

1 **New hadrosaurid (Dinosauria: Ornithopoda) fossils from the uppermost Cretaceous**
2 **of central Patagonia and the influence of paleoenvironment on South American**
3 **hadrosaur distribution**

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5 **Ibiricu Lucio M.** ^{a, b*}, **Casal Gabriel A.** ^{b, c}, **Alvarez Bruno N.** ^{b, d},
6 **De Sosa Tomas Andrea** ^{b, c}, **Lamanna Matthew C.** ^e **Cruzado-Caballero Penelope** ^{f, g, h}

7
8 ^aInstituto Patagónico de Geología y Paleontología (IPGP-CCT CONICET-CENPAT), Boulevard Almirante
9 Brown 2915, Puerto Madryn, Chubut, Argentina. ibiricu@cenpat-conicet.gob.ar.

10 ^bLaboratorio de Paleontología de Vertebrados, Universidad Nacional de la Patagonia San Juan Bosco, Ciudad
11 Universitaria, Ruta provincial n°1, km. 4, Comodoro Rivadavia, Chubut, Argentina. paleogac@gmail.com.

12 ^cLaboratorio de Bioestratigrafía “Dr. Eduardo Musacchio,” Departamento de Geología, Universidad Nacional
13 de la Patagonia San Juan Bosco, Ciudad Universitaria, Ruta provincial n°1, km. 4, Comodoro Rivadavia,
14 Chubut, Argentina. adesosatomas@gmail.com.

15 ^dCentro de Investigaciones y Transferencia Golfo San Jorge, Ciudad Universitaria, Ruta provincial n°1, km. 4,
16 Comodoro Rivadavia, Chubut, Argentina. bruno.n.alvarez@outlook.com.

17 ^eSection of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh,
18 Pennsylvania 15213 USA. lamannam@carnegiemnh.org.

19 ^fÁrea de Paleontología, Departamento de Biología Animal, Edafología y Geología, Universidad de La
20 Laguna, San Cristóbal de La Laguna, Santa Cruz de Tenerife, España. pcruzado@ull.edu.es.

21 ^gInstituto de Investigación en Paleobiología y Geología (IIPG), General Roca, 8332, Río Negro, Argentina.

22 ^hUniversidad Nacional de Río Negro-IIPG, General Roca, Río Negro, Argentina.

23

24 * = corresponding author.

ABSTRACT

25

26 We describe and incorporate fragmentary new cranial and postcranial materials of
27 hadrosaurid ornithopods into the non-avian dinosaur assemblage of the Upper Cretaceous
28 (Coniacian–Maastrichtian) Lago Colhué Huapi Formation of central Patagonia, south-
29 central Chubut Province, Argentina. The fossils come from the upper part of the formation,
30 probably from a stratigraphic interval close to the Cretaceous/Paleogene boundary. The
31 materials belong to at least two ontogenetically distinct individuals that are assigned to
32 Hadrosauridae due to their possession of anatomical features that characterize this derived
33 ornithopod group. Sedimentological inferences reveal that the paleoenvironment of these
34 hadrosaurids was characterized by high-sinuosity, meandering-type fluvial channels,
35 whereas palynological data suggest the existence of low-energy freshwater bodies in the
36 floodplains of these rivers and a warm and humid paleoclimate. The deposition of the upper
37 part of the Lago Colhué Huapi Formation was probably influenced by the Patagonian
38 Atlantic marine transgression, which may have played an important role in the distribution
39 of this sedimentary unit. The new Lago Colhué Huapi Formation hadrosaurid specimens
40 constitute the most stratigraphically recent records of this clade from Argentina. The
41 materials contribute to the interpretation of Upper Cretaceous hadrosaurid
42 paleobiogeography in Patagonian basins; moreover, sedimentological and palynological
43 data suggest that paleoenvironmental conditions may have exerted an important influence
44 on South American hadrosaur distribution, supporting hypotheses of ornithopod faunal
45 turnover during the Late Cretaceous of central Patagonia. Finally, the new remains add to
46 the generally depauperate record of Late Cretaceous ornithopods in the Southern
47 Hemisphere.

48

- 49 *Keywords:* Hadrosauridae, Late Cretaceous, Lago Colhué Huapi Formation, Patagonia,
50 Argentina, paleobiogeography, paleoenvironment.

51 **1. Introduction**

52 Hadrosaurids were the most diverse and derived group within Ornithopoda (Horner
53 et al., 2004; Prieto-Márquez, 2010). The fossil record of this clade is particularly abundant
54 in the Campanian and Maastrichtian of North America and Asia (Lund and Gates, 2006;
55 Kobayashi et al., 2019; McKellar et al., 2019), and indeed, hadrosaurids were one of the
56 most dominant terrestrial herbivore clades in Laurasian Late Cretaceous habitats (Gates et
57 al., 2012; Wosik et al., 2020). In recent years, the fossil record of this herbivorous dinosaur
58 group has increased in South America as well, particularly in Argentine Patagonia (Coria et
59 al., 2012; Cruzado-Caballero and Powell, 2017). However, most Patagonian hadrosaurids
60 are represented by fragmentary remains, which has precluded a robust assessment of their
61 phylogenetic relationships (Prieto-Marquez and Salinas, 2010; Coria, 2011, 2014; Coria et
62 al., 2012; Cruzado-Caballero, 2017). The only other definitive Gondwanan hadrosaur fossil
63 yet identified is the fragmentary holotypic partial skull of the lambeosaurine *Ajnabia*
64 *odysseus* from the Maastrichtian of Morocco (Longrich et al., 2021).

65 Hadrosaurid fossils are commonly found in diverse paleoenvironments such as
66 lower coastal plain channel deposits and upper coastal plain, overbank, and delta plain
67 sediments (Horner et al., 2004). Nevertheless, eggshells and juvenile individuals are
68 generally recovered from upper coastal plain settings (Horner et al., 2004). Moreover,
69 marginal marine environments may have been an ancestral habitat for the clade (Kobayashi
70 et al., 2019).

71 The Coniacian–Maastrichtian Lago Colhué Huapi Formation is the uppermost
72 sedimentary unit of the Chubut Group in the Golfo San Jorge Basin of central Patagonia
73 (Casal et al., 2015). The fossil record of this formation reveals a relatively abundant fauna
74 in which non-avian dinosaurs are well-represented (see Casal et al., 2016; Ibiricu et al.,

75 2020). Here we describe new hadrosaurid materials (specimens UNPSJB-PV 1050 and
76 UNPSJB-PV 1061) from the upper part of the Lago Colhué Huapi Formation, from a
77 stratigraphic interval that is probably close to the Cretaceous/Paleogene boundary.
78 Although fragmentary, the remains are undoubtedly referable to Hadrosauridae and are
79 important because they add to the sparse record of terminal Cretaceous Gondwanan
80 hadrosaurids. Additionally, although the hadrosaurid *Secernosaurus koernerii* comes from
81 the same geographic area (Brett-Surman, 1979), it lacks clear stratigraphic provenance (see
82 below). Therefore, the materials described herein are the first hadrosaurid fossils from the
83 Golfo San Jorge Basin to be associated with precise geographic and stratigraphic
84 information, which in turn casts light on the biostratigraphic and paleobiogeographic range
85 and distribution of South American hadrosaurids during the latest Cretaceous. Furthermore,
86 UNPSJB-PV 1050 and UNPSJB-PV 1061 were associated with palynomorphs and fossil
87 leaves (Vallati et al., 2016, 2020) as well as freshwater stromatolites (Casal et al., 2020).
88 Therefore, the paleoflora (De Sosa Tomas et al., 2017; Vallati et al., 2017) and
89 paleoenvironmental setting (Vallati et al., 2020) of the remains are well known, which in
90 turn supports inferences regarding the association of hadrosaurids with coastal, marine-
91 influenced paleoenvironments and how these environmental preferences shaped the
92 distribution of these dinosaurs. Finally, the first transgression of the Atlantic Ocean across
93 southern South America occurred during the Maastrichtian, affecting multiple Patagonian
94 basins (Spalletti and Franzese, 2007). This marine incursion could have played an
95 important role in influencing the distribution of hadrosaurids in South America and in
96 driving a previously hypothesized turnover of ornithopod faunas on the continent.

97

98

99 2. Geological and paleoenvironmental setting

100 The Golfo San Jorge Basin is located between 44°S and 47°S latitude and 65°W and
101 71°W longitude. Rocks deposited within the basin crop out in the southern portion of
102 Chubut Province and the northern sector of Santa Cruz Province in central Patagonia,
103 Argentina (Fig. 1A). The main sedimentary infill pertains to the Chubut Group (Lesta,
104 1968; Lesta and Ferello, 1972). This group consists of fluviolacustrine units that preserve a
105 rich and important fossil record. The stratigraphically youngest unit of the Chubut Group is
106 the Coniacian–Maastrichtian Lago Colhué Huapi Formation, which was formally separated
107 from the Upper Member of the Bajo Barreal Formation by Casal et al. (2015). Therefore,
108 this unit is placed above the Cenomanian–Turonian Bajo Barreal Formation and, depending
109 on the specific location in the basin, below the Laguna Palacios Formation or the
110 Salamanca Formation (Maastrichtian–Danian *sensu* Barcat et al., 1989; early Danian *sensu*
111 Clyde et al., 2014 and Simeoni, 2014; see Casal et al., 2015). According to Gianni et al.
112 (2018), marked paleobiogeographic changes took place in Patagonia during the
113 Maastrichtian–early Paleocene in tandem with the first Atlantic marine transgression over
114 southern South America (Olivero and Medina, 1994; Aguirre-Urreta et al., 2011). In the
115 Golfo San Jorge Basin, these events coincide with the deposition of the upper section of the
116 Lago Colhué Huapi Formation as well as that of the Salamanca Formation (see below).

117 The Lago Colhué Huapi Formation was deposited under a fluvial regime, in
118 channels that increase in sinuosity toward the top of the formation. The lithology of the unit
119 consists of light-colored sandstones and red mudstones, and, except in the basal portion, is
120 characterized by the absence of pyroclastics, unlike the rest of the units of the Chubut
121 Group (Casal et al., 2015). Its outcrops are well-exposed in the eastern region of the

122 eponymous lake and in the headwaters of the Río Chico in south-central Chubut Province
123 (Fig. 1A).

124 A newly discovered outcrop of the Lago Colhué Huapi Formation at the headwaters
125 of the Río Chico, informally named Cerro del Hadro, has yielded, to date, an association of
126 fossils including stromatolites (Casal et al., 2020), palynomorphs (Vallati et al., 2016,
127 2020), wood fragments, indeterminate eggshells, recently recovered non-avian theropod
128 teeth (Álvarez et al., in prep.), and the hadrosaurid remains that are the focus of this study.
129 The stratigraphic section at the site starts with the light-colored sandstones and red
130 mudstones that characterize the Lago Colhué Huapi Formation (Fig. 1B). This succession is
131 interrupted by an irregular unconformity of concave geometry.

132 The lithofacies analysis presented herein is based on but slightly modified from that
133 proposed by Casal et al. (2020). The sedimentary infill begins with a coarsening downward,
134 intraformational coarse conglomerate [Fig. 1C (Casal et al., 2020: table 1)] followed by a
135 fine conglomerate with low and diffuse-angled crossbedding [Fig. 1D (Casal et al., 2020:
136 table 1)]. The sediments that bear the hadrosaurid remains are ochre and black, coarse- to
137 medium-grained crossbedded sandstones [Fig. 1E (Casal et al., 2020: table 1)]. Above and
138 in direct contact with the sandstones is a finer-grained sedimentary succession that is
139 interpreted as having originated during inundation of the paleovalley, where decantation
140 processes dominated (Fig. 1F). This succession starts with 0.3 m of dark gray laminated
141 mudstone with well-preserved palynomorphs [Fig. 1G (Casal et al., 2020: table 1; Vallati et
142 al., 2020)].

