
33 the specimen was a sexually mature but not fully grown individual. Some distinctive
34 characters present in *Mahuidacursor*, such as the strongly bowed humeral shaft and the
35 weakly developed deltopectoral crest, are shared with other South American basal
36 ornithopods. A phylogenetic analysis including *Mahuidacursor* within a large
37 ornithischian dataset was performed. The results show *Mahuidacursor* to be a basal
38 ornithopod recovered within a polytomy along with *Notohypsilophodon* and the clade
39 Elasmaria (*Talenkauen* + *Macrogryphosaurus*).

40

41

42 **1- INTRODUCTION**

43 The South American record of non-hadrosaurid ornithopod dinosaurs is composed of
44 some partial skeletons and numerous isolated remains, most of them from the
45 Argentinian Patagonia (see tables 1-3 in Cruzado-Caballero et al., 2018). As a result,
46 several species have been defined (i.e. *Gasparinisaura cincosaltensis* Coria and
47 Salgado, 1996; *Notohypsilophodon comodorensis* Martínez, 1998; *Anabisetia saldiviai*
48 Coria and Calvo, 2002; *Talenkauen santacrucensis* Novas, Cambiaso and Ambrosio,
49 2004; *Macrogryphosaurus gondwanicus* Calvo, Porfiri and Novas, 2007).

50 The phylogenetic relationships between these taxa are poorly resolved due largely to the
51 scarcity of cranial material and the incompleteness of the specimens, limiting the
52 presence of overlapping material. In 2007 Calvo and collaborators defined Elasmaria,
53 the first endemic clade of non-hadrosaurid ornithopods from South America. Later,
54 Boyd (2015) reported *Notohypsilophodon* within the clade Elasmaria but relocated this
55 clade within Thescelosaurinae and outside Ornithopoda. More recently, Rozadilla et al.
56 (2016) performed a new phylogenetic analysis comprising a greater number of
57 Argentinian and Antarctic non-hadrosaurid ornithopod taxa. As a result, the location of
58 the clade Elasmaria changed again, appearing as a member of the group Ornithopoda,
59 and the Argentinian and Antarctic non-hadrosaurid ornithopods formed an unresolved
60 polytomy, with *Gasparinisaura* as the sister group of the polytomy. There is some
61 evidence that points to a large set of Gondwanan basal ornithopods that are closely
62 related and may be part of a common clade (i.e. Rozadilla et al., 2016; Herne et al.,
63 2018), but up to now we are far from providing a robust phylogenetic framework. This
64 can only be resolved with the contribution of new fossil discoveries.

65 Here we describe a new ornithopod with clear affinities to certain other ornithopod taxa
66 previously related to the clade Elasmaria. The new specimen was found near the town

67 of Rincón de los Sauces (Neuquén Province, Argentina; Fig. 1). In recent years the area
68 around Rincón de los Sauces has added numerous remains to the dinosaur record,
69 including *Rinconsaurus caudamirus* Calvo and Riga, 2003, *Bonitasaura salgadoi*
70 Apesteguía, 2004, *Petrobrasaurus puestohernandezii* Filippi, Canudo, Salgado, Garrido,
71 García, Cerda and Otero, 2011, *Overosaurus paradasorum* Coria, Filippi, Chiappe,
72 García and Arcucci, 2013, and *Viavenator exxoni* Filippi, Méndez, Gianechini, Juárez
73 Valieri and Garrido, 2018. As regards the ornithopod record this area has added new
74 remains in sedimentary deposits aged between late Coniacian and Campanian (see
75 references in Cruzado-Caballero et al., 2016, 2018 and Jimenez-Gomis et al., *in press*).
76 The new ornithopod is a partial skeleton discovered in the Cerro Overo fossil locality.
77 Previous reports from the same locality include isolated remains belonging to several
78 individuals of different ontogenetic stages, which exhibit affinities with the elasmarians
79 *Macrogryphosaurus* and *Talenkauen* (Cruzado-Caballero et al., 2018; Jimenez-Gomis
80 et al., *in press*). However, these fragmentary remains could not be assigned to a new
81 taxon or to any other known species. On the basis of the new specimen, in this paper we
82 erect a new basal ornithopod genus and species and evaluate its phylogenetic
83 relationships. This research highlights the remarkable diversity of basal ornithopods
84 present in the Upper Cretaceous of Argentina and reinforces the phylogenetic
85 hypothesis that recovers an endemic clade of South American ornithopods.

86
87 *Institutional Abbreviations*— **MAU**, Museo Municipal Argentino Urquiza (Rincón de
88 los Sauces, Neuquén, Argentina); **FMNH**, the Field Museum, Chicago, USA; **MACN**,
89 Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires,
90 Argentina); **MPCA-Pv**, Museo Provincial Carlos Ameghino, Paleovertebrate Collection
91 (Cipolletti, Río Negro, Argentina).

92

93 **2-GEOLOGICAL SETTING**

94 The Neuquén Group (Cenomanian – lower Campanian) consists of a 1,200m-thick red-
95 bed succession that characterizes the Upper Cretaceous succession of the Neuquén Basin
96 (North Patagonia). These deposits were accumulated in a fluvial setting, with minor
97 intercalations of aeolian and shallow lacustrine sediments (Cazau and Uliana, 1973). The
98 outcrops of the group are those with the greatest exposure outside the Andean area of the
99 Basin, bearing a rich and varied fauna of fossil reptiles whose presence has been known
100 to the scientific community since the end of the nineteenth century (Leanza et al., 2004;
101 Garrido, 2010).

102 The fossil remains studied here were recovered from the Bajo de la Carpa Formation
103 (Río Colorado Subgroup), a lithostratigraphic unit included in the upper part of the
104 Neuquén Group with an age estimated to be Santonian (Legarreta and Gulisano, 1989;
105 Bonaparte, 1991; Hugo and Leanza, 2001; Garrido, 2010). Indeed, this unit brought the
106 first vertebrate remains known for the Upper Cretaceous of the Neuquén Basin,
107 comprising crocodiles and fossil snakes found by Roth (1898) and studied by Smith
108 Woodward (1896, 1901).

109 The site where these remains were first found is located in what is currently the
110 university campus of the Universidad Nacional del Comahue in Neuquén, the capital
111 city of the province of Neuquén. Over the decades, a great variety of fossils have been
112 recovered from this location, noteworthy among which are the remains of small
113 abelisaurids and alvarezsaurids (Bonaparte, 1991; Martinelli and Vera, 2007), crocodiles
114 (Bonaparte, 1991; Fiorelli and Calvo, 2007; Martinelli and Pais, 2008), snakes (Caldwell
115 and Albino, 2001), as well as bird remains and bird eggs (Chiappe and Calvo, 1994;
116 Alvarenga and Bonaparte, 1992; Schweitzer et al., 2002; Fernández et al., 2013). A

117 similar faunal association was also found in deposits of this unit outcropping near the
118 locality of Paso Córdoba, Río Negro Province, located approximately 42 km from the
119 city of Neuquén (Gazzera and Calvo, 1991).

120 However, in spite of the rich faunal association recovered from the Bajo de la Carpa
121 Formation in the decades from 1890 to 2000, remains of medium to large-sized
122 dinosaurs were not known for this unit, with the exception of the titanosaur *Bonitasaura*
123 and the later relocation of *Rinconsaurus* and *Overosaurus* within the fluvial deposits of
124 the unit (Filippi, 2015). Since the discovery in 2013 of a new fossiliferous site belonging
125 to the Bajo de la Carpa Formation in the northwestern area of Neuquén Province, located
126 approximately 40 km southwest of the town of Rincón de los Sauces, the number of
127 known species has increased substantially, including a new faunal association composed
128 of sauropod, theropod and ornithopod dinosaurs, as well as a wide variety of turtles and
129 fishes (Filippi et al., 2015, 2016, 2018; Cruzado-Caballero et al., 2016b, 2018).

