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A new ornithopod dinosaur from the Santonian of Northern Patagonia (Rincón de 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 inclunding*Rinconsaurus caudamirus* Calvo and Riga, 2003, *Bonitasaura salgadoi*

70 Apesteguía, 2004, *Petrobrasaurus puestohernandezi* 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

2-GEOLOGICAL SETTING

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

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

The site where these remains were first found is located in what is currently the university campus of the Universidad Nacional del Comahue in Neuquén, the capital city of the province of Neuquén. Over the decades, a great variety of fossils have been recovered from this location, noteworthy among which are the remains of small abelisaurids and alvarezsaurids (Bonaparte, 1991; Martinelli and Vera, 2007), crocodiles (Bonaparte, 1991; Fiorelli and Calvo, 2007; Martinelli and Pais, 2008), snakes (Caldwell and Albino, 2001), as well as bird remains and bird eggs (Chiappe and Calvo, 1994; 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, Macrogryphosaurus*

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 *Macrogryphosaurus* in the concave

227   profile of the ventral side of the cervical centra in *Macrogryphosaurus* as well as in the

228   proportions of the cervical centra (i.e., wider than high in Macrogryphosaurus. as wide

229   as high in Mahuidacursor) and the neural spine of the last cervical (i.e., height

230   significantly increasing in *Macrogryphosaurus* 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 *Macrogryphosaurus*); 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 Macrogryphosaurus

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*, *Macrogryphosaurus* 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*, *Macrogryphosaurus* 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* Nopcsa, 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 *Macrogryphosaurus, 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 *Macrogryphosaurus* (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*, *Macrogryphosaurus*, *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 Charning, 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 *Macrogryphosaurus* 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 *Macrogryphosaurus* 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 45º and 30º. 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

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

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 Marenssi, 2013, *Hexinlusaurus multidens* 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 *Macrogryphosaurus* (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   *Macrogryphosaurus*, 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 *Macrogryphosaurus* 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 *Macrogryphosaurus*,

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 *Macrogryphosaurus* 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 *Macrogryphosaurus* (Calvo et al.,

370 2007). The shafts of the dorsal ribs are anterolaterally to posteromedially compressed.

371 Unlike the dorsal ribs of *Macrogryphosaurus* 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 *Macrogryphosaurus* (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 *Macrogryphosaurus* (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 *Macrogryphosaurus*, *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

4.1.12.1. Carpals

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

4.1.12.2. Metacarpals

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

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*, *Macrogryphosaurus*, *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', 'Rachet', '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 *Macrogryphosaurus*) 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 *Macrogryphosaurus* 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 *Macrogryphosaurus*

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

757 **9-ACKNOWLEDGEMENT**

768

769   **10-REFERENCES**

770   Alvarenga, H., Bonaparte, J.F. 1992. A new flightless land-bird from the Cretaceous of

771   Patagonia. In: K.E. Campbell (Ed.), Papers in Avian Paleontology. Natural

772   History Museum of Los Angeles County, Science Series 36, 51-64.

773   Apesteguía, S. 2004. Bonitasaura salgadoi gen. et sp. nov.: a beaked sauropod from the

774   Late Cretaceous of Patagonia. Naturwissenschaften 91, 493-497.

775   Barrett, P.M.., Butler, R.J, Knoll, F. 2005. Small-bodied ornithischian dinosaurs from

776   the Middle Jurassic of Sichuan, China. Journal of Vertebrate Paleontology 25,

777   823-834.

778   Baron M.G., Norman D.B., Barrett P.M. 2017 Postcranial anatomy of Lesothosaurus

779   diagnosticus (Dinosauria: Ornithischia) from the Lower Jurassic of southern

780   Africa: implications for basal ornithischian taxonomy and systematics.

781   Zoological Journal of the Linnean Society 179, 125-168. doi:

782   10.1111/zoj.12434

783   Bonaparte, J.F. 1991. Los vertebrados fósiles de la Formación Río Colorado, de la

784   ciudad de Neuquén y cercanías, Cretácico superior, Argentina. Revista del

785   Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Paleontología

786   4 (3), 17-123.