143 Vallati et al. (2016) studied the palynoflora of these levels and reported the presence
144 of Maastrichtian species that became extinct at the Cretaceous/Paleogene boundary (Vajda
145 and Bercovici, 2014). Among them, *Quadruplanus brossus* and *Tubulifloridites lilliei*

146 characterize the austral *Nothofagidites/Proteacidites* Province (Herngreen, 1980), whereas
147 *Buttinia andreevi* and *Gabonispuris vigourouxii* typify the tropical to subtropical Palmae
148 Province (Herngreen, 1980). The cooccurrence of species that are characteristic of the
149 tropical and austral provinces, respectively, indicates that, at the latitude of the studied
150 locality, this Patagonian region was located in the Southern Hemisphere transitional zone
151 recognized by Vajda and Bercovici (2014). Species with affinities to Palmae such as
152 *Spinizonocolpites riochiquensis* were also recovered in these deposits, suggesting a warm
153 paleoclimate with at least seasonal rainfall.

154 Above these levels, the sedimentary fill continues with a 0.2 m horizontally
155 laminated white marlstone bed. This bed includes mesocharcoal and a palynoflora
156 dominated by gymnosperms (mainly Podocarpaceae), followed by angiosperms and lesser
157 numbers of spores of Monilophyta, Lycophyta, and Bryophyta, and zygospores of
158 Zygnemataceae. The presence of Zygnemataceae zygospores indicates the presence of a
159 shallow, low-energy, well-oxygenated body of clear water that accords with the
160 reconstruction of a humid and warm paleoclimate (Vallati et al., 2016, 2020). This deposit
161 is laterally related to a stromatolite-bearing horizon [E1; Fig. 1H (Casal et al., 2020: table
162 1)]. Following from the paleoclimatic conditions inferred from the presence of
163 Zygnemataceae zygospores, this laminated microbial deposit would have been located near
164 the shore of a shallow body of water. Above this level, there are alternating green-yellow
165 (Fig. 1F, Lf4) and gray-green (Fig. 1G, Lf5) sandstones followed by the typical red
166 mudstones of the Lago Colhué Huapi Formation with intercalated white carbonate
167 concretions (Fig. 1J, Lf8). The stratigraphic column terminates with a local fissural effusion
168 dominated by the Angostura Basalt (see Fig. 1B), which was dated to 64 Ma by Marshall et
169 al. (1981) and 67 Ma by Clyde et al. (2014). However, in a more complex lateral

170 relationship, depending on the location in the basin, the Lago Colhué Huapi Formation is in
171 some places covered by marine deposits of the Salamanca Formation. This unit represents
172 the first Atlantic marine transgression of the Golfo San Jorge Basin. The age of the
173 Salamanca Formation is Maastrichtian–Danian (*sensu* Barcat et al., 1989) or early Danian
174 (*sensu* Clyde et al., 2014 and Simeoni, 2014).

175 Finally, near Cerro del Hadro, there are other exposures of the Lago Colhué Huapi
176 Formation with plant fossils from horizons related to the stratigraphic level from which the
177 hadrosaurid bones were recovered. Vallati et al. (2020: table 1) noted the presence of
178 *Spinizonocolpites* (a *Nypa*-type pollen grain) in almost every studied outcrop of the
179 formation in the area of the Río Chico headwaters. The extant mangrove palm *Nypa* is
180 restricted to brackish coastal swamps, lagoons, estuaries, rivers, and floodplains. In this
181 sense, it is notable that several large, linear, symmetrical, parallel-veined, palm-like leaf
182 fragments were recovered from reddish claystone at Cerro Hoja Grande, 1.5 kilometers
183 southwest of Cerro del Hadro. If confirmed as those of Arecaceae, these fragmentary leaves
184 could strengthen the presence of this clade in Maastrichtian strata of the Lago Colhué
185 Huapi Formation. Based on this collective evidence, we suggest the probable presence, in
186 the upper levels of this formation, of coastal swamps where *Nypa*-like palms thrived.

187

188 **3. Institutional abbreviations**

189 **CNS-V**, Cátedra de Paleontología, Departamento de Ciencias Naturales,
190 Universidad Nacional de Salta, Salta, Argentina. **FMNH**, Field Museum of Natural
191 History, Chicago, Illinois, USA. **MACN**, Museo Argentino de Ciencias Naturales
192 Bernardino Rivadavia, Buenos Aires, Argentina. **MJHG**, Museo Jorge H. Gerhold,
193 Ingeniero Jacobacci, Río Negro, Argentina. **MLP**, Museo de La Plata, La Plata, Buenos

194 Aires, Argentina. **MPCA-Pv**, Museo Provincial Carlos Ameghino, Paleontología de
195 Vertebrados, Cipolletti, Río Negro, Argentina. **MPEF**, Museo Paleontológico Egidio
196 Feruglio, Trelew, Chubut, Argentina. **MPHN-Pv**, Museo Provincial de Historia Natural,
197 Paleontología de Vertebrados, La Pampa, Argentina. **MRPV**, Museo Regional Provincial
198 de Valcheta, Valcheta, Río Negro Province, Argentina. **UNPSJB-PV**, Universidad
199 Nacional de la Patagonia San Juan Bosco, Paleontología de Vertebrados, Comodoro
200 Rivadavia, Chubut, Argentina.

201

202 **4. Systematic Paleontology**

203 Dinosauria Owen, 1842

204 Ornithischia Seeley, 1887

205 Ornithopoda Marsh, 1881

206 Hadrosauridae Cope, 1869

207 Genus and species indeterminate

208 (Figs. 2–7)

209

210 **Referred specimens:** UNPSJB-PV 1050 (collected *in situ*) and UNPSJB-PV 1061
211 (surface collected after it had rolled a few meters toward the base of the hill). This
212 collection of incomplete cranial and postcranial bones is interpreted to comprise associated
213 partial skeletons of at least two hadrosaurid individuals of differing ontogenetic stages (at
214 least one juvenile and at least one subadult or adult). It consists of the following elements:
215 UNPSJB-PV 1050/1, UNPSJB-PV 1050/2, and UNPSJB-PV 1050/3, dentary fragments;
216 UNPSJB-PV 1061/3, an incomplete middle cervical vertebra; UNPSJB-PV 1050/8 and
217 UNPSJB-PV 1061/4, two incomplete dorsal vertebrae; UNPSJB-PV 1050/4 and UNPSJB-

218 PV 1050/5, two incomplete sacral vertebrae; UNPSJB-PV 1050/6 and UNPSJB-PV 1061/1,
219 two incomplete caudal vertebrae; UNPSJB PV 1050/9, a pedal ungual phalanx; and
220 unidentified fragments.

221 **Locality:** Cerro del Hadro, headwaters of Río Chico, east of southeastern shore of
222 Lago Colhué Huapi, Chubut Province, central Patagonia, Argentina (Fig. 1A).

223 **Horizon and age:** Uppermost Lago Colhué Huapi Formation. Geological studies—
224 particularly those of palynomorphs—support a late Maastrichtian age, probably close to the
225 Cretaceous/Paleogene boundary, for the stratigraphic horizon in question (Vallati et al.,
226 2016, 2020).

227

228 **5. Description and comparisons**

229 *5.1. Dentary*

230 Three edentulous fragments pertaining to at least two dentaries were recovered
231 (UNPSJB-PV 1050/1, UNPSJB-PV 1050/2, and UNPSJB-PV 1050/3; Fig. 2). They are
232 taphonomically distorted and have lost their dorsal and ventral margins. All fragments have
233 narrow, subvertical, parallel dentary alveoli (alveolar sulci), as is characteristic of
234 Hadrosauridae (Horner et al., 2004; Godefroit et al., 2008, 2012; Prieto-Márquez et al.,
235 2016). The septa that separate the alveoli are thin and sheet-like.

236 UNPSJB-PV 1050/1 (Fig. 2A–C) is the smallest fragment, with a length of 26.2 mm
237 and a height of 31.7 mm. It belongs to a left dentary in which the medial surface was flat
238 and the lateral surface convex. It preserves the beginning of the base of the coronoid
239 process on the lateral side and four tooth positions on the medial side. The presence of the
240 tooth row in all dentary fragments indicates that the posterior end of the dental battery
241 nearly surpassed the anterior border of the coronoid process. This is similar to the dentaries

242 of two indeterminate juvenile hadrosaurids from the Salitral Moreno site near General Roca
243 in Río Negro Province, Argentina (specimens MPCA-Pv-SM3 and MPCA-Pv-SM7;
244 Cruzado-Caballero and Coria, 2016). This feature—the position of the posterior end of the
245 tooth row relative to the anterior margin of the coronoid process—has been considered
246 ontogenetically variable in the non-hadrosaurid iguanodontian *Dryosaurus* spp. (Poole,
247 2015). The alveoli are the narrowest of the three dentary fragments, with a width of
248 approximately 3.5 mm.

249 UNPSJB-PV 1050/2 (Fig. 2D–F) is a mediolaterally narrow fragment of a right
250 dentary. In lateral view, the base of the coronoid process and the posterior end of the
251 Meckelian canal are observed, but the fragment does not preserve the suprameckelian
252 foramen. It has eight subvertical tooth positions, each with a width of approximately 4.9
253 mm.

254 UNPSJB-PV 1050/3 (Fig. 2G–I) is another fragment of right dentary, possibly more
255 anteriorly positioned than UNPSJB-PV 1050/2. It is the largest of the three fragments, with
256 a length of 57.4 mm and a height of 38.8 mm. The lateral surface is eroded and the dorsal
257 and ventral borders are broken. There are nine preserved tooth positions. The alveoli are
258 approximately 4.9 mm wide and slightly anterodorsally inclined. Although impossible to
259 confirm, based on the width of the alveoli, this fragment may represent another part of
260 UNPSJB-PV 1050/2; therefore, a similar ontogenetic status is inferred for this fragment.

261

262 5.2. Cervical Vertebra

263 An incomplete cervical vertebra was recovered, consisting of the centrum and the
264 base of the neural arch (UNPSJB-PV 1061/3; Fig. 3). The bone is strongly eroded;
265 therefore, it is not possible to establish whether the centrum and neural arch were fused, but

266 due to the small size of the vertebra it likely represents a juvenile individual. The centrum
267 is strongly opisthocoelous as in cervical vertebrae of the South American hadrosaurids
268 *Lapampasaurus cholinoi* (Coria et al., 2012) and *Secernosaurus koernereri* (Prieto-Márquez
269 and Salinas, 2010) and its articular surfaces are heart-shaped, as is typical of Hadrosauridae
270 (Horner et al., 2004; Coria et al., 2012). The centrum is anteroposteriorly longer than
271 transversely wide and laterally approximately as wide as tall, which indicates that the
272 vertebra was probably situated in the middle of the cervical series. It is transversely
273 constricted at its approximate anteroposterior midpoint (i.e., ‘waisted’), and on the ventral
274 side there is an eroded longitudinal keel or hypapophysis flanked by a marked ventrolateral
275 excavation. The parapophyses are located on the lateral sides of the anterior half of the
276 centrum and are relatively large and oval with their long axis oriented anteroposteriorly.
277 There are two nutrient foramina on the left lateral surface.. The neural canal is wide
278 transversely as in *Lapampasaurus* (see Coria et al., 2012:fig. 3).