130 The presence of two different faunal associations in the Bajo de la Carpa Formation is
131 consistent with variations in the palaeoenvironmental conditions of these deposits
132 according to their location within the palaeogeographic context of the basin (Filippi et
133 al., 2015). An association of aeolian and low-sinuosity to braided fluvial deposits thus
134 characterizes the Bajo de la Carpa Formation at the city of Neuquén and the locality of
135 Paso Córdoba (Heredia and Calvo, 1997, 2002; Garrido and Calvo, 2004; Caldwell and
136 Albino, 2001; Sánchez et al., 2006; Garrido, 2010), whereas a thick succession of
137 muddy floodplains associated with anastomosed fluvial deposits distinguishes this unit
138 in the area southwest of the town of Rincón de los Sauces (Cruzado-Caballero et al.,
139 2018).

140 The bone remains identified as *Mahuidacursor* are from the latter locality. They were
141 recovered from the upper third of the Bajo de la Carpa Formation, which in this area

142 exhibits a total thickness of 108 m. The fossiliferous bed is composed of sandy siltstone
143 interbedded with thin massive mudstone levels. The sandy siltstone shows a faint
144 horizontal stratification, associated with an intense bioturbation developed on top of the
145 bed. Within the palaeoenvironmental context, dominated by the development of an
146 anastomosed fluvial system (Cruzado-Caballero et al., 2018), this fossiliferous level has
147 been interpreted as levee deposits.

148 The preservational features of the *Mahuidacursor* holotype (i.e. an articulated specimen
149 with unabraded and little-weathered bone elements) suggest relatively short subaerial
150 body exposure, which prevented the total disarticulation and dispersion of bones.
151 Because at the time of the discovery the bone remains were partially exposed on the
152 surface, it is possible that the missing pieces of the skeleton have been lost due to recent
153 erosion. However, the action of scavengers prior to the final burial of the body cannot be
154 ruled out.

155

156 **3-MATERIAL AND METHODS**

157 *3.1. Phylogenetic analysis*

158 In this paper, we follow the definition of Sereno (1986, emended) for the clade
159 Iguanodontia, which is ‘the most inclusive group containing *Parasaurolophus walkeri*
160 Parks, 1922 but not *Hypsilophodon foxii* Huxley, 1869 or *Thescelosaurus neglectus*
161 Gilmore, 1913’ (see discussion in Sereno, 2005), and the definition of Calvo et al.
162 (2007) for Elasmaria, which is ‘*Talenkauen santacrucensis*, *Macrogyphosaurus*
163 *gondwanicus*, their most recent common ancestor plus all the descendants’. However,
164 we will not consider the clade Elasmaria to be within the clade Euiguanodontia as in the
165 original publication, due to the status of the clade Euiguanodontia, which was defined
166 by Coria and Salgado (1996) as ‘*Gasparinisaura cincosaltensis*, Dryosauridae,

167 Ankylopollexia (= *Camptosaurus* + *Styracosterna*) and all descendants of their common
168 ancestor', but is inactive, *Gasparinisaura* being positioned among the
169 hypsilophodontids (see discussion in Sereno, 2005).

170

171 3.2. *Palaeohistology*

172 Histological thin sections from a dorsal rib, an ossified tendon and an intercostal plate
173 were prepared by one of us (IAC) at the Museo "Carlos Ameghino" (Cipolletti, Río
174 Negro Province, Argentina). The slices were prepared using standard methods outlined
175 by Chinsamy and Raath (1992) and studied using a petrographic polarizing microscope
176 (Nikon E200 pol). The nomenclature and definitions of structures used in this study are
177 derived from Francillon-Vieillot et al., (1990) and Chinsamy-Turan (2005). The thin
178 sections are deposited in the Museo Municipal Argentino Urquiza (Rincón de los
179 Sauces, Neuquén, Argentina).

180

181 4-SYSTEMATIC PALAEONTOLOGY

182 Dinosauria Owen, 1842

183 Ornithischia Seeley, 1887

184 Ornithopoda Marsh, 1881

185 *Mahuidacursor* nov. gen.

186

187 *Derivation of genus name:* The generic name *Mahuidacursor* is from the Mapuche word
188 'mahuida', which means mountain, in reference to the various mountains of volcanic
189 origin that stand out in the landscape around the town of Rincón de los Sauces, with the
190 suffix '-cursor,' from the Latin for runner.

191 *Diagnosis:* As for the type and only known species.

192

193 *Mahuidacursor lipanglef* nov. sp.

194 *Derivation of species name:* The specific name *lipanglef* is from the Mapuche, in
195 reference to the gracile nature of the specimen, in particular the slender architecture of
196 its forelimbs; the word ‘lipang’ means arm, and ‘lef’, lightly.

197

198 *Holotype:* MAU-Pv-CO-596 consists of a partial articulated postcranial skeleton (Fig.
199 2). The fossil remains are kept within a plaster jacket, in which the left side of the
200 dinosaur skeleton is prepared and well-exposed. By contrast, the right side – which is
201 the side that was cropping out – remains hidden. The skeleton preserves the last four
202 cervical vertebrae (the most anterior of them extracted outside the plaster jacket) and the
203 corresponding ribs, an additional posterior cervical centrum, the most anterior six
204 vertebrae and seven left ribs of the dorsal series, the two scapulae, coracoids and sternal
205 plates, four intercostal plates (those located between the second and sixth dorsal ribs), as
206 well as the right forelimb (also articulated but recovered outside the plaster jacket)
207 including humerus, radius, ulna and almost complete manus (excluding some distal
208 phalanges).

209

210 *Type locality and Horizon:* The Cerro Overo site, near the town of Rincón de los Sauces
211 (Neuquén Province, Argentina); Bajo de la Carpa Formation, Santonian, Upper
212 Cretaceous (Fig. 1).

213

214 *Diagnosis:* Species as for the genus. Medium-sized ornithopod dinosaur diagnosable by
215 the presence of dorsal ribs not distally thickened and bearing a surface restricted to the

216 most anterolateral margin for contact to the preceding intercostal plate (potentially
217 autapomorphic) and the following combination of synapomorphic characters: first
218 dorsal vertebra with rectangular dorsal neural spine; first and second dorsal centra as
219 long as the last cervical centrum; dorsal centra relatively long, and increasing in length
220 only moderately throughout the dorsal sequence; posterior process of the coracoid
221 scarcely developed; humerus length subequal to the scapular length; long and slender
222 scapula; posterior end of the scapular blade narrower than the proximal end of the bone;
223 poorly developed humeral head, rudimentary deltopectoral crest and humeral shaft
224 strongly bowed.

225

226 *Differential diagnosis:* *Mahuidacursor* differs from *Macrogyphosaurus* in the concave
227 profile of the ventral side of the cervical centra in *Macrogyphosaurus* as well as in the
228 proportions of the cervical centra (i.e., wider than high in *Macrogyphosaurus*. as wide
229 as high in *Mahuidacursor*) and the neural spine of the last cervical (i.e., height
230 significantly increasing in *Macrogyphosaurus* and remaining low in *Mahuidacursor*);
231 it differs from *Talenkauen* in the humerus (i.e. the scapula length ratio, which is clearly
232 greater in *Talenkauen*), in the scapula (the ratio of the distal width of the scapular blade
233 to the proximal width being clearly greater in *Talenkauen* than in *Mahuidacursor*), and
234 also in the neural spine of the last cervical (i.e. *Talenkauen* displaying the same
235 condition as *Macrogyphosaurus*); it differs and from *Notohypsilophodon* in the bowing
236 of the humeral shaft, which is gentler in the latter.

