

1 **THE FIRST CAPYBARAS (RODENTIA, CAVIIDAE, HYDROCHOERINAE)**  
2 **INVOLVED IN THE GREAT AMERICAN BIOTIC INTERCHANGE**  
3 **LOS PRIMEROS CARPINCHOS (RODENTIA, CAVIIDAE, HYDROCHOERINAE)**  
4 **PARTICIPANTES DEL GRAN INTERCAMBIO BIÓTICO AMERICANO**

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16 Pages: 22; Figures: 5. Supplementary online material: 3

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18 Heading: VUCETICH *ET AL.*: CAPYBARAS AND THE GABI

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23 **Abstract.** The new combination *Phugatherium dichroplax* nov. comb. (Ahearn and  
24 Lance, 1980) for the North American species “*Neochoerus*” *dichroplax* Ahearn and  
25 Lance, 1980 and “*N.*” *cordobai* Carranza-Castañeda and Miller, 1988 is proposed. Its  
26 biochron is here enlarged (late Early Blancan - latest Blancan; Piacenzian-Gelasian),  
27 being the youngest species of *Phugatherium* and thus extending the biochron of the  
28 genus into the Early Pleistocene. This is the first mention of a Pliocene South American  
29 lineage of capybaras crossing the Panamanian bridge, implying the recognition of a  
30 third lineage of capybaras involved in the Great American Biotic Interchange. The  
31 proposed North American origin of the genus *Neochoerus* is discussed.

32 **Keywords:** Capybaras. Pliocene. North America. GABI

33

34 **Resumen.** LOS CARPINCHOS (RODENTIA, CAVIIDAE, HYDROCHOERINAE) Y  
35 EL GRAN INTERCAMBIO BIÓTICO AMERICANO. Se propone la nueva  
36 combinación *Phugatherium dichroplax* nov. comb. (Ahearn y Lance, 1980) para las  
37 especies “*Neochoerus*” *dichroplax* Ahearn y Lance, 1980 y “*N.*” *cordobai* Carranza-  
38 Castañeda y Miller, 1988 de América del Norte. Esta es la especie más joven del  
39 género. En este trabajo se extiende el biocrón de la especie (Blanquense tardío  
40 Temprano a Blanquense más Tardío; Piacenciano-Gelasiano) así como el del género  
41 hasta el Pleistoceno Temprano. Esta es la primera mención de un linaje de carpinchos  
42 pliocénicos sudamericanos que atraviesan el puente de Panamá, implicando el  
43 reconocimiento de un tercer linaje de carpinchos involucrado en el Gran Intercambio  
44 Biótico Americano. Se discute el origen norteamericano del género *Neochoerus*.

45 **Palabras clave.** Carpinchos. Plioceno. América del Norte. GABI.

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49 THE so called Great American Biotic Interchange (GABI) is the process by which North  
50 and South America, which had been separated during most of the Cenozoic, exchanged  
51 their biotas through the Panamanian corridor (see Morgan, 2008; Woodburne, 2010 and  
52 literature therein). Although there is evidence indicating that the interchange began in  
53 the late Miocene (about 9 Ma), its major phase began during the Late Pliocene and had  
54 its acme in the Latest Pliocene-Early Pleistocene (Woodburne, 2010; Fig. 1). Two  
55 lineages of South American rodents (porcupines and capybaras) were among the legions  
56 that crossed the isthmus from South to North America. Up to date, it was generally  
57 thought that the capybaras that reached North America pertained to the most derived  
58 Pleistocene lineage found in South America, the genera *Neochoerus* Hay 1926 and  
59 *Hydrochoerus* Brisson 1762. Their occurrence in the North American Pliocene raised  
60 several doubts since they would be older than their South American ancestors (Webb,  
61 1985; Woodburne, 2010; Woodburne et al., 2006).