279

280 5.3. Dorsal Vertebrae

281 Two dorsal vertebrae were recovered (UNPSJB-PV 1050/8 and UNPSJB-PV
282 1061/4; Fig. 4). The centrum of UNPSJB-PV 1050/8 (Fig. 4A, B) has been taphonomically
283 crushed but is clearly amphiplatyan, with heart-shaped (dorsoventrally taller than
284 transversely wide) articular surfaces and nutrient foramina on the lateral sides, as is usual
285 for hadrosaurids (Horner et al., 2004;Godefroit et al., 2012; Prieto-Márquez et al., 2016).
286 The lateral surfaces are slightly anteroposteriorly concave. The neural arch is fused to the
287 centrum, suggesting that the element represents a subadult or adult individual, although this
288 cannot be stated definitively in the absence of an osteohistological analysis (Irmis, 2007).
289 The preserved, dorsally facing left prezygapophysis appears to surpass the anterior border

290 of the centrum, and it exhibits a flat, oval articular facet. The neural spine is partly
291 preserved; its base appears to be relatively anteroposteriorly broad and transversely flat.

292 UNPSJB-PV 1061/4 (Fig. 4C–E) is an eroded centrum. It is amphiplatyan and the
293 articular surfaces have the heart-shaped morphology characteristic of hadrosaurids (Horner
294 et al., 2004; Coria et al., 2012; Godefroit et al., 2012; Prieto-Márquez et al., 2016; Cruzado-
295 Caballero and Powell, 2017). As observed in dorsal view, the junction with the neural arch
296 is broken and eroded; therefore, it is not possible to ascertain whether the neural arch and
297 centrum were fused, but based on the tiny size of the bone it presumably represents a
298 juvenile and as such the neurocentral suture was likely unfused. The lateral surfaces are
299 anteroposteriorly concave and exhibit several large, elliptical nutrient foramina as is
300 frequently the case in hadrosaurids [e.g., *Bonapartesaurus rionegrensis* (Cruzado-Caballero
301 and Powell, 2017), *Lapampasaurus*]. On the ventral surface there is a robust sagittal keel
302 that is pierced by smaller foramina, as in the latter hadrosaurid.

303

304 5.4. Sacral Vertebrae

305 Two consecutive sacral vertebrae pertaining to a single individual were found
306 (UNPSJB-PV 1050/4 and UNPSJB-PV 1050/5; Fig. 5). The centra are incomplete and
307 unfused, suggesting that they represent a juvenile or subadult animal; nevertheless, the
308 ontogenetic stage of the specimen cannot be definitively determined without an
309 osteohistological analysis. Based on comparisons with well-preserved hadrosauroid sacral
310 vertebrae [e.g., those of *Eolambia caroljonesa* (McDonald et al., 2012) or the partially
311 preserved sacral elements of *Lapampasaurus*], UNPSJB-PV 1050/4 and UNPSJB-PV
312 1050/5 are interpreted as the posteriormost two sacrals. [In hadrosaurids, the anterior sacral
313 vertebrae resemble the posteriormost dorsals in morphology, whereas the posterior sacrals

314 are, for example, transversely wider and less ‘hourglass-shaped’ in ventral view; see Coria
315 et al. (2012) and McDonald et al. (2012). In other words, the centra become shorter and
316 wider as one moves posteriorly through the hadrosaurid sacrum.] The articular surfaces of
317 the centra (Fig. 5A–D) are elliptical in outline, wider than tall, and amphiplatyan. UNPSJB-
318 PV 1050/4 probably represents the last vertebra in the sacral sequence, and part of its
319 anterior articular surface shows a roughened texture. UNPSJB-PV 1050/4 is more
320 anteroposteriorly compressed than UNPSJB-PV 1050/5, and its neural canal is much
321 narrower in dorsal view. There is a slightly marked groove on the ventral surface of
322 UNPSJB-PV 1050/4, unlike the ventral keel of *Bonapartesaurus* (Cruzado-Caballero and
323 Powell, 2017); conversely, the ventral surface of UNPSJB-PV 1050/5 does not have a
324 groove or keel. The ventral surfaces of both centra exhibit well-developed nutrient
325 foramina, as is also seen in *Lapampasaurus* and *Bonapartesaurus* (Coria et al., 2012;
326 Cruzado-Caballero and Powell, 2017). The sutures for the sacral ribs are partly preserved;
327 they are circular, shared between centra, and occupy almost the entire dorsoventral height
328 of each centrum.

329

330 5.5. Caudal Vertebrae

331 Two caudal vertebrae were found (UNPSJB-PV 1050/6 and UNPSJB-PV 1061/1;
332 Fig. 6). UNPSJB-PV 1061/1 (Fig. 6A–D) displays typical hadrosaurid anterior caudal
333 vertebral features such as an anteroposteriorly short, amphiplatyan centrum with
334 subhexagonal to circular articular surfaces and transverse processes that arise from the
335 centrum at right angles (Horner et al., 2004; Prieto-Márquez and Salinas, 2010; Cruzado-
336 Caballero and Powell, 2017). The centrum is marginally taller than wide and considerably
337 wider and taller than long. Its lateral surfaces are anteroposteriorly concave, pierced by

338 small nutrient foramina, and ornamented by well-marked horizontal rugosities. The ventral
339 surface of the centrum does not have hemapophyseal facets; coupled with its
340 anteroposteriorly short proportions, this indicates that UNPSJB-PV 1061/1 is one of the
341 anteriormost five vertebrae in the tail (Horner et al., 2004). The preserved fragments of
342 transverse processes are subtriangular in cross-section. The zygapophyses are
343 taphonomically affected; nevertheless, the preserved left prezygapophysis is strongly
344 dorsally projected and surpasses the level of the anterior margin of the centrum. Only the
345 base of the neural spine is preserved, and it is anteroposteriorly short and transversely
346 narrow.

347 UNPSJB-PV 1050/6 (Fig. 6E–H) is a small, amphiplatyan centrum with the
348 hexagonal articular surfaces typical of hadrosaurid caudal vertebrae (Horner et al., 2004;
349 Prieto-Marquez and Salinas, 2010; Cruzado-Caballero and Powell, 2017). It is
350 approximately as long as wide and slightly wider than tall. The lateral surfaces are gently
351 anteroposteriorly concave and pierced by irregularly distributed nutrient foramina.
352 Hemapophyseal facets are present on the ventral surface, indicating that the centrum
353 belongs to the middle or posterior region of the caudal series. Well-developed foramina are
354 also present and irregularly distributed on the ventral surface. As seen in dorsal view, the
355 neural canal is narrow, particularly at its anteroposterior midpoint, and sutures for the
356 neural arch are evident. These unfused neurocentral sutures suggest that the element
357 belongs to a juvenile individual.

358

359 *5.6. Pedal Ungual Phalanx*

360 A small, eroded pedal ungual phalanx (UNPSJB-PV 1050/9; Fig. 7) was also
361 recovered from the Cerro del Hadro site. It is arrowhead-shaped in dorsal and ventral

362 views, as in other hadrosaurids (Horner et al., 2004; Prieto-Márquez and Norell, 2010; see
363 Fig. 7A, B). The phalanx has a well-marked, concave proximal articular surface. Its distal
364 end is broken and eroded, though what remains of this end is rugose. The dorsal surface of
365 the ungual is slightly convex, whereas the ventral surface is flat. Both surfaces are
366 perforated by irregularly distributed nutrient foramina.

367

368 **6. Discussion**

369 *6.1. Latest Cretaceous Ornithopods from South-Central Patagonia*

370 The specimens described herein were recovered from a small area; moreover, no
371 other fossil vertebrates were discovered within several meters of the site. Although the
372 bones were not thin sectioned for paleohistological study, their size, incomplete ossification
373 and/or fusion (in some cases), and the porous surface texture of selected axial elements
374 permits tentative ontogenetic stage interpretations (see Farke and Yip, 2019). Specifically,
375 the fossils support the presence of at least two growth stages among the materials, including
376 juvenile and subadult/adult specimens; therefore, we interpret that they represent at least
377 two ornithopod individuals. Although the fragmentary nature of UNPSJB-PV 1050 and
378 UNPSJB-PV 1061 precludes a taxonomic determination to the genus or species level, we
379 are confident in referring the specimens to Hadrosauridae. This assignment is supported by
380 the following features: the general morphology of the alveolar sulci of the dentary
381 fragments; the dorsoventrally compressed, opisthocoelous cervical vertebral centrum; the
382 heart-shaped articular surfaces of the dorsal vertebral centra; the hexagonal articular
383 surfaces of the caudal vertebral centra; and the characteristically arrowhead-shaped pedal
384 ungual (Horner et al., 2004; Prieto-Marquez, 2007). These features stand in contrast to
385 those of earlier diverging iguanodontians, in which the dorsal centra retain suboval anterior

386 and posterior articular surfaces and the caudal centra are rectangular in outline.
387 Furthermore, the recovered pedal unguis lacks the prominent lateral groove present in non-
388 hadrosaurid iguanodontians (Norman et al., 2004).

389 Definitive ornithomimid fossil records from the Lago Colhué Huapi Formation include
390 the partial postcranial skeleton of the medium-sized elasmarian *Sektensaurus*
391 *sanjuanboscoi* (Luna et al., 2003; Ibiricu et al., 2010, 2019, 2020). This specimen was
392 recovered from an ephemeral island near the southeastern shore of Lago Colhué Huapi that
393 is exposed when the water level is low (Ibiricu et al., 2020). The age of the stratigraphic
394 level within the formation where this herbivorous dinosaur was recovered is considered to
395 be Campanian to ?early Maastrichtian (Casal et al., 2007, 2015; Lamanna et al., 2019a).

396 Two other ornithomimids have been reported from the latest Cretaceous of central
397 Patagonia: the supposed ceratopsian *Notoceratops bonarellii* (Tapia, 1918) and the
398 hadrosaurid *Secernosaurus koerneri* (Brett-Surman, 1979). The holotypic and only known
399 specimen of *Notoceratops*, a left dentary, was described as having been collected from the
400 Lago Colhué Huapi area near the source of the Río Chico (Tapia, 1918). Although no
401 specific stratigraphic location was provided, the only terrestrial Cretaceous unit that crops
402 out in this region is the Lago Colhué Huapi Formation (Casal et al., 2015, 2016).

403 Consequently, the *Notoceratops* dentary undoubtedly comes from this unit. The
404 interpretation of this taxon as a ceratopsian is controversial and is complicated by the fact
405 that its holotype is currently missing (Coria and Cambiaso, 2007; Rich et al., 2014). Based
406 on the known ornithomimid fossil record of the Lago Colhué Huapi Formation—as well as
407 the total absence of ceratopsian fossils from Late Cretaceous strata elsewhere in the
408 Gondwanan landmasses—the most parsimonious interpretation, in our view, is that this

409 dinosaur is a hadrosaurid ornithopod (see below as well as Ibiricu et al., 2010 and
410 references therein).

411 By contrast, the taxonomic placement of *Secernosaurus* within Hadrosauridae is
412 well supported (Prieto-Marquez and Salinas, 2010). The holotype of this hadrosaurid was
413 reportedly recovered from the “San Jorgé (sic) Formation” (Brett-Surman, 1979), a rock
414 unit that does not exist in the Golfo San Jorge Basin (see Casal et al., 2016). Later, Ibiricu
415 et al. (2010) and Prieto-Marquez and Salinas (2010) concluded that this specimen was
416 derived from the Upper Member of the Bajo Barreal Formation, based on its documented
417 geographic provenance from two miles east of the Río Chico headwaters. However, as
418 pointed out by Casal et al. (2016), the continental Cretaceous strata in question are now
419 assigned to the Lago Colhué Huapi Formation. Furthermore, we contend that the
420 *Secernosaurus* holotype was recovered from the uppermost (Maastrichtian, see below)
421 portion of this formation, from the same general stratigraphic level as the specimens
422 described herein.