237

238 *4.1. Description and comparison.*

239 *4.1.1. Cervical vertebrae*

240 Five cervical vertebrae are preserved (Figs. 2-3). One of them is an eroded centrum
241 found isolated but near the rest of the skeleton. The four most posterior ones were found
242 in anatomical connection even though the first of them was extracted apart from the
243 plaster jacket containing the main body of the individual. The cervical centra are
244 anteroposteriorly elongated whereas they are almost as wide as high (see Supporting
245 Information 2). The latter is a different condition from that of *Macrogyphosaurus*
246 whose cervical centra are wider than high (Calvo et al., 2007). The anteroposterior
247 length increases posteriorly except for the last vertebra, in which it decreases, this
248 pattern being similar to *Talenkauen*, *Macrogyphosaurus* and *Gasparinisaura* (see
249 Supporting Information 2; Cambiaso, 2007). The length:height ratio of the most anterior
250 cervical centrum is more than 1.5, as in the anterior cervical centra of *Thescelosaurus*,
251 *Parksosaurus*, *Talenkauen*, *Macrogyphosaurus* and *Dryosaurus altus* Marsh, 1894
252 (Boyd, 2015; Han et al., 2017) and unlike those of most ornithischians (i.e.
253 *Lesothosaurus diagnosticus* Galton, 1978; *Haya* Makovicky, Kilbourne, Sadleir and
254 Norell, 2011; *Zalmoxes robustus* Nopcea, 1899; *Yinlong downsi* Xu, Forster, Clark and
255 Mo, 2006; Boyd, 2015; Han et al., 2017). The centra are spool-shaped and bear a well-
256 defined ventral keel, as in basal ornithopods (i.e. *Haya*, *Hypsilophodon*,
257 *Macrogyphosaurus*, *Notohypsilophodon*; Calvo et al., 2007; Makovicky et al., 2011;
258 Ibiricu et al., 2014; Boyd, 2015) and the iguanodontian *Valdosaurus canaliculatus*
259 Galton 1977 (Barrett et al., 2011). This keel is sharper in its anterior part than in the
260 posterior part, like in other basal ornithopods (i.e. Butler et al., 2011). In lateral view,
261 the ventral border of the centra is almost straight, as in other basal ornithopods (i.e.
262 *Thescelosaurus*, *Talenkauen*; Gilmore, 1915; Novas et al., 2004) and unlike the concave
263 border of *Changchunsaurus parvus* Zan Shu-Qin, Chen Jun, Jin Li-Yong and Li Tao,
264 2005 and *Macrogyphosaurus* (Calvo et al., 2007; Butler et al., 2011). The articular

265 surfaces are heart-shaped and amphicoelous, as in most ornithischians (i.e.
266 *Thescelosaurus*, *Gasparinisaura*, *Macrogyphosaurus*, *Talenkauen*,
267 *Notohypsilophodon*; Calvo et al., 2007; Cambiaso, 2007), this differs from the slightly
268 opisthocoelous cervical vertebrae of iguanodontians (Galton, 1974; Norman et al.,
269 2004). In lateral view, all the centra show an open neurocentral suture indicating an
270 immature stage (Irmis, 2007; see discussion below; Figs. 2 B, 3 C-D). The neural spines
271 are dorsoventrally low, lateromedially narrow and triangle-shaped in lateral view. The
272 dorsoventral development of the neural spines is rudimentary, as in most ornithischians,
273 and differs from the prominent neural spines of *Thescelosaurus*, *Tenontosaurus tilletti*
274 Ostrom, 1970, *Heterodontosaurus tucki* Crompton and Channing, 1962, *Scelidosaurus*
275 *harrisonii* Owen, 1861 and *Stegosaurus stenops* Marsh, 1887 (Han et al., 2017). The
276 last neural spine is low as in other basal ornithopods (i.e. *Thescelosaurus*) and unlike in
277 *Macrogyphosaurus* and *Talenkauen* where it increases significantly in height (Novas et
278 al., 2004; Cambiaso, 2007). The transverse processes are located dorsally to the neural
279 arch, as in *Macrogyphosaurus* and in the most posterior cervical vertebra of
280 *Talenkauen* (Cambiaso, 2007). They are dorsoventrally narrow and laterally oriented.
281 The prezygapophyses are located anteriorly to the base of the neural spine, and their
282 articular surface is oval-shaped, flat and is directed upwards and inwards. The
283 postzygapophyseal processes are long and are curved backwards and outwards. They
284 extend well above the level of the neural canal. The angle formed by this paired process
285 is between approximately 45° and 30°. The postzygapophyseal processes are gently
286 arched, as in most ornithischians (i.e. *Hypsilophodon*, *Talenkauen*, *Notohypsilophodon*;
287 Galton, 1974; Novas et al., 2004; Ibiricu et al., 2014) and unlike iguanodontians
288 (Norman, 1986; Weishampel et al., 2003). The articular surface of the

289 postzygapophyses is located at the end of that process; it is oval-shaped, flat and faces
290 ventrolaterally.

291

292 4.1.2. *Cervical Ribs*

293 Three posterior cervical ribs are well preserved and articulated (Fig. 3 A-B). The two
294 most anterior ribs are anteroposteriorly projected, exceeding posteriorly the end of their
295 corresponding centrum. They are parallel to the anteroposterior axis of the centrum,
296 sharpening posteriorly, and are dorsoventrally narrow. In the first rib, the *capitulum* and
297 *tuberculum* form a right angle whereas in the second one the *capitulum* and *tuberculum*
298 are anteriorly directed. By contrast, the last cervical rib is similar to the dorsal ribs but
299 its length is approximately half that of the first dorsal rib. It is ventrally directed,
300 lateromedially narrow and anteroposteriorly widened.

301

302 4.1.3. *Dorsal vertebrae*

303 The dorsal series preserves the first six vertebrae in articulation (Fig. 2 and 4). The
304 centra are spool-shaped, constricted at mid-length and rectangular in lateral view. The
305 dorsal centra show ventral keels, but they are less prominent than in those of the
306 cervicals. A similar ventral keel is also seen in *Yueosaurus tiantaiensis* Zheng, Jin,
307 Shibata, Azuma and Yu, 2012, *Changchunsaurus*, *Talenkauen*, *Notohypsilophodon*,
308 *Macrogryphosaurus*, *Hypsilophodon*, *Trinisaura santamartaensis* Coria, Moly,
309 Reguero, Santillana and Marensi, 2013, *Hexinlusaurus multidentis* Barrett, Butler and
310 Knoll, 2005 and *Jeholosaurus shangyuanensis* Xu, Wang and You, 2000, unlike in
311 *Koreanosaurus boseongensis* Huh, Lee, Kim, Lim and Godefroit, 2011, *Orodromeus*
312 *makelai* Horner and Weishampel, 1988 and *Oryctodromeus cubicularis* Varricchio,

313 Martin and Katsura, 2007 (Novas et al., 2004; Calvo et al., 2007; Huh et al., 2011;
314 Ibiricu et al., 2014). Their ventral surfaces are concave in lateral view. All dorsal
315 vertebrae have amphiplatyan centra with heart-shaped articular surfaces, as in
316 *Thescelosaurus*, *Talenkauen*, *Notohypsilophodon* and *Macrogyphosaurus* (Galton,
317 1974; Novas et al., 2004; Calvo et al., 2007; Ibiricu et al., 2014). The first and second
318 dorsal vertebrae are similar in anteroposterior length to the last cervical vertebra
319 (measurements in Supporting Information 2). Afterwards, the dorsal centra increase in
320 length posteriorly, as in basal ornithopods and the parksosaurid *Thescelosaurus*
321 (Norman et al., 2004; Brown et al., 2011). This contrasts with *Talenkauen* and
322 *Macrogyphosaurus*, in which the first dorsal vertebra is shorter than the last cervical
323 and posteriorly the length decreases, and with the parksosaurid *Orodromeus*, in which
324 the dorsal series decreases in length posteriorly (Scheetz, 1999; Cambiaso, 2007). As
325 the vertebrae are included in the matrix and are articulated, it is not possible to observe
326 the right side and measure their lateromedial width and dorsoventral height. As in the
327 case of the cervical vertebrae, the dorsal centra have neurocentral sutures that are not
328 entirely fused (Fig. 4 A and D). The dorsal vertebrae bear parapophyses above the
329 neurocentral suture. The height of the dorsal neural arch pedicels is low, as in most
330 ornithischians and unlike in stegosaurians (Han et al., 2017). The dorsal neural spines
331 are short, rectangular and lateromedially narrow; the dorsoventral height and
332 anteroposterior width are roughly similar, as in basal ornithopods but unlike in
333 iguanodontians, where the dorsoventral height is more than twice the anteroposterior
334 width (Han et al., 2017). By contrast, in *Talenkauen* and *Macrogyphosaurus* the neural
335 spine has a greater anteroposterior width than dorsoventral height (Cambiaso, 2007).
336 The second neural spine is rectangular in lateral view, unlike *Macrogyphosaurus*,
337 which does not show this shape until the third vertebra, and *Talenkauen*, until the fifth