787   Boulenger, G.A. 1881. Sur l'arc pelvien chez les dinosauriens de Bernissart. Bulletin de

788   l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 3 (1),

789   600-608.

790   Boyd, C.A. 2015. The systematic relationships and biogeographic history of

791   ornithischian dinosaurs. PeerJ 3, e1523; DOI 10.7717/peerj.1523

792   Boyd, C.A., Clealand, T.P., Novas, F. 2011. Osteogenesis, homology, and function of

793   the intercostal plates in ornithischian dinosaurs (Tetrapoda, Sauropsida).

794   Zoomorphology 130, 305-313.

795   Brown, C.M., Boyd, C.A., Russell, A.P. 2011. A new basal ornithopod dinosaur

796   (Frenchman Formation, Saskatchewan, Canada), and implications for late

797   Maastrichtian ornithischian diversity in North America. Zoological Journal of

798   the Linnean Society 163, 1157-1198

799   Butler, R.J. 2005. The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot

800   Formation (Lower Jurassic) of South Africa and Lesotho. Zoological Journal of

801   the Linnean Society 145 (2), 175-218.

802   Butler, R.J., Galton, P.M., Porro, L.B., Chiappe, L.M., Henderson, D.M., Erickson,

803   G.M. 2009. Lower limits of ornithischian dinosaur body size inferred from a

804   new Upper Jurassic heterodontosaurid from North America. Proceedings of the

805   Royal Society B 277, 375e381.

806   Butler, R.J., Liyong, J.., Jun, C, Godefroit, P. 2011.The postcranial osteology and

807   phylogenetic position of the small ornithischian dinosaur Changchunsaurus parvus

808   from the Quantou Formation (Cretaceous, Aptian-Cenomanian) of Jilin

809   Province, north-eastern China. Palaeontology 54 (3), 667-683.

810   Butler, R.J., Smith, R.M.H., Norman, D.B. 2007. A primitive ornithischian dinosaur

811   from the Late Triassic of South Africa, and the early evolution and

812   diversification of Ornithischia. Proceedings of the Royal Society B: Biological

813   Sciences.

814   Caldwell, M.W., Albino, A.M. 2001. Palaeoenvironment and palaeoecology of three

815   Cretaceous snakes: Pachyophis, Pachlyrhachis, and Dinilysia. Acta

816   Palaeontologica Polonica 46, l-86.

817   Calvo, J.O., González Riga, B.J. 2003. Rinconsaurus caudamirus gen. et sp nov., a new

818   titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia,

819   Argentina. Revista Geológica de Chile, 30 (2), 333-353. Calvo, J., Porfiri, J.D.,

820   Novas, F.E. 2007. Discovery of a new ornithopod dinosaur from the Portezuelo

821   Formation (Upper Cretaceous), Neuquén, Patagonia, Argentina. Arquivos do

822   Museu Nacional, Rio de Janeiro 65, 471-483.

823   Cambiaso, A.V. 2007. Los ornitópodos e iguanodontes basales (Dinosauria,

824   Ornithischia) del Cretácico de Argentina y Antártida. Tesis de la Universidad de

825   Buenos Aires, 412pp.

826   Canale, J.I., Cerda, I.A., Novas, F.E., Haluza, H. 2016. New small-sized abelisaurid

827   (Theropoda: Ceratosauria) from the early Late Cretaceous of northwest

828   Patagonia, Argentina. Cretaceous Research 62, 18-28.

829   Cazau, L.B., Uliana, M.A. 1973. El Cretácico superior continental de la Cuenca

830   Neuquina. 5° Congreso Geológico Argentino. Actas, 3, 131-163.

831   Cerda, I..A., Casal, G.A., Martinez, R.D., Ibiricu, L,M. 2015 Histological evidence for a

832   supraspinous ligament in sauropod dinosaurs. The Royal society Open Science

833   2, 150369. http://dx.doi.org/10.1098/rsos.150369

834   Chiappe, L.M., Calvo, JO. 1994 Neuquenornis volans, a new Late Cretaceous bird

835   (Enantiornithes: Avisauridae) from Patagonia, Argentina. Journal of Vertebrate

836   Paleontology 14 (2). 230-246

837 Chinsamy, A. 2005. The microstructure of dinosaur bone: deciphering biology with

838   fine-scale techniques. John Wiley and Sons.