423 Based on their hadrosaurid affinities, overall morphology, and closely comparable
424 geographic and inferred stratigraphic provenance from the Lago Colhué Huapi Formation,
425 it is possible that UNPSJB-PV 1050 and UNPSJB-PV 1061 pertain to *Secernosaurus*
426 *koernerii*. Nevertheless, this is difficult to determine due to the fragmentary nature of the
427 new fossils. Interestingly, during recent fieldwork in the Río Chico area, two of the present
428 authors (LMI, GAC) located a ‘historic-looking’ abandoned quarry that yielded an
429 indeterminate bone fragment. Based on information provided by people living in the area,
430 this quarry—which is at the same stratigraphic level as that which yielded UNPSJB-PV
431 1050 and UNPSJB-PV 1061—may have been opened by a team from the Field Museum
432 (Chicago) during their 1923 expedition that discovered the *Secernosaurus* holotype. As

433 such, though this is difficult to establish with certainty, we suspect that *Secernosaurus* may
434 come from the same horizon of the Lago Colhué Huapi Formation as the new hadrosaurid
435 materials described herein.

436 Recently, Becerra et al. (2018a) reported fragmentary new hadrosaurid materials
437 belonging to more than one individual, found several kilometers away from the bones
438 described herein. Nevertheless, they came from the same stratigraphic level, i.e., the
439 uppermost section of the Lago Colhué Huapi Formation.

440 In sum, at the moment, the latest Cretaceous (Campanian–Maastrichtian)
441 ornithopod record of the Golfo San Jorge Basin includes the medium-sized elasmarian
442 *Sektensaurus*, the probable hadrosaurid *Notoceratops* (originally considered a ceratopsian),
443 and unquestionable hadrosaurids: the *Secernosaurus* holotype, the materials reported by
444 Becerra et al. (2018a), and UNPSJB-PV 1050 and UNPSJB-PV 1061. Continued
445 paleontological exploration of exposures of the Lago Colhué Huapi Formation in the area
446 of the Río Chico and Lago Colhué Huapi promises to increase understanding of the
447 Cretaceous herbivorous dinosaur assemblage of central Patagonia.

448

449 *6.2. Paleoenvironmental Influences on South American Hadrosaurid Distribution*

450 Casamiquela (1964), Brett-Surman (1979), and Bonaparte (1984) were the first to
451 describe Patagonian hadrosaurid remains and to analyze the likely mode of arrival of these
452 dinosaurs to the Southern Hemisphere. According to these and later authors, a dispersal
453 event occurred from North America to South America no later than the late Campanian
454 (Fig. 8A), probably via the Proto-Antillean volcanic arc (see Cruzado-Caballero and
455 Powell, 2017). This is evidenced by the South American record of Hadrosauridae, which is
456 concentrated in the Campanian–Maastrichtian of Argentina (see Cruzado-Caballero, 2017

457 and Cruzado-Caballero et al., 2018 and references therein; Table 1). Subsequently, a second
458 dispersal of hadrosaurids from South America to Antarctica took place, no later than the
459 mid-Maastrichtian (Fig. 8A). This is supported by the occurrence of definitive and putative
460 Antarctic fossils of these derived ornithopods, which have so far been recovered only from
461 middle–upper Maastrichtian horizons of the López de Bertodano Formation of the James
462 Ross Basin (see Reguero et al., 2016: table 1; Lamanna et al., 2019b: table 1; E. Roberts
463 pers. comm. to MCL).

464 Cruzado-Caballero et al. (2018) described a fauna of small- to medium-sized
465 elasmarian ornithopods in Santonian and more ancient Upper Cretaceous horizons in
466 northern Patagonia that ultimately gave way to an assemblage of larger-bodied elasmarians
467 and hadrosaurids during the Campanian–Maastrichtian. The presence of *Sektensaurus* and
468 other ornithopod fossils with clear non-hadrosaurid affinities (LMI pers. obs.) recovered
469 from the eastern shore of Lago Colhué Huapi and ephemeral islands in this lake [from
470 strata that are regarded as Campanian to ?early Maastrichtian in age (see Casal et al., 2007;
471 Lamanna et al., 2019a)] confirm that this large-bodied elasmarian-dominated fauna also
472 occurred in central Patagonia. Therefore, at least in the Golfo San Jorge Basin, and
473 probably in more southern areas of South America as well (see below), this fauna may have
474 persisted until the latest Campanian or early Maastrichtian. In sum, in the Lago Colhué
475 Huapi Formation, two temporally successive ornithopod faunas are observed: a
476 Campanian–?early Maastrichtian assemblage dominated by elasmarians and potentially
477 other non-hadrosaurid ornithopods, and a late Maastrichtian fauna dominated by
478 hadrosaurids, which, as evidenced by the fossils described herein (and those reported by
479 Becerra et al., 2018a), may have been the only ornithopod clade to survive to the latest
480 Maastrichtian in central Patagonia. Although this hypothesized elasmarian-to-hadrosaurid

481 faunal turnover could be an artifact of taphonomic or preservational biases, it appears to
482 constitute an authentic ecological replacement, at least in central Patagonia. Nevertheless, it
483 is important to note that some elasmarians may have coexisted with hadrosaurids,
484 specifically during the late Campanian–early Maastrichtian, suggesting the existence of
485 some form of niche partitioning between these ornithopod groups (Novas et al., 2019).
486 However, the hadrosaurid fossil record strongly suggests that, subsequent to at least the
487 middle Maastrichtian, these highly specialized herbivores were the only ornithopods
488 present in Patagonia (i.e., in the Neuquén, Cañadón Asfalto, Golfo San Jorge, and Austral-
489 Magallanes basins). This, in turn, suggests that hadrosaurids were well-adapted to
490 paleoecological conditions in Patagonia during the latest Cretaceous. Moreover, recent
491 histological studies of Antarctic Campanian–Maastrichtian ornithischians (i.e., elasmarians
492 and ankylosaurs) indicate that the growth patterns of these high latitude (>60° S) taxa were
493 similar to those of related forms from Patagonia. This, in turn, suggests that the distribution
494 of Gondwanan ornithopods was not strongly influenced by physiological aspects and that
495 these animals were adapted to cope with significant temperature variations throughout the
496 year (see Cerda et al., 2019; Garcia-Marsà et al., 2020). Interestingly, the only other
497 herbivorous dinosaurs that unquestionably shared the Patagonian latest Cretaceous
498 paleoenvironment with ornithopods were ankylosaurs and titanosaurs (seemingly the only
499 sauropods to survive to the end of the Cretaceous worldwide), suggesting that these groups
500 of animals may have not directly competed for resources and niches available at that time
501 (Coria, 2011). Nevertheless, titanosaurian fossils are generally uncommon in marine-
502 influenced paleoenvironments (Gasparini et al., 2001) such as that which yielded the
503 hadrosaurids UNPSJB-PV 1050 and UNPSJB-PV 1061 (see below). In particular,
504 titanosaurian fossils recovered from the Lago Colhué Huapi Formation are associated with

505 depositional settings that are characterized by braided fluvial channels that are less sinuous
506 than are those from the uppermost portion of the unit. These low-sinuosity rivers are
507 indicative of inland paleoenvironments, which in turn suggests that these derived sauropods
508 were adapted to these types of habitats (Butler and Barrett, 2008).

509 The sedimentary paleoenvironment of the middle (Campanian–?early
510 Maastrichtian) section of the Lago Colhué Huapi Formation—the strata that have yielded
511 non-hadrosaurid ornithopods such as *Sektensaurus*—corresponds to anastomosing
512 multichannel fluvial systems that exhibited seasonal fluctuations (Allard and Casal, 2013;
513 Casal et al., 2014, 2019). This fluvial channel morphology indicates that the fauna present
514 during the deposition of the middle section of the formation lived inland, well away from
515 the paleoshoreline. Furthermore, the presence of desiccation cracks, saponite and sepiolite
516 clays (Pozo Rodríguez and Casas Sainz de Aja, 1992; Zaaboub et al., 2005; Casal et al.,
517 2015), and external iron oxide crusts and abundant hematite in permineralized titanosaur
518 bones (Casal et al., 2019; Casal and Nillni, 2020) indicates the existence of a seasonally dry
519 or semiarid climate (Allard and Casal, 2013; Casal et al., 2015, 2019). Conversely, the
520 strata that yielded the hadrosaurids UNPSJB-PV 1050 and UNPSJB-PV 1061, placed some
521 40–50 meters higher in section, contain a relatively abundant fossil record, including
522 stromatolites, palynomorphs (e.g., *Buttinia andreevi*, *Gabonispuris vigourouxii*), wood,
523 theropod teeth, and indeterminate eggshell fragments (Fig. 9). This diversity of fossil
524 material is congruent with the relative abundance of palynoflora during the latest
525 Maastrichtian, at least in central Patagonia (Barreda et al., 2012). In particular,
526 palynomorphs from Cerro del Hado, which were preserved in a shallow, lagoon-like
527 freshwater body, suggest a latest Maastrichtian age for this section (close to the
528 Cretaceous/Paleogene boundary), and are indicative of a warm, humid paleoclimate (Vallati

529 et al., 2016, 2020). The paleoenvironment of these upper levels of the Lago Colhué Huapi
530 Formation is interpreted as having been characterized by high sinuosity, meandering-type
531 fluvial channels. In many cases, these appear as abandoned channels associated with wide
532 floodplains (Casal et al., 2015, 2019) adjacent to a larger body of water that was fed by
533 these meandering rivers. In this regard, rising sea levels may have inundated valleys,
534 causing rivers to slow and overflow, forming lagoon-like features on the floodplains. These
535 large freshwater bodies could have been related to the proximity of the marine
536 transgression represented by the Salamanca Formation.

537 The uppermost, latest Maastrichtian levels of the Lago Colhué Huapi Formation are
538 laterally related to marine deposits (see Casal et al., 2015 and references therein) of the
539 Salamanca Formation (Maastrichtian–Danian *sensu* Barcat et al., 1989; early Danian *sensu*
540 Clyde et al., 2014 and Simeoni, 2014). Specimens UNPSJB-PV 1050 and UNPSJB-PV
541 1061 (as well as the aforementioned stromatolites, palynomorphs, wood, theropod teeth,
542 and eggshells) were recovered from sediments indicative of warm, low energy, shallow
543 lagoons within paleovalleys. Moreover, as mentioned above, this interpretation, which is
544 based on stratigraphic evidence, is further supported by the presence of baculate Arecaceae
545 pollen grains, specifically *Spinizonocolpites* (*Nypa*-type palms, which may have played an
546 important role in late Maastrichtian paleocommunities; see Barreda et al., 2012). Modern
547 *Nypa* are found in continental brackish to coastal marine environments (Vallati et al., 2016,
548 2017; De Sosa Tomas et al., 2017); therefore, this indicates that the new central Patagonian
549 hadrosaurids were directly associated with coastal plain paleoenvironments and
550 paleoecosystems. Interestingly, charcoalfied plant material identified at Cerro del Hadro
551 (Vallati et al., 2020) indicates that wildfires were relatively common in the
552 paleoenvironment represented by the upper section of the Lago Colhué Huapi Formation. A

553 similar ecological pattern has been described for other well-known latest Cretaceous
554 habitats that were also frequented by hadrosaurids (see Vajda et al., 2013).