338 vertebra (Cambiaso, 2007). The anteroposterior width increases posteriorly. The last
339 neural spine increases significantly in height, so it is almost as dorsoventrally high as
340 anteroposteriorly wide. This spine, though somewhat eroded, shows a widening on its
341 left side at the dorsal end that may be similar to the sixth dorsal vertebra of
342 *Thescelosaurus*, the last seven dorsal of *Hypsilophodon* and the posterior vertebrae of
343 *Talenkauen* (Galton, 1974; Cambiaso, 2007; Brown et al., 2011). The transverse
344 processes are short, robust and anteroposteriorly elliptical in cross-section. They lie at
345 the level of the zygapophyses, as is characteristic of basal ornithopods (Norman et al.,
346 2004). They are oriented laterally and slightly dorsally, as in most ornithischians and
347 unlike in thyreophorans, whose transverse processes are dorsolaterally oriented (i.e.
348 more than 40° above the horizontal; Han et al., 2017). The prezygapophyses are located
349 anteriorly to the base of the neural spine and the postzygapophyses are located in the
350 base. Articulation between the zygapophyses of the dorsal vertebrae is flat and smooth,
351 with a rounded outline, as is common in ornithischians (i.e. *Orodromeus* and
352 *Thescelosaurus*; Han et al., 2017) and unlike some ceratopsians (i.e. *Auroraceratops*
353 *rugosus* You, Li, Ji, Lamanna and Dodson, 2005; Han et al., 2017). The articular faces
354 of the prezygapophyses are upward and inward, whereas those of the postzygapophyses
355 are downward and outward. Finally, ossified epaxial tendons are present along the
356 vertebral column, as in other ornithopods (Han et al., 2017).

357

358 4.1.4. Dorsal ribs

359 Seven dorsal ribs are preserved in anatomical articulation (Fig. 2). The *tuberculum* is
360 greatly reduced and is represented only as a boss on the angle of the rib, as in
361 *Macrogyphosaurus* and *Thescelosaurus*, and unlike *Talenkauen*, whose most anterior
362 ribs have a well-developed *tuberculum* (Calvo et al., 2007; Cambiaso, 2007; Brown et

363 al., 2011). The third rib is the most complete, with a length of 425 mm (see Supporting
364 Information 2). In the third to fifth ribs, the anterior edge bears a lateral surface marked
365 with slight rugosities in the distal third (Fig. 2 A-C). This area is associated with the
366 articulation or juxtaposition of the intercostal plates (Fig. 2 A-C). The location of this
367 area differs with respect to other basal ornithopods (*Hypsilophodon*, *Parksosaurus*,
368 *Talenkauen*), in which the area is located on the posterior margin (Brown et al., 2011).
369 By contrast, this surface has not been observed in *Macrogyphosaurus* (Calvo et al.,
370 2007). The shafts of the dorsal ribs are anterolaterally to posteromedially compressed.
371 Unlike the dorsal ribs of *Macrogyphosaurus* and *Talenkauen*, in *Mahuidacursor* the
372 ribs do not present an anteroposterior thickening of their ventral half or end (Calvo et
373 al., 2007).

374

375 4.1.5. Intercostal plates

376 *Mahuidacursor* bears intercostal plates, as in *Lesothosaurus*, *Othnielosaurus consors*
377 Galton 2007, *Parksosaurus*, *Thescelosaurus*, *Hypsilophodon*, *Talenkauen* and
378 *Macrogyphosaurus* (see Boyd et al., 2011). There are four intercostal plates preserved,
379 which are in articulation with the contiguous dorsal ribs (Fig. 2 C). The anterior edge of
380 the intercostal plate is below the posterior edge of the dorsal rib, and the posterior edge
381 of the intercostal plate lies above the anterior edge of the dorsal rib. The posterior and
382 ventral edges of the plates are broken. These are lateromedially narrow and have a
383 rectangular outline, unlike the diamond-shaped plates of *Talenkauen* or the subcircular
384 plates of *Macrogyphosaurus* (Calvo et al., 2007; Cambiaso, 2007; measurements in
385 Supporting Information 2).

386

387 4.1.6. Scapula

388 Both scapulae are preserved and are fused with the coracoids (Fig. 5 A-B). Only the left
389 scapula is visible, due to the right scapula being hidden by the matrix. The left scapula
390 is anteroposteriorly straight and lateromedially narrow. It is slightly convex in lateral
391 view. It has a length of 410 mm, slightly shorter than the length of the humerus (440
392 mm; see Supporting Information 2). The condition of a humerus subequal to the
393 scapula, as present in *Mahuidacursor*, is common among ornithischians, but differs
394 from *Agilisaurus louderbacki* Peng 1990, *Hexinlusaurus*, *Gasparinisaura* and
395 *Talenkauen* (Cambiaso, 2007; Han et al., 2017). The scapula of *Mahuidacursor* is 30%
396 longer than that of *Talenkauen* and is half as wide at its anterior end as in *Talenkauen*
397 (Cambiaso, 2007). The ratio between the humerus length and scapula length is 1.07,
398 which is similar to other North American ornithopods (*Thescelosaurus neglectus*
399 USNM7757= 1.06-1.14; *Parksosaurus* ROM84= 1.02; *Scutellosaurus* P1.175= 1.1) and
400 *Anabisetia* (1.03), but diverges from *Talenkauen* (1.26; Cambiaso, 2007). The anterior
401 end is expanded, as in basal ornithopods and basal iguanodontians (Ibiricu et al., 2014).
402 The posterior end is clearly narrower than the anterior end as in basal styracosternans
403 (e.g. *Mantellisaurus*, Norman, 1986) and unlike *Talenkauen* (Cambiaso, 2007), where
404 the posterior end is only slightly narrower, and other basal ornithopods, where the
405 posterior end of the scapula is wider (e.g. *Hypsilophodon*, *Tenontosaurus*; Galton, 1974;
406 Tennant, 2010). The posterior end is asymmetrical and finishes between the third and
407 fourth dorsal vertebrae. The dorsal and ventral borders are divergent towards the distal
408 end, and as in *Dryosaurus* and all the more derived non-hadrosaurid iguanodontians the
409 scapula is flared distally (Norman, 2004). The posterior border is relatively straight,
410 similar to *Eocursor parvus* Butler, Smith, and Norman 2007, *Zalmoxes*, *Mantellisaurus*

411 and *Yinlong* and unlike basal ornithopods (i.e. *Hypsilophodon* or *Haya*), *Dryosaurus*,
412 *Tenontosaurus* and *Camptosaurus*; Han et al., 2017).

413 The scapula has an acromial process that is very well developed, as in *Talenkauen*,
414 *Anabisetia*, *Thescelosaurus*, *Camptosaurus* and some basal ornithopods (Galton 1974;
415 Cambiaso, 2007; Carpenter and Wilson, 2008). It has a dorsoventrally narrow neck that
416 is approximately 60.7% of the maximum width of the blade. This is different from the
417 robust scapula of *Talenkauen*, in which the width of the neck is approximately 41.25%
418 of the maximum width of the blade (Cambiaso, 2007).