839 Chinsamy, A, Raath, M.A., 1992. Preparation of fossil bone for histological

840   examination. Palaeontologia Africana 29, 39-44.

841 Coria, R., Calvo, J.O. 2002. A new iguanodontian ornitthopod from Neuquen basin,

842   Patagonia, Argentina. Journal of Vertebrate Paleontology 22 (3), 503-509.

843 Coria, R., Salgado, L. 1996. A basal iguanodontian (Ornithischia: Ornithopoda) from

844   the Late Cretaceous of South America. Journal of Vertebrate Paleontology 16,

845   445-457.

846 Coria, R., Filippi, L.S., Chiappe, L.M., García, R., Arcucci, A.B. 2013. Overosaurus

847   paradasorum gen. et sp. nov., a new sauropod dinosaur (Titanosauria:

848   Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina.

849   Zootaxa 3683 (4), 357-376.

850 Coria, R.., Moly, J.J, Reguero, M.., Santillana, S, Marenssi, S. 2013. A new ornithopod

851   (Dinosauria; Ornithischia) from Antarctica. Cretaceous Research 41, 186-193.

852 Crompton, A.W.., Charig, AJ. 1962. A new ornithischian from the Upper Triassic of

853   South Africa. Nature 196, 1074-1077.

854 Cruzado-Caballero, P, Filippi, L.S., Méndez, A.H., Garrido, A.C., Juárez Valieri, R.D.

855   2016. New record of ornithopod dinosaur from the Plottier Formation (Upper

856   Cretaceous), Patagonia, Argentina. Annales de Paléontologie 102, 145-150.

857 Cruzado-Caballero, P, Filippi, L.S., Méndez, A.H., Garrido, A.C., Díaz-Martínez, I.

858   2018. First ornithopod remains from Bajo de la Carpa Formation (Santonian,

859   Upper Cretaceous), northern Patagonia, Argentina. A new view about the

860   biodiversity of Late Cretaceous South American ornithopods. Cretaceous

861   Research 83, 182-193.

862   Cruzado-Caballero, P., Méndez, A.H., Filippi, L.S., Juárez Valieri, R.D., Garrido, A.C.

863   2016b. Palaeobiodiversity of the Bajo de la Carpa Formation (Santonian, Upper

864   Cretaceous) in the Cerro Overo-La Invernada area, northern Patagonia,

865   Argentina. VII Jornadas Internaciones sobre Paleontología de Dinosaurios y su

866   Entorno. Libro de Resúmenes, 53–55. Sala de los Infantes, Burgos (Spain).

867   Doering, A. 1882. Geología. In: Informe oficial de la Comisión agregada al Estado

868   Mayor General de la Expedición al Río Negro (Patagonia) realizada en los

869   meses de Abril, Mayo y Junio de 1879, bajo las órdenes del General Julio A.