555 At the site from which the hadrosaurid *Lapampasaurus cholinoi* was recovered,
556 Coria et al. (2012) described a tidally influenced, marginal marine paleoenvironment that
557 transitioned to a restricted, low-energy marine environment by the lower portion of the
558 upper Campanian?–lower Maastrichtian Allen Formation. Moreover, multiple hadrosaurid
559 fossils have been reported from the La Colonia Formation (Campanian–Maastrichtian,
560 Cañadón Asfalto Basin) (Hill et al. 2002; Gasparini et al., 2015), from a low-energy
561 restricted environment, probably in the central, mixed-energy zone within an estuary
562 (Gasparini et al., 2001; Boyd et al., 2006; see also Cúneo et al., 2014). Body and
563 ichnofossil evidence of hadrosaurids associated with coastal and/or marginal marine
564 paleoenvironments has also been found in other, chronologically equivalent formations in
565 Argentina and other South American countries (Table 1). The same condition characterizes
566 the strata from which UNPSJB-PV 1050 and UNPSJB-PV 1061 were collected, suggesting
567 that South American hadrosaurids may have typically been associated with these kinds of
568 paleoenvironmental patterns or conditions (see below and Table 1). Nevertheless, although
569 Coria (2011) also noted that Patagonian hadrosaurids have mostly been recovered from
570 marine-influenced depositional settings, he could not completely dismiss the possibility of
571 the presence of these ornithopods in more inland regions as well. According to Coria
572 (2011), the observed distribution of Patagonian hadrosaurids may therefore be an artifact of
573 the fossil record. In the Lago Colhué Huapi Formation, however, at least two distinct,
574 temporally successive, well-characterized paleoenvironments are present, the older of the
575 two representing an inland habitat and the younger an environment that was much closer to
576 the paleoshoreline. These settings yield two distinct ornithopod assemblages—the older

577 populated by elasmarians and the younger hadrosaurid-dominated—thus supporting the
578 hypothesis that these latter herbivorous dinosaurs may have been specifically adapted to
579 coastal paleoenvironments.

580 As mentioned above, in a regional context, the Salamanca Formation is probably
581 laterally related to the Lago Colhué Huapi Formation. The Maastrichtian levels of the
582 Salamanca Formation probably represent an Atlantic marine incursion into central
583 Patagonia (Barcat et al., 1989). This marine incursion attained its maximum during the
584 latest Maastrichtian, probably related to the climax of thermal subsidence linked with sea
585 level rise (Spalletti and Franzese, 2007). Moreover, although the Maastrichtian–Paleocene
586 marine transgressions across Patagonia occurred in a context of global sea level decline,
587 based on geodynamic processes, Gianni et al. (2018) recently suggested that dynamic
588 subsidence of the edge of the flat-slab could have caused sudden Atlantic marine
589 transgression during the Maastrichtian–early Paleocene (represented by the Salamanca
590 Formation) in the Golfo San Jorge Basin. In this regard, the putative asynchronous
591 transgression may have taken advantage of topographic depressions (e.g., fluvial valleys) in
592 the area, which may in turn have favored the generation of estuaries. Therefore, the marine
593 transgression may have started near the source of the Río Chico during the Maastrichtian
594 instead of the early Paleogene (i.e., Danian, see Clyde et al., 2014; Simeoni, 2014).
595 Moreover, this marine transgression would have been contemporaneous with the marine
596 arms of the so-called Pampeano Embayment (= Pacha Sea) and the North Patagonian
597 Embayment (= Kawas Sea), which according to Apesteguía et al. (2012) may have reached
598 as far as the North Patagonian (= Somuncurá) Massif in Chubut. Nevertheless, this marine
599 transgression clearly also extended to south-central Chubut.

600 In a geochronological context, the materials described herein come from the upper
601 portion of the Lago Colhué Huapi Formation. According to Casal et al. (2016), these levels
602 are partially or completely correlative with the Allen and Loncoche formations of the
603 Neuquén Basin, the Los Alamos, Coli Toro, and Angostura Colorada formations of the
604 North Patagonian Massif, and the Paso del Sapo and La Colonia formations of the Cañadón
605 Asfalto Basin. Furthermore, this correlation may be also extrapolated to the Austral-
606 Magallanes Basin of southernmost Argentina (e.g., Chorrillo Formation; see Novas et al.,
607 2019) and Chile (Dorotea Formation, see George et al., 2020). Finally, UNPSJB-PV 1050
608 and UNPSJB-PV 1061 constitute the first unquestionable Argentinean evidence of latest
609 Maastrichtian (i.e., close to the Cretaceous/Paleogene boundary) hadrosaurids, with the
610 possible exceptions of trackways from the Maastrichtian–Danian Yacoraite Formation of
611 Jujuy and Salta provinces in the northwestern part of the nation (Alonso, 1980, 1989;
612 Alonso and Marquillas, 1986; Díaz-Martínez et al., 2016; see Table 1). (Note, however,
613 that the purported hadrosaurid nature of many of these trackways is in doubt; Leonardi,
614 1994; C. Meyer pers. comm. to MCL.)

615 In sum, the distribution of hadrosaurids in Patagonia appears to be directly related to
616 coastal environments, suggesting a positive association between South American members
617 of this clade and these kinds of habitats. This was also directly linked to the ongoing
618 Atlantic marine transgression that influenced Patagonian basins during the Maastrichtian
619 (Gasparini et al., 2001) and that probably also impacted South American hadrosaurid
620 distribution (Fig. 8B). Moreover, this is congruent in Patagonia as a whole, where marine
621 transgression occurred during the Maastrichtian and persisted into the early Paleogene
622 (Novas et al., 2019; see also Malumián and Nájuez, 2011). In contrast, in the Northern
623 Hemisphere, the peak marine transgression occurred during the Campanian, followed by

624 regression during the Maastrichtian. Furthermore, marine-influenced environments may
625 have been a selected habitat for the hadrosaurid clade early in its evolution during the
626 Campanian of North America (Kobayashi et al., 2019). Whether or not this could have
627 affected the dispersal capabilities of these dinosaurs remains unknown.

628

629 **7. Conclusions**

630 We report fragmentary new remains that unquestionably pertain to hadrosaurid
631 ornithopods from the uppermost part of the Lago Colhué Huapi Formation (Chubut Group,
632 Golfo San Jorge Basin), close to the Cretaceous/Paleogene extinction event. The fossils
633 represent at least two ontogenetic stages (i.e., juvenile and subadult/adult) individuals.
634 Furthermore, we contend that the stratigraphically controversial holotypic partial skeleton
635 of the hadrosaurid *Secernosaurus koeneri* was also recovered from the Lago Colhué Huapi
636 Formation, probably from the same stratigraphic level as the materials described herein. At
637 the moment, all hadrosaurid fossils from central Patagonia (i.e., the Golfo San Jorge Basin)
638 have been recovered from the uppermost portion of the Lago Colhué Huapi Formation.
639 Therefore, at least in central Patagonia, these ‘duckbilled dinosaurs’ appear to have been
640 restricted to the final stages of the Cretaceous.

641 Reconstruction of the latest Maastrichtian paleoenvironment frequented by these
642 hadrosaurids indicates the occurrence of freshwater bodies and a warm, humid climate.
643 These paleoenvironmental inferences are supported by a rich and relatively abundant
644 palynoflora recovered from the same horizons. Furthermore, in a broader geological
645 context, the paleoenvironment preserved in the uppermost portion of the Lago Colhué
646 Huapi Formation may have been affected by an Atlantic marine transgression that resulted
647 in the generation of estuaries and lagoons.

648 Interestingly, two temporally successive ornithopod assemblages seem to be present
649 in the latest Cretaceous (Campanian–Maastrichtian) of southern South America. In the
650 Lago Colhué Huapi Formation, specifically, the earlier, elasmarian-dominated fauna occurs
651 in the middle (Campanian–?lower Maastrichtian) section of the unit, associated with
652 anastomosing multichannel fluvial systems and seasonally arid conditions indicative of an
653 inland paleoenvironment. The younger of the two faunas is present in the uppermost (upper
654 Maastrichtian) part of the formation and is clearly dominated by hadrosaurids. The
655 paleoenvironment inhabited by these latter ornithopods was characterized by a warm,
656 humid paleoclimate and high sinuosity, meandering-type channels and wide floodplains
657 adjacent to larger, lagoon-like bodies of water related to marine transgression. The largely
658 disjunct stratigraphic occurrence of elasmarians and hadrosaurids would appear to support a
659 previously proposed hypothesis of Patagonian ornithopod faunal turnover during the Late
660 Cretaceous. Nevertheless, it could also be an artifact of changing paleoenvironments and
661 differing habitat preferences between the two groups. Elasmarians and hadrosaurids may
662 have coexisted during the Campanian–early Maastrichtian, suggesting some type of niche
663 partitioning between the two clades during this interval. After the middle Maastrichtian,
664 however, the only ornithopods in Patagonia appear to have been hadrosaurids, suggesting
665 that these animals may have replaced elasmarians, possibly due to their being better
666 adapted to the environmental conditions and resources that prevailed at that time. This
667 could be also related to greater dietary flexibility in these herbivores relative to other
668 ornithopods (see Chin et al., 2017; Wosik et al., 2020). Therefore, the floral richness and
669 paleoenvironmental conditions of the upper portion of the Lago Colhué Huapi Formation
670 may have benefited hadrosaurids. As mentioned above, however, distinctions in
671 paleoenvironmental preferences between these two groups could also have played a role in

672 generating this apparent pattern. In this context, the distribution and putative turnover of
673 ornithopod faunas may have been directly related to the influence of marine transgressions
674 that strongly affected conditions in these Late Cretaceous paleoenvironments. In sum, (1)
675 the distribution of Late Cretaceous ornithopods in southern South America was directly
676 related to paleoenvironmental conditions; (2) the proximity of the paleoshoreline, which
677 shows a positive association, could have favored hadrosaurids over earlier-diverging
678 ornithopods such as elasmarians; and (3) the Atlantic marine transgression may have played
679 an important role in the distribution of hadrosaurids (probably starting in the northern and
680 central Patagonian basins and ending in the southernmost Patagonian basin, the Austral-
681 Magallanes Basin). Nevertheless, these hypotheses must remain tentative in the event that
682 non-hadrosaurid ornithopods are eventually recovered from the latest Cretaceous (i.e., latest
683 Maastrichtian) of South America.

684 Finally, in a broad context, the hadrosaurid materials described herein add to the
685 generally meager record of ornithopods in the Late Cretaceous of the Southern Hemisphere.
686 Moreover, these fossils add information and support to the putative paleoenvironmental and
687 geochronological correlation of the Lago Colhué Huapi Formation of the Golfo San Jorge
688 Basin to the Loncoche and Allen formations of the Neuquén Basin, the Angostura
689 Colorada, Los Alamos, and Coli Toro formations, which are well exposed in the
690 occidental section of the North Patagonian (= Somuncurá) Massif, and the La Colonia and
691 Paso del Sapo formations of the Cañadón Asfalto Basin.

692

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705

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1091 **Figure captions**

1092

1093 **Fig. 1. A,** Locality map and general geographic and geological context of Cerro del Hadro,
1094 the site in the Lago Colhué Huapi Formation of central Patagonia, Argentina that yielded
1095 the new hadrosaurid fossils (modified from Casal et al., 2020). **B,** Stratigraphic column and
1096 photograph of Cerro del Hadro showing the location of the fossils. **C–J,** Lithofacies present
1097 at the Cerro del Hadro site. **C,** Intraformational coarse conglomerate (Lf1). **D,**
1098 Intraformational fine conglomerate (Lf2). **E,** Coarse- to medium-grained sandstone that
1099 yielded the hadrosaurid remains (Lf3). **F,** Succession of fine- to coarse-grained sandstone
1100 (Lf4). **G,** Gray laminated mudstone with well-preserved palynomorphs (Lf5). **H,**
1101 Stromatolite (Lf6). **I,** White marlstone with palynomorphs (Lf7). **J,** Red mudstone typical
1102 of the Lago Colhué Huapi Formation (Lf8). Abbreviation: **Lf,** lithofacies.

1103

1104 **Fig. 2.** Hadrosauridae indet., fragments of left (UNPSJB-PV 1050/1) and right (UNPSJB-
1105 PV 1050/2; UNPSJB-PV 1050/3) dentaries. UNPSJB-PV 1050/1 in medial (**A**), ventral (**B**),
1106 and lateral (**C**) views. UNPSJB-PV 1050/2 in medial (**D**), ventral (**E**), and lateral (**F**) views.
1107 UNPSJB-PV 1050/3 in medial (**G**), ventral (**H**), and lateral (**I**) views. Abbreviations: **als,**
1108 alveolar sulci, **cp?**, coronoid process, **mkc,** Meckelian canal.