419

420 4.1.7. Coracoid

421 Both coracoids are preserved and are co-ossified with the scapula (Fig. 5 A and C-D).
422 They are robust and subrectangular in shape, as in most of the basal ornithopods
423 (Norman et al., 2004). They are anteroposteriorly wide and lateromedially narrow,
424 similar to those in *Talenkauen* but not as wide as in the latter (Cambiaso, 2007;
425 Supporting Information 2). The lateral side is flat and the posterior border is strongly
426 convex, unlike the slightly sinuous border of *Talenkauen* (Cambiaso, 2007). A circular
427 coracoid foramen and an ellipsoidal concave area below are observed in the lateral side
428 as in *Talenkauen*, in which the concave area is slightly smaller and shallower. The
429 foramen does not directly contact the scapulocoracoid suture. Unlike in *Talenkauen*,
430 *Trinisaura*, *Thescelosaurus*, *Parksosaurus*, *Hypsilophodon*, *Haya*, *Changchunsaurus*
431 and *Orodromeus*, the posterior border of the coracoid is weakly concave between the
432 glenoid and the posteroventral tip of the coracoid (Gilmore, 1915; Parks, 1926; Galton,
433 1974; Scheetz, 1999; Cambiaso, 2007; Butler et al., 2011; Makovicky et al., 2011; Coria
434 et al., 2013). The posterior process of the coracoid is weakly hooked, unlike *Talenkauen*

435 and *Trinisaura*, which have a strongly developed hook, and like *Heterodontosaurus*,
436 *Stormbergia dangershoeki* Butler, 2005 and *Notohypsilophodon* (Butler, 2005;
437 Cambiaso, 2007; Coria et al., 2013; Ibiricu et al., 2014), in which the posterior process
438 of the coracoid is more rounded. The glenoid is smaller than the area of the suture with
439 the scapula.

440

441 4.1.8. Sternum

442 The two sternal plates are present and fused (Fig. 5 E-F). They are almost complete,
443 except for a small part of the posterior margin of both sternal plates and the end of the
444 posterior process of the left sternum (measurements in Supporting Information 2).

445 These plates are triradiate and hatchet-shaped, as in *Macrogyphosaurus*, *Lurdusaurus*
446 *arenatus* Taquet and Russell, 1999 and derived iguanodontians, and unlike the kidney-
447 shaped sternal plates of other basal ornithopods (i.e. *Hypsilophodon*, *Parksosaurus*,
448 *Tenontosaurus*; Galton, 1974a; Taquet and Russell, 1999; Norman, 2004; Norman et al.,
449 2004; Calvo et al., 2007; Han et al., 2017). The main body is projected anteroposteriorly
450 and is V-shaped. The anterior end of the main body is lateromedially narrower than the
451 posterior border, unlike *Lurdusaurus* and the more derived iguanodontians, where the
452 width of the main body is almost constant (Taquet and Russell, 1999; Norman, 2004).

453 The mid-posterior edges are markedly curved backward unlike in styracosternans,
454 where they curve forward and inward (i.e. *Iguanodon bernissartensis* (Boulenger,
455 1881), *Mantellisaurus atherfieldensis* (Hooley, 1925); Norman, 1980, 1986). Due to this
456 curvature, there are two deep concave zones, unlike the gentle concavities present in
457 *Iguanodon* and *Mantellisaurus* (Norman, 1980, 1986).

458 The anterior side is thick and rounded. The posterior processes curve backward and
459 outward. These are short and rod-shaped, unlike in *Lurdusaurus* and more derived
460 iguanodontians (Norman, 2004). As the two sternal plates are in anatomical connection
461 with the rest of the bones, only the ventral side can be observed. On this side, there is a
462 sagittal ridge in the fusion between the plates. The parascapular spine is absent, as is
463 common in ornithischians and unlike in *Huayangosaurus taibaii* Dong, Tang and Zhou
464 1982 (Dong et al., 1982).

465

466 4.1.9. Humerus

467 A complete right humerus was found in articulation with the ulna and radius (Fig. 6). It
468 is slender and long, and the shaft is relatively straight in anterior view, whereas it is
469 slightly sigmoid in profile. However, the humeral shaft is strongly laterally bowed (Fig.
470 6 A-B), as in *Talenkauen*, *Trinisaura*, *Anabisetia* and *Notohypsilophodon* (see Rozadilla
471 et al., 2016: Fig. 7) and unlike in most cerapodans, which usually have a rather straight
472 humeral shaft (i.e. *Hypsilophodon*, Galton, 1974: Fig. 28; *Haya*, Makovicky et al.,
473 2011: Fig. 3A).

474 The humerus is longer than the ulna, as is typical in basal ornithopods (the ulna is about
475 80% as long as the humerus; Norman et al., 2004; see Supporting Information 2). The
476 shaft is more slender than the humerus of *Talenkauen* (Novas et al., 2004). The anterior
477 and posterior borders are divergent at the proximal end. The anterior border is almost
478 straight whereas the posterior border is concave in lateral view. The proximal end is
479 anteroposteriorly wide and lateromedially flattened. The head of the humerus is in the
480 middle of the proximal end of the shaft in lateral view. It has a smooth and subspherical
481 articular surface that is poorly developed, in contrast to the strongly developed articular
482 surface in *Talenkauen* (Fig. 6 E). The deltopectoral crest is weakly developed, in the

483 form of an elongated, thickened edge that extends for approximately half the total length
484 of the humerus (Fig. 6 A-B). This is a feature that it shares with the members of the
485 clade Elasmaria *Talenkauen* and *Notohypsilophodon* and the iguanodontians *Anabisetia*
486 and *Gasparinisaura* but not with more developed ornithopods (i.e. *Thescelosaurus*,
487 *Dryosaurus*, *Camptosaurus*, *Iguanodon*; Novas et al., 2004). Distally, the crest merges
488 smoothly with the shaft and does not form a prominent angle on the humeral shaft. The
489 bicipital groove is shallow and wide in its proximal part. Below the crest the shaft is
490 subcircular in cross-section. The distal condyles are subequal in size, with a prominent
491 intercondylar groove.

492

493 4.1.10. Radius

494 The radius is complete and was found in articulation with the humerus, the ulna and the
495 carpals (Fig. 7). The radius is straight but the distal end appears to be weakly twisted
496 about its longitudinal axis. It is gracile, as in *Talenkauen*, *Anabisetia*, *Dryosaurus* and
497 basal ornithopods (Cambiaso, 2007). The length of the radius is about 70% that of the
498 humerus, as is typical in basal ornithopods (Norman et al., 2004; see Supporting
499 Information 2). It is slightly shorter than the ulna. Distally, the radial shaft is somewhat
500 twisted. Proximally, the shaft is ellipsoidal in cross-section; it is circular in the middle
501 and becomes more triangular distally. The proximal articular surface is slightly concave
502 and rugose. The distal articular surface has two concave areas for the articulation of the
503 carpal bones. As is characteristic of basal ornithopods, a shallow sulcus occupies the
504 proximal surface for articulation with the humerus (Norman et al., 2004). The medial
505 side of the shaft is convex and presents a ridge along almost all its length. The lateral
506 side of the shaft is flat, with an elongate facet for attachment to the ulna.

507

508 4.1.11. Ulna

509 A complete right ulna was found in articulation with the humerus, the radius and the
510 carpals (Fig. 8). In proximal view, the ulna is triangular in cross-section, with a
511 regularly convex lateral border, a concave medial border and a slightly concave anterior
512 articular border for the radius. The diaphysis is mediolaterally bowed in anterior view
513 and straight in medial view, similar to the iguanodontians *Zalmoxes*, *Iguanodon*,
514 *Ouranosaurus nigeriensis* Taquet, 1976 and *Camptosaurus* and unlike *Haya* and
515 *Tenontosaurus* (Galton, 1974; Taquet, 1979; Norman, 1980; Weishampel et al., 2003;
516 Tennant, 2010; Makovicky et al., 2011). It is slightly longer than the radius. The shaft is
517 roughly triangular in cross-section, with a concave medial surface. The proximal end is
518 anteroposteriorly wider than the distal end. The anterior process develops into a rounded
519 triangular crest that progressively merges with the ulnar shaft. The lateral process is less
520 developed. Between the anterior process and the lateral coronoid process there is a
521 shallow triangular depression into which the head of the radius fits in lateral view.