870   Roca. III Parte, Geología 299-530pp.

871   Dollo, L. 1888. Iguanodontidae et Camptonotidae. Comptes Rendus de Academie des

872   Sciences (Paris) CVI, 775-777.

873   Dong, Z., Tang, Z., Zhou, S. 1982. Note on the new Mid-Jurassic stegosaur from

874   Sichuan Basin, China. Vertebrata PalAsiatica 20, 83-87.

875   Fernández M.S., García, R.A., Fiorelli, L., Scolaro, A., Salvador, R.B., Cotaro, C.N..,

876   Kaiser, GW., Dykes, G.J. 2013. A Large Accumulation of Avian Eggs from the

877   Late Cretaceous of Patagonia (Argentina) Reveals a Novel Nesting Strategy in

878   Mesozoic Birds. PLoS ONE 8, 4, e61030.

879   Filippi, L. 2015. Los dinosaurios sauropoda del Cretácico Superior del norte de la

880   Cuenca Neuquina, Patagonia, Argentina. Boletín del Instituto de Fisiografía y

881   Geología 58, 19-28.

882   Filippi, L.S., Canudo, J.I., Salgado, L., Garrido, A., García, R., Cerda, I., Otero, A.

883   2011. A new sauropod from the Plottier Formation of Patagonia (Argentina).

884   Geologica Acta 9 (1), 1-12.

885   Filippi, L., Martinelli, A.G., Garrido, A.C. 2015. Una nueva asociación de dientes de

886   vertebrados para la Formación Bajo de la Carpa (Santoniense, Cretácico

887   Superior) en Rincón de los Sauces, Neuquén, Argentina. Spanish. Journal of

888   Palaeontology 30 (2), 223-238.

889   Filippi, L.., Méndez, AH., Juárez Valieri, R.D., Garrido, A.C. 2016. A new

890   brachyrostran with hypertrophied axial structures reveals an unexpected

891   radiation of latest Cretaceous abelisaurids. Cretaceous Research 61, 209-219.

892   Filippi, L., Méndez, A.H., Gianechini, F.A., Juárez Valieri, R.D., Garrido, A.C. 2018.

893   Osteology of Viavenator exxoni (Abelisauridae; Furileusauria) from the Bajo de

894   la Carpa Formation, NW Patagonia, Argentina. Cretaceous Research 83, 95-119.

895   Fiorelli, L., Calvo, J.O. 2007. The first "Protosuchian" (Archosauria: Crocodyliformes)

896   from the Cretaceous (Santonian) of Gondwana. Arquivos do Museu Nacional 65

897   (4), 417–459.

898   Francillon-Vieillot, H., De Buffrénil, V., Castanet, J., Geraudie, J.., Meunier, FJ. 1990.

899   Microstructure and mineralization of vertebrate skeletal tissues. In: Carter, J.G.

900   (Ed.), Skeletal biomineralization: patterns, processes and evolutionary trends,

901   vol. 1. Van Nostrand Reinhold, New York, pp. 471–530.

902   Galton, P.M. 1974a. The ornithischian dinosaur Hypsilophodon (Huxley, 1869) from

903   the Wealden of the Isle of Wight. Bulletin of the British Museum (Natural

904   History) Geology 25, 1-152.

905   Galton, P.M. 1977. The ornithopod dinosaur Dryosaurus and a Laurasia-Gondwanaland

906   connection in the Upper Jurassic. Nature 268, 230-232.

907   Galton, P.M. 1978. Fabrosauridae, the basal family of ornitischian dinosaurs (Reptilia:

908   Ornitischia). Paläontologische Zeitschrift 52 (1/2), 138-159.

909   Galton, P.M. 2007. Teeth of ornithischian dinosaurs (mostly Ornithopoda) from the

910   Morrison Formation (Upper Jurassic) of the Western United States. In: K.

911   Carpenter (ed.), Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs.

912   Indiana University Press, Bloomington, In: K. Carpenter (ed.), Horns and Beaks:

913   Ceratopsian and Ornithopod Dinosaurs. Indiana University Press, Bloomington,

914   17-47.

915   Garrido, A.C., Calvo, J.O. 2004. Reasignación litoestratigráfica de los niveles

916   portadores de Megaloolithus patagonicus Calvo et al., (Dinosauria: Sauropoda)

917   en las bardas de la ciudad de Neuquén. Ameghiniana (Suplemento) 41 (4), 47R.

918   Gazzera, C.E., Calvo, J.O. 1991. Asignación de los estratos de la Formación La Balsa a

919   la Formación Río Colorado, Senoniano de la Cuenca Neuquina. Ameghiniana 28

920   (3-4), 408.