1109

1110 **Fig. 3.** Hadrosauridae indet., middle cervical vertebra (UNPSJB-PV 1061/3). **A,** anterior,
1111 **B,** posterior, **C,** ventral, and **D,** laterodorsal views. Abbreviations: **as,** anterior articular
1112 surface, **lve,** lateroventral excavation, **nc,** neural canal, **pp,** parapophysis, **ps,** posterior
1113 articular surface.

1114

1115 **Fig. 4.** Hadrosauridae indet., dorsal vertebrae (UNPSJB-PV 1050/8 and UNPSJB-PV
1116 1061/4). UNPSJB-PV 1050/8 in left (**A**) and right (**B**) lateral views. UNPSJB-PV 1061/4 in
1117 anterior (**C**), left lateral (**D**), and ventral (**E**) views. Abbreviations: **as**, anterior articular
1118 surface, **fo**, foramen, **nc**, neural canal, **ns**, neural spine, **prz**, prezygapophysis, **ps**, posterior
1119 articular surface.

1120

1121 **Fig. 5.** Hadrosauridae indet., sacral vertebrae, UNPSJB-PV 1050/4 and UNPSJB-PV
1122 1050/5 in anterior (**A, B**), posterior (**C, D**), dorsal (**E**), and ventral (**F**) views.
1123 Abbreviations: **as**, anterior articular surface, **fo**, foramen, **nc**, neural canal, **ps**, posterior
1124 articular surface, **sr**, sacral rib.

1125

1126 **Fig. 6.** Hadrosauridae indet., caudal vertebrae. UNPSJB-PV 1050/6 in anterior (**A**), right
1127 lateral (**B**), posterior (**C**), and left lateral (**D**) views. UNPSJB-PV 1061/1 in anterior (**E**),
1128 dorsal (**F**), posterior (**G**), and ventral (**H**) views. Abbreviations: **as**, anterior articular
1129 surface, **fo**, foramen, **nc**, neural canal, **ns**, neural spine, **prz**, prezygapophysis, **ps**, posterior
1130 articular surface, **rug**, rugosities.

1131

1132 **Fig. 7.** Hadrosauridae indet., pedal ungual phalanx (UNPSJB-PV 1050/9) in dorsal (**A**),
1133 ventral (**B**), proximal (**C**), and distal (**D**) views.

1134

1135 **Fig. 8.** Late Cretaceous hadrosaurid paleobiogeography in the Western Hemisphere. **A**,
1136 Hypothesized hadrosaurid dispersal events from North America to South America (no later
1137 than the late Campanian) and from South America to Antarctica (no later than the mid-
1138 Maastrichtian). Paleogeographic reconstruction redrawn after Blakey (2016). **B**,

1139 Hadrosaurid distribution in southern South America and the influence of marine
1140 transgression on Patagonian basins. Abbreviations: **An**, Antarctica, **NA**, North America,
1141 **SA**, South America. Red points in **B** indicate body fossil records; question mark indicates
1142 putative hadrosaurid ichnofossils.

1143

1144 **Fig. 9.** Schematic paleoecological reconstruction (not to scale) of the upper section of the
1145 Lago Colhué Huapi Formation at the headwaters of the Río Chico, Golfo San Jorge Basin,
1146 central Patagonia, Argentina (modified from Vallati et al., 2020). Genera in parentheses
1147 represent modern analogues for selected plant fossils.

1148

1149 **Table 1.** Comprehensive overview of the body and ichnofossil record of South American
1150 hadrosaurids with associated paleoenvironmental interpretations. Abbreviations: **Ar**,
1151 Argentina, **Bo**, Bolivia, **Ca**, Campanian, **Ch**, Chile, **e**, early, **l**, late, **m**, middle, **Ma**,
1152 Maastrichtian, **Pa**, Paleocene, **Pe**, Peru, **Sa**, Santonian. *Very probably not a hadrosaurid
1153 ichnofossil (C. Meyer pers. comm. to MCL). †Reposited at the MACN according to the
1154 relevant Paleobiology Database entry (collection 51594).

1155 **Table 1.** Comprehensive overview of the body and ichnofossil record of South American hadrosaurids with associated
 1156 paleoenvironmental interpretations. Abbreviations: **Ar**, Argentina, **Bo**, Bolivia, **Ca**, Campanian, **Ch**, Chile, **e**, early, **l**, late, **m**, middle,
 1157 **Ma**, Maastrichtian, **Pa**, Paleocene, **Pe**, Peru, **Sa**, Santonian. *Very probably not a hadrosaurid ichnofossil (C. Meyer pers. comm. to
 1158 MCL). †Reposited at the MACN according to the relevant Paleobiology Database entry (collection 51594).
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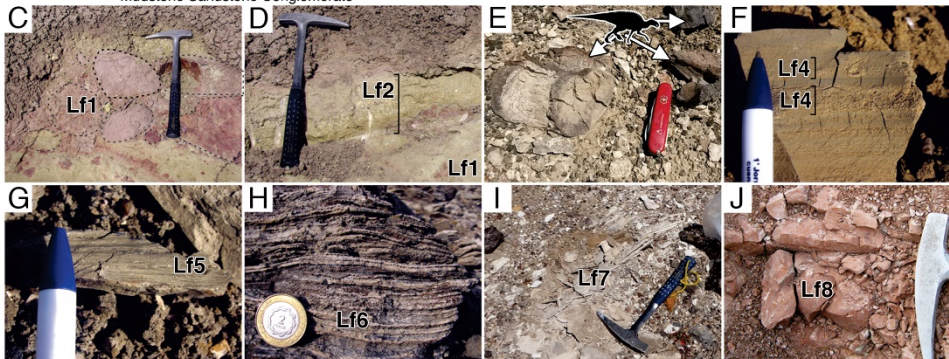
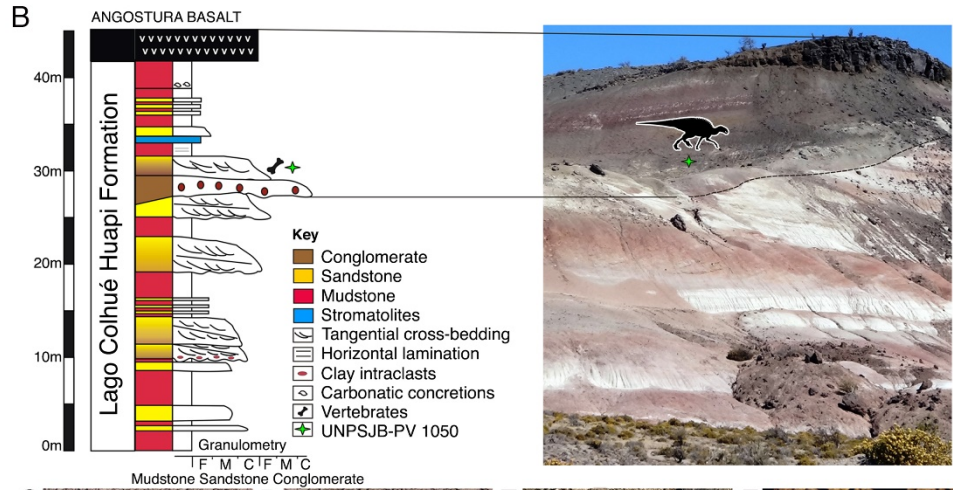
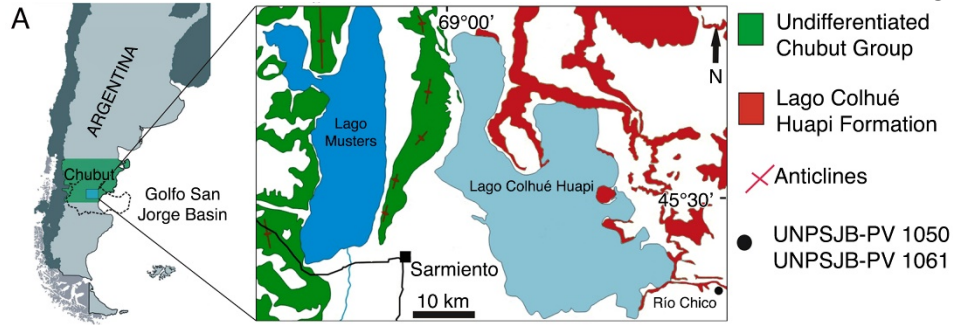
Taxon/specimen	Specimen number(s)	Formation (nation)	Stage(s)	Paleoenvironment (source)	Taxon/specimen source(s)
Body fossils					
<i>Bonapartesaurus rionegrensis</i>	MPCA-Pv-SM2	Allen (Ar)	m/l Ca–e Ma	“Moderate-energy fluvial” (Cruzado-Caballero and Powell, 2017)	Powell, 1987; Juárez Valieri et al., 2010; Cruzado-Caballero and Powell, 2017
‘ <i>Kritosaurus</i> ’ <i>australis</i> (= <i>Secernosaurus koernerii</i> ?)	MACN-RN various	Los Alamos (Ar)	l Ca–e Ma	“Lacustrine environment mixed with shallow marine sediments” (Andreis, 1987)	Bonaparte, 1984; Bonaparte et al., 1984; Bonaparte and Rougier, 1987; Salinas et al., 2006; Prieto-Marquez and Salinas, 2010; Coria, 2014; Becerra et al., 2018b
<i>Lapampasaurus cholinoi</i>	MPHN-Pv-01	Allen (Ar)	m/l Ca–e Ma	“Marginal marine conditions with tidal influence” (translated) (Coria et al., 2012)	González Riga and Casadío, 2000; Juárez Valieri et al., 2010; Coria et al., 2012
<i>Secernosaurus koernerii</i>	FMNH PP13423	Lago Colhué Huapi (Ar)	l Ma	Floodplain, proximal to paleoshoreline (this paper)	Brett-Surman, 1979; Prieto-Marquez and Salinas, 2010; this paper
Hadrosauridae indet. (= ‘ <i>Willinakaqe salitralensis</i> ’)	MPCA-Pv-SM various	Allen (Ar)	m/l Ca–e Ma	?	Juárez Valieri et al., 2010; Coria, 2014; Cruzado-Caballero and Coria, 2016; Cruzado-Caballero and Powell, 2017
Hadrosauridae indet.	Not reported	Allen (Ar)	m/l Ca–e Ma	?	Corsolini, 2014; Coria, 2016; Cruzado-Caballero, 2017