62 Capybaras are a unique group of rodents, with ever-growing cheek teeth that  
63 increase in size and change in occlusal morphology through life. The change is caused  
64 partly by generation of structures after birth and by their allometric growth (Vucetich et  
65 al., 2005, 2014a; Deschamps et al., 2007, 2009). These characteristics caused some  
66 confusion when interpreting the fossil record, and led to regard them as taxonomically  
67 highly diverse. Small species with simple dental morphology were considered as  
68 primitive, and large species with complicated cheek teeth, as derived. In the past ten  
69 years Vucetich et al. (2005) began the revision of the late Miocene –Pliocene South  
70 American capybaras and stated that in each locality small specimens were juveniles of  
71 the species represented by large specimens. This new taxonomic paradigm led to a  
72 reduction of nominal taxa and a better comprehension of the species limits (Vucetich et

73 al., 2005, 2014a, b; Deschamps et al., 2007, 2009). They also made the first  
74 phylogenetic analyses that helped to understand their relationships, resulting in the  
75 Pleistocene clade *Nechoerus-Hydrochoerus* the sister group of the Pliocene  
76 *Phugatherium* (Pérez et al, 2014; Vucetich et al., 2014a). All this new knowledge  
77 showed that extinct species had short stratigraphic ranges (Fig. 1) (partly because of  
78 their physiological requirements) and relatively wide geographic distributions,  
79 establishing them useful as biostratigraphic tools (Deschamps et al., 2013).

80 In this paper, we begin the revision of the genus *Nechoerus* Hay 1926 with the  
81 study of the Pliocene North American species *N. dichroplax* Ahearn and Lance, 1980  
82 and *N. cordobai* Carranza-Castañeda and Miller, 1988.

83

#### 84 MATERIALS AND METHODS

85 The following materials housed in the American Museum of Natural History  
86 were revised: F: AM 107680 (crashed skull with crashed left and right P4-M3), 107685  
87 (edentulous partial left dentary), 107688 (partial dentary), 107689 (right dentary with  
88 p4-m1), 107691 (left maxillary fragment with M2-3), 107692 (partial palate with left  
89 P4-M3 and right P4-M1 and M3); 107694 (left M1-M2 and partial M3 and right P4-  
90 M2), 107695 (maxillary fragment with left M3), and the cast F: AM 105010 of TRO  
91 564 (left dentary fragment with p4-m2 assigned in schedis to ? *Hydrochoerus* and to  
92 *Nechoerus* (?) *pinckneyi* by Mones in 1978). The following illustrations (Ahearn and  
93 Lance, 1980; Mones, 1980) were also used in this study: F: AM 107686 (partial dentary  
94 with p4) , 107693 (right m1-m2), UALP 1183 (right M3) and 1225 (left m3), and SAF  
95 9-13 (left m1-m2).

96 They were compared with *Phugatherium catacliticum* Ameghino, 1887 from  
97 the early Pliocene Monte Hermoso Formation, Argentina, *P. novum* (Ameghino, 1908)

98 from the early late Pliocene Chapadmalal Formation, Argentina, *Hydrochoeropsis*  
99 *dasseni* Kraglievich, 1930 from the late Pliocene Uquía Formation, Argentina,  
100 *Nechoerus* sp. (MMH 08-04-02 and UNSGH 645) from the Pleistocene of southern  
101 Buenos Aires Province, Argentina, and illustrations of *Phugatherium saavedrai*  
102 (Hoffstetter, Villarroel and Rodrigo, 1984) from the Pliocene Umala Formation,  
103 Bolivia, and *Nechoerus cordobai* Carranza-Castañeda and Miller, 1988 from the late  
104 Pliocene of San Miguel de Allende, Guanajuato, Mexico.

105 Although in many papers about the GABI the authors use the “short Pleistocene”  
106 for the chronologic Time scale (e.g. Morgan, 2008; Woodburne, 2010), here the  
107 International Stratigraphic Chart with the Plio-Pleistocene boundary at 2.588 Ma is  
108 followed.

109 ***Institutional abbreviations.*** **F: AM**, Frick Collection, American Museum of Natural  
110 History, New York, USA; **Fcs**, Facultad de Ciencias Sociales, Universidad Nacional del  
111 Centro, Argentina; **IGCU**, Museo de Paleontología de Vertebrados del Instituto de  
112 Geología de la Universidad Autónoma de México; **MACN Pv**, Museo Argentino de  
113 Ciencias Naturales, Vertebrate Paleontology Collection, Buenos Aires, Argentina; **MD**,  
114 Museo Darwin, Punta Alta, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina;  
115 **MMH**, Museo de Monte Hermoso, Monte Hermoso, Argentina; **MMP**, Museo  
116 Municipal de Mar del Plata, Mar del Plata, Argentina; **MNHN Bol**, Museo Nacional de  
117 Historia Natural, La Paz, Bolivia; **UALP**, University of Arizona, Laboratory of  
118 Paleontology, Tucson, USA; **UNSGH**, Cátedra de Geología Histórica, Universidad  
119 Nacional del Sur, Argentina.