921   Gilmore, C.W. 1913. A new dinosaur from the Lance Formation of Wyoming.

922   Smithsonian Miscelanea Collection 61, 1-5.

923   Goloboff, P., Farris, J.C., Nixon, K.C. 2008. TNT, a free program for phylogenetic

924   analysis. Cladistics 24, 774-786.

925   Han, F., Forster, C.A., Xu, X.., Clark, JM. 2017. Postcranial anatomy of Yinlong

926   downsi (Dinosauria: Ceratopsia) from the Upper Jurassic Shishugou Formation

927   of China and the phylogeny of basal ornithischians. Journal of Systematic

928   Palaeontology 1-29.

929   Heredia, S., Calvo, J.O. 1997. Sedimentitas eólicas en la Formación Río Colorado

930   (Grupo Neuquén) y su relación con la fauna del Cretácico superior.

931   Ameghiniana 34 (1), 120.

932   Heredia, S., Calvo, J.O. 2002. Estratigrafía de las bardas de la ciudad de Neuquén,

933   Argentina. 15° Congreso Geológico Argentino. Actas, 699-705.

934   Herne, M.C., Tait, A.M., Weisbecker, V., Hall, M., Nair, J.P., Cleeland, M., Salisbury,

935   S.W. 2018. A new small-bodied ornithopod (Dinosauria, Ornithischia) from a

936   deep, high-energy Early Cretaceous river of the Australian–Antarctic rift system.

937   PeerJ 5:e4113

938   Horner, J.R., Weishampel, D.B. 1988. A comparative embryological study of two

939   ornitischian dinosaurs. Nature 332, 256-257.

940   Huh, M., Lee, D.-G., Kim, J.-K.., Lim, J-D., Godefroit, P. 2011. A new basal

941   ornithopod dinosaur from the Upper Cretaceous of South Korea. Neues Jahrbuch

942   für Geologie und Paläontologie, Monatshefte 259/1, 1-24.

943   Huxley, T.H. 1869. On Hypsilophodon, a new genus of Dinosauria. Proceedings of the

944   Geological Society of London 204, 3-4.

945   Ibiricu, L.M., Martínez, R.D., Luna, M., Casal, G.A. 2014. A reappraisal of

946   Notohypshilophodon comodorensis (Ornithischia: Ornithopoda) from the Late

947   Cretaceous of Patagonia, Argentina. Zootaxa 3786 (4), 401-422.

948   Irmis, R.B. 2007 Axial skeleton ontogeny in the Parasuchia (Archosauria:

949   Pseudosuchia) and its implications for ontogenetic determination in archosaurs.

950   Journal of Vertebrate Paleontology 27, 350-361.

951   Jiménez-Gomis, C., Cruzado-Caballero, P., Gasca, J.M., Filippi, L. *in press*. New

952   fossils of ornithopod dinosaurs from the Santonian (Upper Cretaceous) of the

953   Bajo de la Carpa Formation of North Patagonia (Neuquén, Argentina).

954   Geogaceta 63

955   Leanza, H., Apesteguia, S., Novas, F.E., De La Fuente, M.S. 2004. Cretaceous

956   terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod

957   assemblages. Cretaceous Research 25, 61-87.

958   Maddison, W.P., Maddison, D.R. 2010. Mesquite: a modular system for evolutionary

959   analysis. Version 2:73. Available at mesquiteproject.org. Accessed May 30,

960   2012.

961   Makovicky, P.J., Kilbourne, B.M., Sadleir, R.W., Norell, M.A. 2011. A new basal

962   ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia.

963   Journal of Vertebrate Paleontology 31 (3), 626-640.

964   Marsh, O.C. 1879. Notice of new Jurassic reptiles. American Journal of Science Serie 3

965   18, 501-505.

966   Marsh, O.C. 1887. Principal characters of American Jurassic dinosaurs. Pt. IX. The

967   skull and dermal armor of Stegosaurus. American Journal of Science Serie 3 34,

968   413-417.