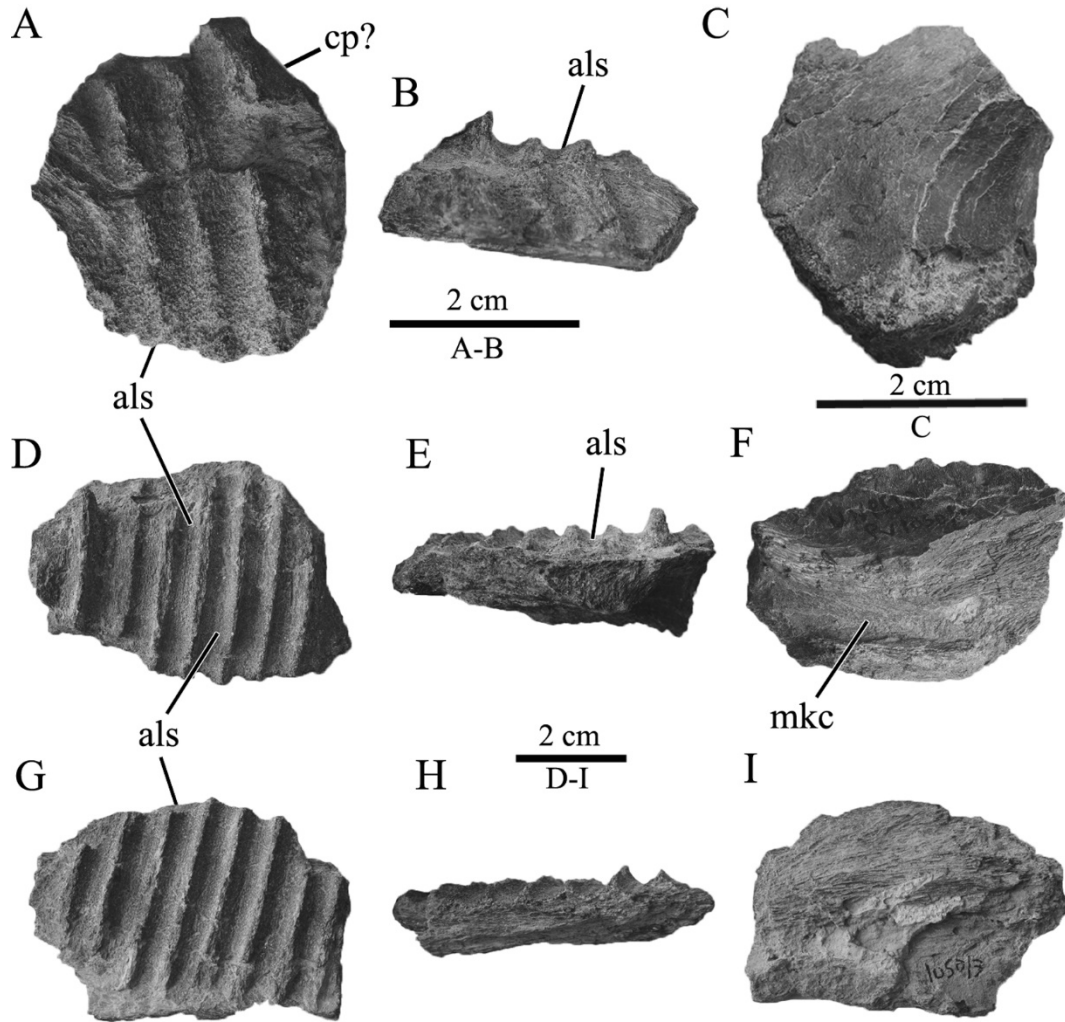
Hadrosauridae indet.	Not reported	Allen (Ar)	m/l Ca–e Ma	“Supratidal environment in close proximity to the coast” (Salgado et al., 2007)	Salgado et al., 2007
Hadrosauridae indet.	MPCA-Pv-25442–25445	Allen? (Ar)	l Ca–e Ma?	?	Cruzado-Caballero, 2017
Hadrosauridae indet.	MACN-PV RN 1085	Allen or Los Alamitos (Ar)	l Ca–e Ma	“Continental environment developed close to a marginal-litoral (sic) place” (Martinelli and Forasiepi, 2004)	Martinelli and Forasiepi, 2004
Hadrosauridae indet.	MLP 62-XII-13-1	Angostura Colorada/Coli Toro (Ar)	Ca–e/m Ma	Marine-influenced? (Casamiquela, 1964)	Casamiquela, 1964
Hadrosauridae indet.	MJHG.Pa26/9/14-1–14-57	Angostura Colorada/Coli Toro (Ar)	e Ca–m Ma	?	Cruzado-Caballero, 2015, 2017
Hadrosauridae indet. †	MACN? (numbers not reported)	Coli Toro (Ar)	Ca–Ma	Lacustrine (Casamiquela, 1978; Powell, 2003)	Casamiquela, 1978, 1980; Powell, 2003
Hadrosauridae indet.	Not reported	Dorotea (Ch)	l Ma	“Marine-influenced,” “associated with littoral environments”; “fluvial, shoreface, and deltaic” (Novas et al., 2019; George et al., 2020)	Jujihara et al., 2014; Soto-Acuña et al., 2014; Novas et al., 2019; George et al., 2020
Hadrosauridae indet.	MPEF-PV 10872, 10873, 10875	La Colonia (Ar)	Ca–Ma	“Low-energy restricted environments... probably in the central mixed-energy zone within an estuary” (Gasparini et al., 2015)	Gasparini et al., 2015

Hadrosauridae indet.	Not reported	La Colonia (Ar)	Ca–Ma	“Low-energy restricted environments... probably in the central mixed-energy zone within an estuary” (Gasparini et al., 2015)	Hill et al., 2002
Hadrosauridae indet.	UNPSJB-PV 1050, 1061	Lago Colhué Huapi (Ar)	1 Ma	Floodplain, proximal to paleoshoreline (this paper)	This paper
Hadrosauridae indet.	Not reported	Lago Colhué Huapi (Ar)	1 Ma	“Distal floodplains” (Becerra et al., 2018a)	Becerra et al., 2018a
Hadrosauridae indet.	MJHG.Pa26/9/14-59–61	Los Alamos (Ar)	1 Ca–e Ma	?	Cruzado-Caballero, 2015, 2017
Hadrosauridae indet.	MRPV 431/P–437/P	Los Alamos? (Ar)	1 Ca–e Ma	“Continental environment developed close to a marginal-litoral (sic) place” (Martinelli and Forasiepi, 2004)	Martinelli and Forasiepi, 2004; Cruzado-Caballero, 2017
Hadrosauridae indet.	Not reported	Los Alamos? (Ar)	1 Ca?–e Ma?	?	Cruzado-Caballero et al., 2018
Hadrosauridae indet.	MPEF-PV 1914–1928	Paso del Sapo (Ar)	Ca–Ma	“Littoral environment of the ‘Senoniano lacustre’” (translated) (Apesteguía et al., 2012)	Apesteguía and Cambiaso, 1999; Apesteguía et al., 2012
Hadrosauridae indet.	Not reported	Río Colorado? (Subgroup) (Ar)	Sa?–Ca?	?	Cruzado-Caballero et al., 2018
Ichnofossils					
<i>Hadrosaurichnus australis</i>	CNS-V 10.020	Yacoraite (Ar)	Ma	“Tidal flat” (Alonso, 1980)	Alonso, 1980, 1989

<i>Hadrosaurichnus titacacaensis</i>	N/A (specimens not collected)	Upper Vilquechico (Pe)	Ma	“Probably deposited in a mixed, deltaic-shallow marine environment, and might represent a progradational deltaic sequence” (Jaillard et al., 1993)	Jaillard et al., 1993
<i>Hadrosauropodus</i> isp.	N/A (specimen not collected)	Yacoraite (Ar)	Ma–Pa	“Lagoon with some tidal influence” (Díaz-Martínez et al., 2016)	Díaz-Martínez et al., 2016
<i>Taponichnus donottoi</i> *	N/A (specimen not collected)	Yacoraite (Ar)	1 Ma	“Coastal area with periodically flooded beaches” (Alonso and Marquillas, 1986)	Alonso and Marquillas, 1986; Alonso, 1989; Leonardi, 1994
<i>Telosichnus saltensis</i> *	N/A (specimen not collected)	Yacoraite (Ar)	1 Ma	“Coastal area with periodically flooded beaches” (Alonso and Marquillas, 1986)	Alonso and Marquillas, 1986; Alonso, 1989; Leonardi, 1994
<i>Tridigitichnus inopinatus</i> *	Not reported	Angostura Colorada (Ar)	Ca–Ma	“Flood plain... not very far from the sea-coast” (translated) (Casamiquela, 1987; Leonardi, 1994)	Casamiquela, 1987; Leonardi, 1994; Díaz-Martínez et al., 2015
?Hadrosauridae indet.	N/A (specimen not collected)	El Molino (Bo)	Ma	“Seasonal migration route along the shoreline and deltas of an ancient lake system” (Meyer et al., 2021)	Meyer et al., 2021
?Hadrosauridae indet.*	N/A (specimen not collected)	El Molino? (Bo)	1 Ma	?	Leonardi, 1994
?Hadrosauridae indet.	N/A (specimen not collected)	Couches Rouges (Pe)	Sa?–Ma?	“Flood plain” (Leonardi, 1994)	Leonardi, 1994; Noblet et al., 1995

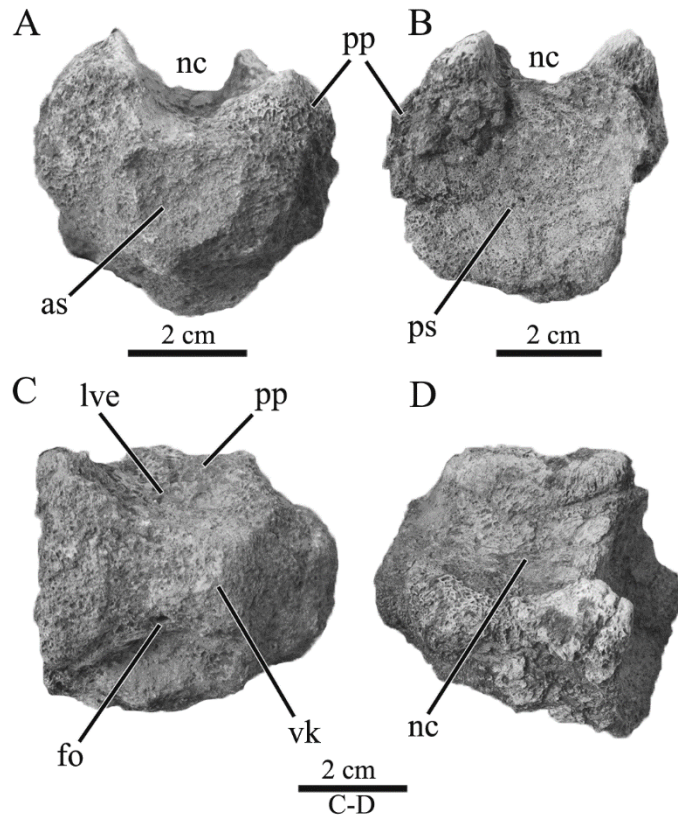
1160	?Hadrosauridae indet.*	N/A (specimen not collected)	Yacoraite? (Ar)	1 Ma?	?	Leonardi, 1994
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1197 **Figure 3**



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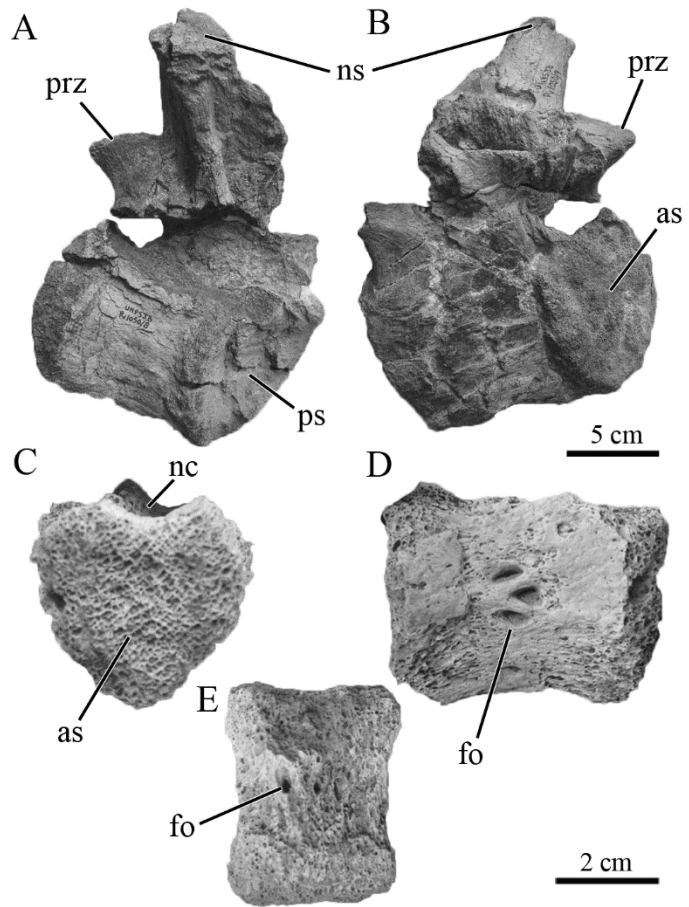
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1203 **Figure 4**