120 ***Nomenclature and anatomical abbreviations.*** Tooth terminology is explained in Fig. 2.  
121

122 **TAXONOMICAL BACKGROUND**

123 Mones (1991), in his last revision of the family Hydrochoeridae, recognized five  
124 valid species for the genus *Nechoerus* Hay 1926: *N. dichroplax* Ahearn and Lance,  
125 1980; *N. tarijensis* (Ameghino, 1902); *N. fontanai* (Rusconi, 1933); *N. sulcidens* (Lund,  
126 1839), and *N. aesopi* (Leidy, 1853).

127 The geographic and stratigraphic provenance of the type specimens of each  
128 taxon reported by Mones (1991) is: *N. dichroplax*, Arizona, North America, late  
129 Blancan, late Pliocene; *N. tarijensis*, Bolivia, Tarija, Ensenadan?, middle Pleistocene?  
130 (currently Ensenadan, Pleistocene in age; Tonni et al., 2009); *N. fontanai*, Argentina,  
131 Buenos Aires, late Pliocene-early Pleistocene, “Puelchense” (currently considered  
132 Pleistocene in age; Soibelzon et al., 2005); *N. sulcidens*, Brasil, Lagoa Santa, Lujanian,  
133 late Pleistocene, and *N. aesopi*, North America, South Carolina, Rancholabrean, late  
134 Pleistocene (Fig. 1).

135 According to Mones (1984, 1991) *N. dichroplax* is also reported for the late  
136 Pliocene of Guanajuato, Mexico through its synonyms *Nechoerus* sp. nov. A and B  
137 Carranza-Castañeda, Ferrusquía-Villafranca and Miller, 1981 (or *N. cordobai* and  
138 *Nechoerus* sp. respectively in Carranza-Castañeda and Miller, 1988). In this way, the  
139 late Pliocene record of North American capybaras includes one species, *Nechoerus*  
140 *dichroplax*, or three, *N. dichroplax*, *N. cordobai*, and *Nechoerus* sp.

141 Other capybaras recorded in the Plio-Pleistocene of North America include  
142 *Nechoerus aesopi*, *N. pinckneyi* Hay, 1923 and *Hydrochoerus holmesi* Simpson, 1928  
143 whose validity is controversial (see Mones, 1991; Baskin and Thomas, 2007; Morgan,  
144 2005, 2008). Even the Pliocene provenance of some of them is dubious (Sanders, 2002:  
145 101-102; Morgan, 2008: 122).

## 146 SYSTEMATIC PALEONTOLOGY

147 Order RODENTIA Bowdich, 1821

148 Suborder HYSTRICOGNATHI Tullberg, 1899  
149 Superfamily CAVIOIDEA (Fischer, 1817) Kraglievich, 1930  
150 Family CAVIIDAE Fischer, 1817  
151 Subfamily HYDROCHOERINAE (Gray, 1825) Gill, 1872: Weber, 1928 sensu Kraglievich,  
152 1930  
153 Genus *Phugatherium* Ameghino, 1887  
154 **Type species.** *Phugatherium cataclisticum* Ameghino, 1887; fixed by monotypy.  
155 Montehermosan, early Pliocene, Argentina.  
156 **Included species.** *P. cataclisticum*, *P. novum*, *P. saavedrai*, *P. dichroplax*  
157 **Additions to the diagnosis** (see Vucetich et al., 2014a). The p4 (Fig. 1) with C3 well  
158 defined by deep h.2i. and h.3i. at least reaching 50% of the width of the tooth, equal in  
159 depth or h.3i. deeper; both within the pr.I (ahead the h.f.e.).  
160 **Distribution.** Montehermosan-Chapadmalalan (Zanclean-early Piacenzian) of South  
161 America, and late Early-latest Blancan (Piacenzian- Gelasian) of North America (Fig.  
162 1).  
163 ***Phugatherium dichroplax* nov.comb.**  
164 Figures 3.1-2, 3.9, 4.1-3  
165 *Nechoerus dichroplax* Ahearn and Lance, 1980  
166 *Nechoerus lancei* Mones, 1980  
167 *Nechoerus cordobai* Carranza-Castañeda and Miller, 1988 (= *Nechoerus* sp. nov. A  
168 Carranza-Castañeda, Ferrusquía-Villafranca and Miller, 1981)  
169 *Nechoerus* sp. nov. B Carranza-Castañeda, Ferrusquía-Villafranca and Miller, 1981  
170 (= *Nechoerus* sp. Carranza-Castañeda and Miller, 1988)  
171 **Holotype.** F: AM 107691, left M2-M3.