969   Marsh, O.C.1894. The typical Ornithopoda of the American Jurassic. American Journal

970   of Science Serie 3 48, 85-90.

971 Martinelli, A.G., Vera, E.I. 2007. Achillesaurus manazzonei, a new alvarezsaurid

972   theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation,

973   Río Negro Province, Argentina. Zootaxa 1582, 1-17.

974 Martinelli, A.G., Pais, D.F. 2008. A new baurusuchid crocodyliform (Archosauria) from

975   the Late Cretaceous of Patagonia (Argentina). Comptes Rendus Paleovol 7 (6),

976   371-381.

977 Martínez, R. 1998. Notohypsilophodon comodorensis gen. et sp. nov. Un

978   Hypsilophodontidae (Ornithischia, Ornithopoda) del Cretácico Superior de

979   Chubut, Patagonia Central. Acta Geológica Leopoldensia 21 (46/47), 119-135.

980 Nopcsa, F. 1899. Dinosaurierreste aus Siebenbürgen (Schädel von Limnosaurus

981   transsylvanicus nov. gen. et spec.), Denkschriften der Kaiserlichen Akademie

982   der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 68, 555-591.

983 Norman, D.B. 1980. On the ornithischian dinosaur Iguanodon bernissartensis from

984   Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 178,

985   1-103. Norman, D.B. 1986. On the anatomy of Iguanodon atherfieldensis

986   (Ornithischia: Ornithopoda). Bulletin de l'Institut Royal des Sciences Naturelles

987   de Belgique 56, 281-372.

988 Norman, D.B. 2004. Basal Iguanodontia, In: Weishampel, D.B., Dodson, P., Osmólska,

989   H. (Eds.), The Dinosauria, Second Edition. University of California Press,

990   Berkeley, pp. 413–437.

991 Norman, D.B., Sues, H.D., Witmer, L.M., Coria, R.A. 2004. Basal ornithopoda, In:

992   Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, Second

993   Edition. University of California Press, Berkeley, pp. 393–412.

994 Novas, F.E., Cambiaso, A.V., Ambrosio, A. 2004. A new basal iguanodontian
995   (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia.
996   Ameghiniana 41 (1), 75-85.

997 Novas, F.E., Agnolin F., Brissón Egli F., Gianechini F., Cerda I.A. 2018. Osteology of a
998   new specimen of Buitreraptor gonzalezorum (Theropoda, Coelurosauria).
999   Cretaceous Research 83, 127-167.

1000 Organ C.L., Adams J. 2005. The histology of ossified tendons in dinosaurs. Journal of
1001   Vertebrate Paleontolgy 25, 602-613.

1002 Ostrom, J.H. 1970. Stratigraphy and Paleontology of the Cloverly Formation (Lower
1003   Cretaceous) of the Bighorn Basin Area, Wyoming and Montana. Peabody
1004   Museum of Natural History, Yale University, 35, 234 p.

1005 Owen, R. 1861. A monograph of the fossil Reptilia of the Lias Formations. I.
1006   Scelidosaurus harrisonii. Palaeontographical Society Monographs, Part 1, 1-14.

1007 Parks, W.A. 1922. Parasaurophus walkeri, a new genus and species of crested
1008   trachodont dinosaur. Geological Series 13, 1-32.

1009 Peng G. 1990. A new small ornithopod (Agilisaurus louderbacki gen. et sp. nov.) from
1010   Zigong, China. Newsletter of the Zigong Dinosaur Museum 2, 19-27.

1011 Roth, S. 1898. Apuntes sobre la geología y paleontología de los territorios del Río
1012   Negro y Neuquén. Revista Museo de La Plata 9, 1-56.

1013 Rozadilla, S., Agnolin, F. L., Novas, F. E., Aranciaga Rolando, A. M., Motta, M. J.,
1014   Lirio, J. M., Isasi, M. P. 2016. A new ornithopod (Dinosauria, Ornithischia)
1015   from the Upper Cretaceous of Antarctica and its palaeobiogeographical
1016   implications. Cretaceous Research 57, 311-324.