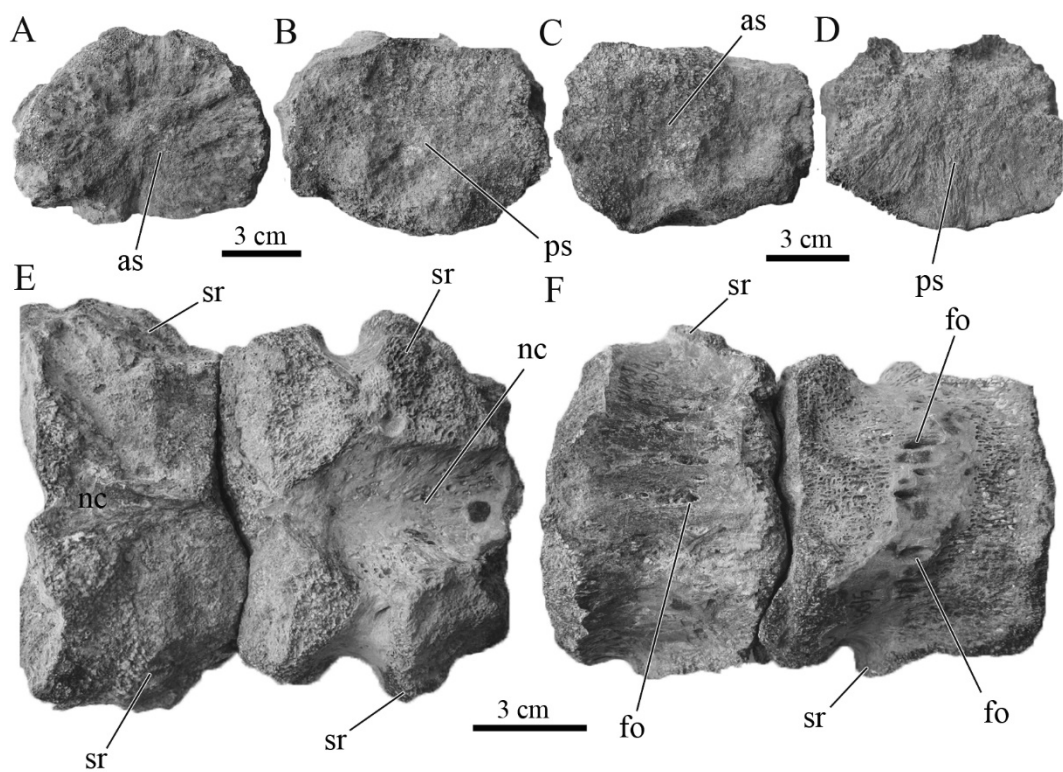


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1207 **Figure 5**



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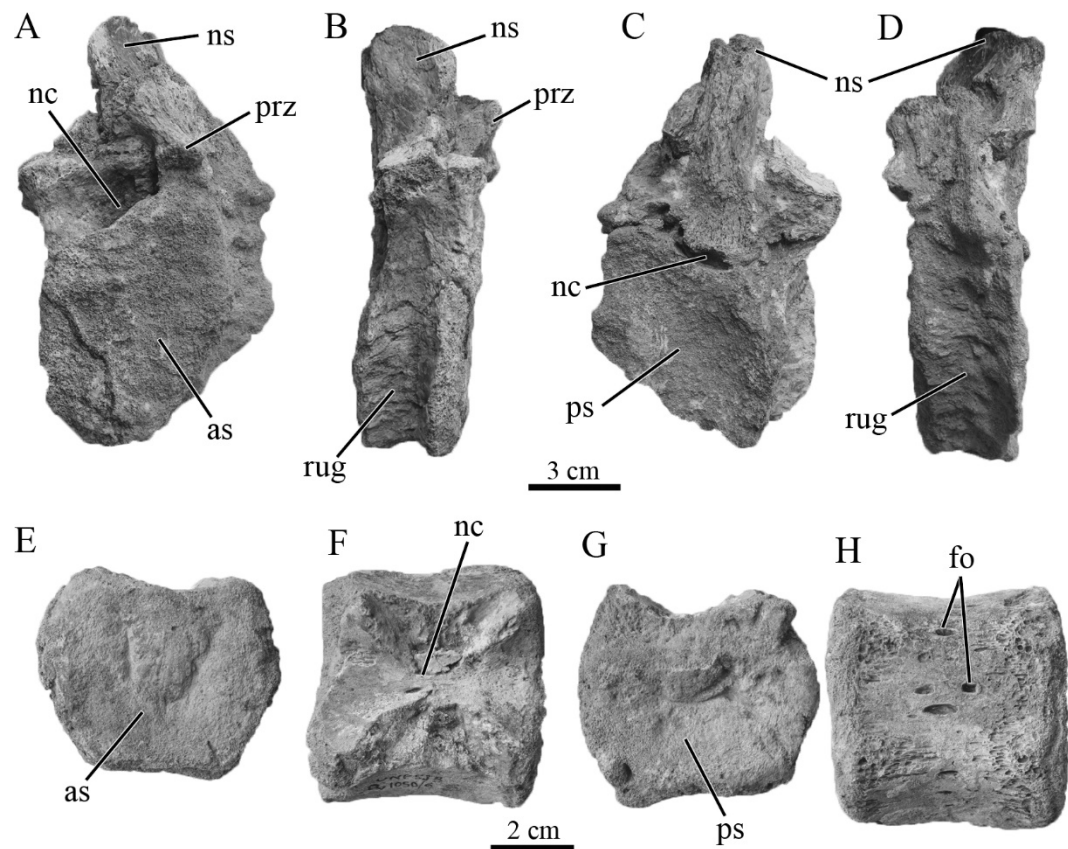
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1213 **Figure 6**



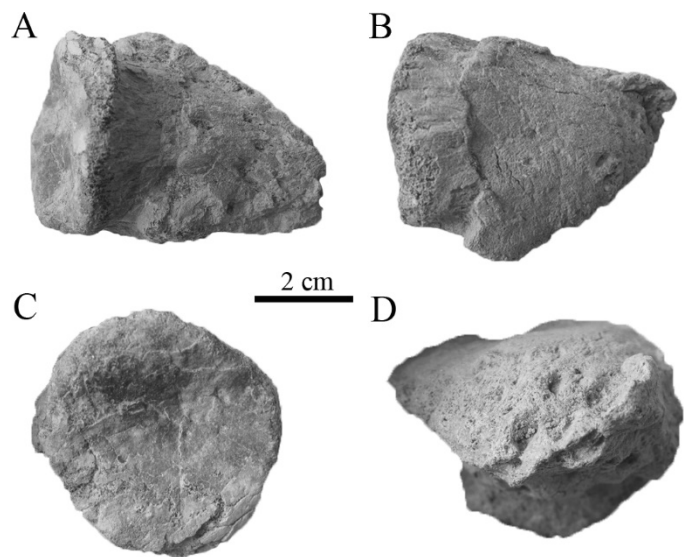
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1218 **Figure 7**



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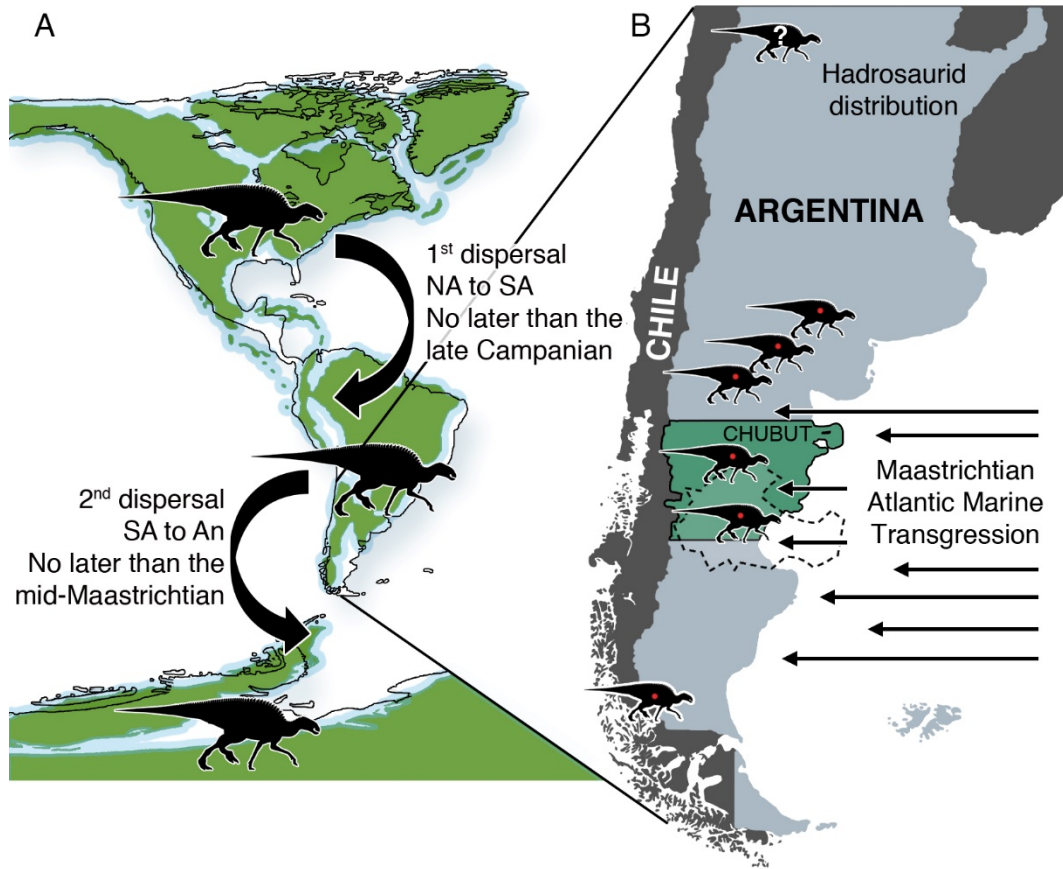
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1228 **Figure 8**



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




















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1233 **Figure 9**



References

	Podocarpaceae (<i>Dacrycarpus</i>)		Liliaceae (<i>Lilium?</i>)		<i>Catinipollis geiseltalensis</i>		<i>Spinizonocolpites riochiquensis</i>
	Dicksoniaceae (<i>Dicksonia</i>)		Areaceae (<i>Nypa</i>)		<i>Ovoidites</i> sp.		Sandstones
	Proteaceae (<i>Protea</i>)		Stromatolite		<i>Azolla</i> sp. 1 Vallati et al. 2017		Crossbedded sandstones
	Zygnemataceae (<i>Zygnema</i>)		Eggsbells		<i>Gabonisporis vigourouxii</i>		Mudstones
	Salviniaceae (<i>Azolla</i>)		<i>Dacrycarpites australiensis</i>		<i>Zlavisporis reticulatus</i>		Laminated siltstones
	Marsileaceae (<i>Marsilea</i>)		<i>Cibotidites</i> sp.		<i>Liliacitites kaitangataensis</i>		White marlstones
	Ricciaceae (<i>Riccia</i>)		<i>Proteacidites scabroratus</i>				La Angostura Basalt
							Probable Maastrichtian sea