522 On the proximodorsal surface of the ulna, the articular facet for the proximal part of the
523 radius is large, triangular in shape and concave. The ulna progressively tapers distally.
524 The ulna has a weak olecranon process, a feature seen in *Notohypsilophodon* but not in
525 basal euornithopods (Martínez, 1998; Makovicky et al., 2011; Fig. 9A-B and E). The
526 distal surface articulates with the carpus and is moderately smooth and convex.

527

528 4.1.12. Hand

529 The right wrist and hand are preserved articulated and moderately complete, but
530 partially masked by sediment and dorsally collapsed (Fig. 8 and 9); the wrist is slightly
531 displaced from its anatomical contact with the ulna and radius.

532

533 *4.1.12.1. Carpals*

534 The carpals are ovoid, as in basal neornithischians (i.e. *Hexinlusaurus*, *Hypsilophodon*,
535 *Haya*; Galton, 1974; Barrett et al., 2005; Makovicky et al., 2011) and unlike the block-
536 shaped carpals of ankylopollexians (i.e. *Camptosaurus*, *Mantellisaurus*; Norman, 1986;
537 Carpenter and Wilson, 2008) and stegosaurians (i.e. *Stegosaurus*; Han et al., 2017). The
538 intermedium-ulnare articulation is free, as is common in ornithischians and unlike in
539 stegosaurs, where it is fused (i.e. Han et al., 2017). The articulation between the carpals
540 and metacarpal I is free, as in other basal ornithopods (i.e. *Hypsilophodon*; Galton,
541 1974) and unlike in ankylopollexians, where it is co-ossified as two blocks (i.e.
542 *Mantellisaurus*; Norman, 1986).

543

544 *4.1.12.2. Metacarpals*

545 Metacarpals of digits I to IV are preserved. The metacarpals are slender and
546 morphologically close to those of other basal ornithopods (i.e. *Hypsilophodon*; Galton,
547 1974), whereas they clearly differ from the metacarpals with block-like proximal ends
548 of ankylopollexians and heterodontosaurids (Butler et al., 2008; Han et al., 2017). The
549 metacarpals are sub-rounded in cross-section and lack extensor pits. Metacarpal I is
550 elongated and is more than 50% the length of metacarpal II, and metacarpal II is
551 subequal to metacarpal III in length (see Supporting Information 2), as is common in
552 ornithischians but unlike in ankylopollexians (Han et al., 2017).

553

554 *4.1.12.3. Phalanges*

555 The total phalangeal count of the digits cannot be determined, due to the loss of the
556 distal phalanges. The preserved phalanges lack extensor pits, as is common in
557 ornithischians (Han et al., 2017).

558

559 **5-HISTOLOGICAL ANALYSIS**

560 In order to assess the minimum age and ontogenetic growth stage of *Mahuidacursor*,
561 histological thin sections were made from one dorsal rib. Although the ontogenetic
562 stages of non-avian dinosaur specimens have usually been inferred from long bone
563 histology (i.e. Canale et al., 2016; Novas et al., 2018), dorsal ribs have recently been
564 demonstrated to be useful for at least minimum age estimation when long bones are not
565 available (i.e. Waskow and Sander, 2014; Waskow and Mateus, 2017). Since
566 *Mahuidacursor* preserves intercostal plates, we also include one of these in our
567 histological analysis. Its inclusion provides a good opportunity to study the histology of
568 these particular structures, allowing comparison with other taxa and testing previous
569 hypotheses about their origin (Boyd et al., 2011). An ossified tendon was also sampled
570 for histological analysis.

571 A total of five slides were analysed in the present study, one from the ossified tendon
572 and two from each of the other elements. The slides from the dorsal rib correspond to
573 transverse sections obtained from the proximal portion of the shaft and from the
574 *capitulum*. For the intercostal plate, two transverse (i.e. perpendicular to the rib axis)
575 sections were obtained.

576

577 *5.1. Histological description*

578 Dorsal rib: The rib has a compact cortex that surrounds a marrow cavity filled with
579 cancellous bone (Fig. 10 A-B). The cortical thickness is markedly reduced in the
580 *capitulum*. The transition between the perimedullary cortex and the cancellous bone is
581 rather distinct. The cancellous bone is secondary in origin, comprising different layers
582 of lamellar bone formed during different episodes of remodelling. The inner cortex is
583 also highly remodelled, exhibiting several generations of secondary osteons. This
584 remodelling is not homogeneous, being more pronounced in some areas than in others
585 where secondary osteons reach the outer cortex. The primary bone in the shaft consists
586 of well-vascularized fibrolamellar bone tissue (Fig. 10 B-C). The primary osteons are
587 longitudinally arranged, and their density tends to decrease in the outermost portion of
588 the cortex. The cortical bone exhibits Sharpey's fibres (Fig. 10 D), which are more
589 abundant and densely grouped in some areas (i.e. the anterolateral region in the shaft)
590 than in others. Lines of arrested growth (LAGs) and in some instances annuli are
591 recorded in both sections (Fig. 10 D). Whereas six LAGs are preserved in the shaft,
592 only four are recorded in the *capitulum*. Whereas the two innermost preserved LAGs in
593 the shaft are well spaced, the outer four are more closely grouped. Unlike those
594 observed in the shaft, the outermost preserved LAGs in the *capitulum* are formed in a
595 layer of almost avascular tissue, very similar to a thick annulus (Fig. 10 E). Immediately
596 before the outermost preserved LAG, a layer of well-vascularized fibrolamellar bone is
597 present (Fig. 10 F).

598 Intercostal plate: The cross-sections reveal a thin structure composed of two thin layers
599 of compact bone enclosing a thick band of cancellous bone (Fig. 10 G). The boundaries
600 between compact and cancellous bone are distinct. The bony trabeculae of the
601 cancellous bone are thin and formed by secondarily deposited lamellar tissue. The
602 cortical bone is formed by poorly vascularized parallel-fibred bone (Fig 10 H-I). Some

603 regions of the lateral cortex exhibit a degree of variation with regard to the intrinsic
604 fibre orientation. Although these fibres are mostly oriented in parallel to the outer
605 surface, they change their orientation from parallel to perpendicular to the
606 anteroposterior axis of the plate (Fig. 10 I). Secondary osteons are abundant in the
607 compacta (Fig. 10 J). At least three closely spaced LAGs are preserved. No noticeable
608 histological differences are found between the two cortices.

609 Ossified tendon: The only sampled tendon exhibits a compact appearance in cross-
610 section, which mostly corresponds with dense Haversian bone (Fig. 10 K). Several
611 superimposed generations of secondary osteons are longitudinally oriented. Remains of
612 primary bone tissue are preserved in the outermost region of the compacta (Fig. 10 L).
613 The primary bone is avascular and monorefringent under polarized light. The bone cell
614 lacunae are rounded or elongated, and circumferentially arranged. Poorly defined
615 growth marks are also discernible (Fig. 10 L).

616

617 **6-PHYLOGENETIC ANALYSIS**

618 To assess the phylogenetic relationships of *Mahuidacursor* and other Argentinean
619 ornithopods, we analysed the dataset proposed by Han et al., (2017), with the addition
620 of the taxa *Mahuidacursor*, *Macrogyphosaurus*, *Talenkauen*, *Notohypsilophodon* and
621 *Diluvicursor* as well as a new character in the matrix (see Supporting Information 1). At
622 present, *Mahuidacursor* can be coded for 9.5% of the morphological characters
623 included in the dataset (i.e. 37 out of 381 characters).