1017 Ruiz-Omeñaca, J.I., Canudo, J.I., Cuenca-Bescós, G., Cruzado-Caballero, P., Gasca,

1018   J.M., Moreno-Azanza, M. 2012. A new basal ornithopod dinosaur from the

1019   Barremian of Galve, Spain. Comptes Rendus Palevol 11 (6), 435-444.

1020 Sánchez, M.L., Gómez, M.J., Heredia, S. 2006. Sedimentología y paleoambientes del

1021   Subgrupo Río Colorado (Cretácico Superior), Grupo Neuquén, en las bardas de

1022   la ciudad de Neuquén y alrededores. Revista de la Asociación Geológica

1023   Argentina 61 (2), 236-255.

1024 Scheetz, R.D. 1999. Osteology of Orodromeus makelai and the phylogeny of basal

1025   ornithopod dinosaurs. Ph.D. Thesis Montana State University - Bozeman206 p.

1026 Schweitzer, M.H., Jackson, F.D., Chiappe, L.M., Schmitt, J.G.., Calvo, J.O., Rubilar,

1027   D.E. 2002. Late Cretaceous avian eggs with embryos from Argentina. Journal of

1028   Vertebrate Paleontology 22 (1), 191-195.

1029 Sereno, P.C. 1986. Phylogeny of the bird-hipped dinosaurs. National Geographic

1030   Research 2, 234-256.

1031 Sereno, P.C. 2005. Stem Archosauria version 1.0. TaxonSearch.

1032   http://www.taxonsearch.org/Archive/stem-archosauria-1.0.php

1033 Smith Woodward, A.S. 1896. On two Mesozoic crocodilians Notosuchus nov. gen. and

1034   Cynodontosuchus nov. gen. from the red sandstones of the Territory of

1035   Neuquén (Argentina). Anales del Museo de la Plata. Paleontología 4, 1-20.

1036 Smith Woodward, A.S. 1901. On some extinct reptiles from Patagonia of the genera

1037   Miolania, Dinilysia and Genyodectes. Proccedings of the Royal Society of

1038   London 1, 169-184.

1039 Taquet, P. 1976. Geologie et Paleontologie du gisement de Gadoufaoua (Aptian du

1040   Niger). Cahiers de Paleontologie, 1-191.

1041 Taquet, P., Russell, D.A. 1999. A massively - constructed iguanodont from

1042   Gadoufaoua, Lower Cretaceous of Niger. Annales de Paléontologie, 85 (1), 85-

1043   96.

1044 Tennant, J. 2010.Osteology of a near-complete skeleton of Tenontosaurus tilletti

1045   (Dinosauria: Ornithopoda) from the Cloverly Formation, Montana, USA. MSci

1046   University of Manchester, 196pp.

1047 Varricchio, D.J., Martin, A.J., Katsura, Y. 2007. First trace and body fossil evidence of

1048   a burrowing, denning dinosaur. Proceedings of the Royal Society B: Biological

1049   Sciences 274, 1361-1368.

1050 Waskow, K., Mateus, O. 2017. Dorsal rib histology of dinosaurs and a crocodylomorph

1051   from western Portugal: skeletochronological implications on age determination

1052   and life history traits. Comptes Rendus Palevolution 16 (4), 425-439.

1053 Waskow, K., Sander, P.M. 2014. Growth record and histological variation in the dorsal

1054   ribs of Camarasaurus sp. (Sauropoda). Journal of Vertebrate Paleontology 34

1055   (4), 852-869.

1056 Weishampel, D.B., Jianu, C.M., Csiki, Z., Norman, D.B. 2003. Osteology and

1057   phylogeny of Zalmoxes (n. g.), an unusual Euornithopod dinosaur from the latest

1058   Cretaceous of Romania. Journal of Systematic Palaeontology 1(2), 85-12.

1059 Xu, X., Forster, C.A.., Clark, J.M, Mo, J. 2006. A basal ceratopsian with transitional

1060   features from the Late Jurassic of northwestern China. Proceedings of the Royal

1061   Society, B 273 (1598), 2135-2140.

1062 Xu, X., Wang, X.-L., You, H.-L. 2000. A primitive ornithopod from the early

1063   cretaceous Yixian Formation of Liaoning. Vertebrata PalAsiatica 10, 318-325.

1064   You H., Li, D., Ji, Q., Lamanna, M.C., Dodson, P. 2005. On a new genus of basal

1065   neoceratopsian dinosaur from the Early Cretaceous of Gansu Province, China.

1066   Acta Geologica Sinica 79 (5), 593-597.

1067   Zan, S.-Q., Chen, J., Jin, L.-Y., Li, T. 2005. A primitive ornithopod from the Early

1068   Cretaceous Quantou Formation of Central Jilin, China. Vertebrata Palasiatica 43

1069   (3), 182-193.

1070   Zheng, W., Jin, X., Shibata, M., Azuma, Y., Yu, F. 2012. A new ornithischian dinosaur

1071   from the Cretaceous Liangtoutang Formation of Tiantai, Zhejiang Province,

1072   China. Cretaceous Research 34, 208-219.

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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)

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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)

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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)

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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)

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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)

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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)

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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

A

B

V?

mc

IV

III   II

I

C

D

mc

I

II   III

IV

Marasuchus lilloensis
Silesaurus opolensis
Herrerasaurus ischigualastensi
Eoraptor lunensis
Diluvicursor pickeringi
Laquintasaura venesuelae
Micropachycephalosaurus hongtuy
Gasparinisaura cincosaltensis
Zephyrosaurus schaffi
Koreanosaurus boseongensis
Yueosaurus tiantaiensis
Orodromeus makelai
Jeholosaurus shangyuanensis
Hypsilophodon foxii
Changchunsaurus parvus
Hexinlusaurus multidens
Haya griva
Yandusaurus hongheensis
Agilisaurus louderbacki
Lesothosaurus diagnosticus
Eocursor parvus
Pisanosaurus mertii
Thescelosaurus neglectus
Parksosaurus warreni
Wannanosaurus yansiensis
Goyocephale lattimorei
Homalocephale calathocercos
Prenocephale prenes
Stegoceras validum
Abrictosaurus consors
Fruitadens haagarorum
Tianyulong confuciusi
Manidens condorensis
Echinodon becklessi
Pegomastax africanus
Heterodontosaurus tucki
Scutellosaurus lawleri
Emausaurus ernsti
Scelidosaurus harrisonii
Isaberrysaura mollensis
Huayangosaurus taibaii
Stegosaurus stenops
Hesperosaurus mjosi
Minmi paravertebra
Gargoyleosaurus parkpinorum
Euoplocephalus tutus
Pinacosaurus grangeri
Gideonmantellia amosanjuanae
Notohypsilophodon comodorensis
Mahuidacursor
Talenkauen santacrucensis
Macrogryphosaurus gondwanicus
Zalmoxes robustus
Tenontosaurus tilletti
Dryosaurus altus
Camptosaurus dispar
Ouranosaurus nigeriensis
Probactrosaurus gobiensis
Mantellisaurus atherfieldensis
Albalophosaurus yamaguchiorum
Chaoyangsaurus youngi
Yinlong downsi
Stenopelix valdensis
Psittacosaurus lujiatunensis
Psittacosaurus mongoliensis
Xuanhuaceratops niei
Hualianceratops wucaiwanensis
Liaoceratops yanzigouensis
Koreaceratops hwaseongensis
Auroraceratops rugosus
Archaeoceratops oshimai
Yamaceratops dorngobiensis
Aquilops americanus
Mosaiceratops azumai
Leptoceratops gracilis
Bagaceratops rozhdestvenskyi
Protoceratops andrewsi

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