624 The character distribution was analysed with Mesquite 2.75 (Maddison and Maddison,
625 2010). The resulting matrix included 77 species-level taxonomic units (73 ingroup taxa
626 and 4 outgroups) coded across 381 characters which were treated as equally weighted,
627 and it was run with TNT v1.5 (Goloboff et al., 2008). Twenty-one characters (2, 23, 31,

628 39, 125, 163, 196, 203, 204, 222, 227, 238, 243, 247, 268, 292, 296, 302, 306, 320, 361)
629 were treated as ordered (additive) because they form transformation series. A new
630 character (381) was added: intercostal plates; 0, absence or 1, presence.

631 The most parsimonious trees were sought using the ‘New Technology Search’ option
632 with the ‘Sectional Search’, ‘Ratchet’, ‘Drift’ and ‘Tree Fusing’ options. The maximum
633 number of trees stored in memory was set to 10000. Bremer support values were
634 calculated using a Bremer Support script made by Goloboff (2008) with the default
635 setting (1000 replicates). The bootstrap values were calculated using the resampling
636 function of TNT, with the standard (sample with replacement) and traditional search
637 options and 1000 replicates, and the results were expressed as absolute frequencies.

638 166 most parsimonious trees were obtained with a tree length of 1232 steps, a
639 consistency index (CI) of 0.364 and a retention index (RI) of 0.706. The strict consensus
640 tree is presented in Fig. 11. As in Han et al. (2017), the strict consensus tree shows poor
641 resolution in some areas (Fig. 11).

642 The resulting topology resembles previously published hypotheses, with the exception
643 of the appearance of *Gideonmantellia amosanjuanae* Ruiz-Omeñaca, Canudo, Cuenca-
644 Bescós, G. Cruzado-Caballero, Gasca and Moreno-Azanza, 2012 as the closest
645 outgroup taxon to the taxa *Notohypsilophodon* and *Mahuidacursor* in polytomy and to
646 the sister clade Elasmaria (*Macrogryphosaurus* + *Talenkauen*), which is located as the
647 sister group to the clade Iguanodontia.

648 In our analysis, the group composed of the South American ornithopods
649 *Notohypsilophodon* + *Mahuidacursor* + [*Macrogryphosaurus* + *Talenkauen*] is defined
650 by the presence of two unambiguous synapomorphies in all trees: a rudimentary
651 deltopectoral crest that is at most a thickening on the anterolateral margin of the
652 humerus (character 277:1) and a humeral shaft that is strongly bowed laterally along its

653 length (character 280:1). There are also four unambiguous synapomorphies in some
654 trees: the anterior cervical centra with a ratio of length to height greater than 1.5
655 (character 234:0); sternal plates shafted or hatchet-shaped (rod-like posterolateral
656 process, expanded anterior end) (character 265:1); anterior trochanter that is broadened,
657 prominent, 'wing' or 'blade'-shaped, and subequal in anteroposterior width to the
658 greater trochanter (character 353:1); and the presence of intercostal plates (character
659 381:1). All of them are coded for *Mahuidacursor* except character 353.

660

661 7-DISCUSSION

662 The phylogenetic relationships among the basal members of Ornithopoda remain
663 tangled, as none of the recent hypotheses shows strong support values (Boyd, 2015;
664 Rozadilla et al., 2016; Baron et al., 2017; Herne et al., 2018). The conservative anatomy
665 shown by basal ornithopods, as well as the presence of large number of homoplasies
666 among most taxa (Butler et al., 2009; Rozadilla et al., 2016), makes it difficult to clarify
667 the presence of subclades. However, the special features observed in the forelimbs of
668 *Mahuidacursor* and certain other South American ornithopods (i.e. *Notohypsilophodon*,
669 *Talenkauen* and *Macrogyphosaurus*) help bring to light the existence of a
670 monophyletic clade.

671 The diversity of ornithopods in South America is not as great as in the northern
672 hemisphere but it is still possible to differentiate two distinct groups: a first group
673 formed by small-sized ornithopods such as *Gasparinisaura* and *Anabisetia*, and a
674 second group composed of medium-sized ornithopods such as *Notohypsilophodon* and
675 the clade Elasmaria. It is with the latter group that *Mahuidacursor* shows the greater
676 affinity. *Mahuidacursor* is a medium-sized ornithopod, with a morphotype that is more
677 slender than *Macrogyphosaurus* and *Talenkauen*, as can be observed in its longer

678 cervical and dorsal vertebrae. The elongation of the dorsal vertebrae entails an increase
679 in the length of the thorax and an increase in the space between the dorsal ribs, which is
680 uniquely covered by rectangular intercostal plates. This is unlike *Macrogyphosaurus*
681 and *Talenkauen*, which present an anteroposterior thickening of the dorsal ribs that
682 helps cover the space between the ribs. Moreover, *Mahuidacursor* has a deltopectoral
683 crest of the humerus and lateral process of the ulna that are weakly developed, which
684 may suggest a partial loss of forelimb movement or poor musculature. This would
685 imply a tendency to adopt a bipedal or poorly quadrupedal posture (Maidment et al.,
686 2012; Rozadilla et al., 2016). It would be in accordance with the presence of a slender
687 forelimb and a small hand, as in other medium-sized ornithopods considered bipedal
688 (*Notohypsilophodon*, *Parksosaurus*, *Talenkauen*, *Thescelosaurus*; Parks, 1926; Galton,
689 1974; Cambiaso, 2007; Ibiricu et al., 2014).

690 Furthermore, it has been proposed that the Argentinian elasmarians, along with other
691 closely related ornithopods from Gondwana, exhibit adaptations for a specialized
692 cursorial mode of life (Rozadilla et al., 2016; Herne et al., 2018). Of these anatomical
693 features, those located in the forearms (the bowed humerus and the poorly developed
694 deltopectoral crest) can be observed in *Mahuidacursor*. The absence of a tail or hind
695 limbs in the holotype of *Mahuidacursor* precludes the verification of additional
696 cursorial features (i.e. a slender and bunched foot with a narrow metatarsal IV,
697 expanded chevrons; Herne et al., 2018).

698 In addition to the above mentioned features, *Mahuidacursor* is well differentiated from
699 other ornithischians as well as from all other members of the South American
700 ornithopod clade by a wide set of anatomical features (i.e. dorsal ribs not distally
701 thickened and bearing a surface restricted to the most anterolateral margin for contact to
702 the preceding intercostal plate; first dorsal vertebra with rectangular dorsal neural spine;

703 first and second dorsal centra as long as the last cervical centrum; dorsal centra
704 relatively long, and increasing in length only moderately throughout the dorsal
705 sequence; posterior process of the coracoid scarcely developed; humerus length
706 subequal to the scapular length; long and slender scapula; posterior end of the scapular
707 blade narrower than the proximal end of the bone; poorly developed humeral head).

708 In the light of the histological analysis, the absence of an External Fundamental System
709 (i.e. a peripheral band of lamellar or parallel-fibred bone with closely packed growth
710 lines) in the sampled rib indicates that the individual was not somatically mature at the
711 time of death (Chinsamy-Turan, 2005). Microstructural changes in the compacta close
712 to the outer cortex (i.e. a reduction in the spacing between LAGs and a reduction in the
713 density of vascular spaces) suggest that the individual represented by the specimen had
714 nevertheless reached sexual maturity (Chinsamy-Turan, 2005). This combination of
715 microstructural features suggests that the individual corresponds to a sexually mature
716 subadult specimen. On the basis of the number of preserved LAGs, we infer a minimum
717 age of six years. The histological data are congruent with the presence of scars of the
718 neurocentral suture on the dorsal vertebrae, which indicates that skeletal maturity had
719 not been achieved at the moment of death.

720 Regarding the histological data from the intercostal plate, calcified cartilage is entirely
721 absent in *Mahuidacursor*. This contrasts with the data provided by Boyd et al. (2011)
722 for two specimens of *Thescelosaurus* sp. and *Hypsilophodon*. Such an absence was also
723 reported for *Talenkauen* (Boyd et al., 2011). The presence of calcified cartilage in the
724 intercostal plates of *Thescelosaurus* and *Hypsilophodon* was interpreted by Boyd et al.
725 (2011) as evidence for endochondral ossification in these elements. Although our data
726 do not support an endochondral origin for the intercostal plates, the absence of calcified
727 cartilage does not refute this hypothesis. As reported for *Talenkauen*, the high amount

728 of secondary cancellous bone in the intercostal plate reveals that the primary bone
729 formed in the element has been eroded.

730 In the case of the ossified tendon, the most noticeable feature reported in
731 *Mahuidacursor* is related to the nature of its primary bone. Unlike what is reported for
732 other ornithopod dinosaurs (i.e. Adams and Organ, 2005; Cerda et al., 2015), the
733 primary bone does not appear to be formed by coarse bundles of mineralized
734 collagenous fibres oriented in parallel to the main axis of the tendon. Such fibres can be
735 easily individualized under polarized light because they are delineated by thin bright
736 lines. Although the primary extracellular matrix in the *Mahuidacursor* tendon is also
737 monorefringent in cross-section, it is not possible to recognize individual mineralized
738 fibres. The unexpected histological variation observed in the *Mahuidacursor* tendon
739 with regard to other ornithopod dinosaurs may be attributed to various, not mutually
740 exclusive causes (i.e. the pattern of formation, ontogenetic stage). Given the high degree
741 of secondary remodelling in the sample, it is not possible at the moment to determine
742 the causes of the observed histological variations.

743

744 **8-CONCLUSION**

745 The articulated fossil remains of an ornithopod found in the Santonian Cerro Overo site
746 near Rincón de los Sauces (Neuquén Province, Argentina) reveal the presence of a new
747 taxon, *Mahuidacursor lipanglef*.

748 *Mahuidacursor* is a gracile, medium-bodied ornithopod with a slender forelimb.

749 Judging by the histological data, the holotype specimen corresponds to a sexually
750 mature but not fully grown individual. *Mahuidacursor* is a member of an unnamed
751 clade together with the South American ornithopods *Notohypsilophodon*,

752 *Macrogryphosaurus* and *Talenkauen*. This clade is defined by two unambiguous
753 synapomorphies in all trees and four unambiguous synapomorphies in some trees.
754 Furthermore, *Mahuidacursor* is well differentiated from other South American basal
755 ornithopods by a broad set of characters.

756

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768

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1074 Figure captions

1075 Figure 1. Map showing the location of the Cerro Overo site (Rincón de los Sauces,
1076 Neuquén, Argentina). (1 column / 80mm wide)

1077

1078 Figure 2. Holotype of *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) in
1079 left lateral (A-B) and dorsal (D) views. Detail of the intercostal plates in (C).
1080 Abbreviations: aa, articulation area; dr, dorsal rib; ip, intercostal plate. Scale bar: 5 cm.
1081 (2 columns / 166 mm wide)

1082

1083 Figure 3. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) articulated
1084 cervical vertebrae in left lateral (A) and dorsal (B) views. Isolated cervical vertebra in
1085 right and left lateral (C-D), anterior (E), dorsal (F), ventral (G) and posterior (H) views.
1086 Abbreviations: cr, cervical rib; nc, neural canal; ns, neural spine; poz,
1087 postzygapophyseal process; prz, prezygapophyseal process; vk, ventral keel. Scale bar:
1088 5 cm. (2 columns / 166 mm wide)

1089

1090 Figure 4. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) articulated dorsal
1091 vertebrae in left lateral (A) and dorsal (B) views. Isolated dorsal vertebra in right and
1092 left lateral (C-D), anterior (E), dorsal (F), ventral (G) and posterior (H) views.
1093 Abbreviations: nc, neural canal; ns, neural spine; poz, postzygapophysis; tp, transverse
1094 process. Scale bar: 5 cm. (2 columns / 166 mm wide)

1095

1096 Figure 5. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) pectoral girdle.
1097 Left scapula in lateral (A-B) view. Right and left coracoids in anterior (C-D) view.
1098 Right and left sternal plate in anterior (E-F) views. Abbreviations: acf, articular coracoid
1099 facet; cf, coracoid foramen; dr, deltoid ridge; g, glenoid; gf, glenoid fossa; pp, posterior
1100 process; sr, sagittal ridge; vp, ventral process. Scale bar: 5 cm. (2 columns / 166 mm
1101 wide)

1102
1103 Figure 6. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right humerus in
1104 medial (A), lateral (B), posterior (C), anterior (D), proximal (E) and distal (F) views.
1105 Abbreviations: hh, humeral head; rc, radial condyle; uc, ulnar condyle. Scale bar: 5 cm.
1106 (2 columns / 166 mm wide)

1107
1108 Figure 7. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right radius in
1109 anterior (A), posterior (B) and medial (C) views. Scale bar: 5 cm. (1 column / 80 mm
1110 wide)

1111
1112 Figure 8. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right ulna and
1113 hand in posterior (A), anterior (B), lateral (C), medial (D) and proximal (E) views.
1114 Abbreviations: dc, distal condyle; dfr, distal face for radius; lp, lateral process; mp,
1115 medial process; op, olecranon process. Scale bar: 5 cm. (2/3 columns / 110 mm wide)

1116

1117 Figure 9. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right manus in
1118 dorsal (A-B) and ventral (C-D) views. Abbreviations: mc, metacarpal; I, II, III, IV, V,
1119 digits I, II, III, IV, V. Scale bar: 5 cm. (1 column / 80mm wide)

1120

1121 Figure 10. Bone histology of *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-
1122 596) dorsal rib (A-F), intercostal plate (G-J) and ossified tendon (K, L). Arrowheads in
1123 all the pictures indicate the presence of lines of arrested growth. A, C, E, H, I, K: cross-
1124 polarized light with lambda compensator; B, F, G, L: plane-polarized light; D: cross-
1125 polarized light; J: normal transmitted light. (A) General view of the proximal shaft of
1126 the rib in cross-section showing the distribution of the compact and cancellous bone.
1127 (B) Detail of compact bone (square inset in A). (C) Detail of the primary tissue
1128 composed of fibrolamellar bone (square inset in B). Scattered secondary osteons in
1129 different stages of development are observed toward the inner region. (D) Abundant
1130 Sharpey's fibres in the outer cortex. (E) General view of the compact and cancellous
1131 bone of the rib at the level of the *capitulum*. (F) Detailed view (square inset in E) of the
1132 external cortex. Note the major histological variation in the compact bone tissue. (G)
1133 General view of the intercostal plate in transverse section. (H) Detail of the cortical
1134 bone in the lateral cortex (square inset at the bottom of G). (I) Detail of the cortical bone
1135 in the medial cortex (square inset at the top of G). Note the variable orientation of the
1136 intrinsic fibres. (J) Detail of the secondary osteons in the cortical bone. (K) General
1137 view of the highly remodelled tissue of the ossified tendon. (L) Remains of primary
1138 bone preserved in the outer cortex (square inset in K). Abbreviations: bt, bony
1139 trabeculae; its, intertrabecular space; ms, medial surface; ls, lateral surface; lsf,
1140 longitudinally sectioned fibres; lvs, longitudinally oriented vascular spaces; Sf,

1141 Sharpey's fibres; so, secondary osteons; tsf, transversally sectioned fibres. (2 columns /
1142 166 mm wide)

1143

1144 Figure 11. Strict consensus of 166 most parsimonious trees resulting from the 'New
1145 Technology Search' implemented in TNT, showing the suggested systematic position of
1146 *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) within Ornithopoda.
1147 Numbers above the branches are Bremer support values and numbers beneath the
1148 branches represent bootstrap values after 1000 replicates. Bootstrap values lower than
1149 20 are not shown. (2 columns / 166 mm wide)

1150