172 **Type locality.** Dry Mountain (=111 Ranch; Mones, 1991; Morgan, 2005), San Simon  
173 Creek, Graham County, Arizona.

174 **Holotype of synonyms.** *Nechoerus lancei* UALP 1183, large palatal fragment with  
175 right P4-M3 and left P4-M1 and M3; *Nechoerus cordobai* IGCU 6170, skull fragment.

176 **Emended diagnosis.** *P. dichroplax* differs from the other species of *Phugatherium* by  
177 the deep h.s.e. of pr.IIb of m3 that reaches 50% of the prism width (Fig. 3.9). In p4 h.2i.  
178 and h.3i. reach 75% the prism width defining a long drop-shaped C3 (Figs. 1, 3.1–2);  
179 pr.I has thin walls more lingually divergent than in the other species. M3 with external  
180 fissures in almost every prism, deeper (up to 35% the width of the prism) in prisms 4  
181 and 5 (Figs. 4.1–4), intermediate in depth between *P. novum* (Fig. 4.6) and *P.*  
182 *catacliticum* (Figs. 2.3, 4.7).

183 **Geographic and temporal distribution.** The localities mentioned by Ahearn and Lance  
184 (1980) and Mones (1980); plus San Miguel de Allende, Guanajuato, Mexico (Carranza-  
185 Castañeda and Miller (1988) and Inglis-1A, Citrus County, Florida; late Early Blancan  
186 to Latest Blancan (Fig. 1).

187 **Relationships of *Phugatherium dichroplax***

188 “*Nechoerus*” *dichroplax* was defined by Ahearn and Lance in 1980 upon remains  
189 found in North America (Arizona and Florida). The materials of the hypodigm from  
190 Florida (Sommer’s Pit and Mule Pen Quarry) listed but not illustrated by Ahearn and  
191 Lance (1980), as well as those from the Macasphalt Shell Pit and Kissimmee River  
192 (Morgan and Hulbert, 1995; Morgan, 2005: Table 1) have not been revised. Mones  
193 (1980) described the species *N. lancei* upon the same remains (holotype UALP 1183  
194 from the 111 Ranch Beds, Graham County, Arizona). The type specimens of each  
195 species are not the same, but they are included in the hypodigm of the other. Mones  
196 (1981) reported this issue and synonymized both species as *Nechoerus dichroplax*



197 Ahearn and Lance, 1980 by priority. Later, Mones (1984) included in the synonymy two  
198 species described on materials from the early Blancan (late Pliocene) of Guanajuato,  
199 Mexico: *Neochoerus* sp. nov. A and *N.* sp. nov. B (*N. cordobai* and *Neochoerus* sp.  
200 respectively, in Carranza-Castañeda and Miller, 1988).

201 The assignment of the specimens to the genus *Neochoerus* raised several doubts  
202 from the beginning. Mones (1980) said that the morphological cranio-dental features of  
203 “*N. lancei*” suggested that the generic assignment of the species could be controversial  
204 because of the structure of the p4 very similar to that of *Chapalmatherium irenense*  
205 Reig 1958 (Fig. 3.3; currently considered a juvenile specimen of *Phugatherium*  
206 *catacliticum*, Fig. 3.7; see Vucetich et al., 2014b and Deschamps et al., 2013), and the  
207 structure of the M3 similar to “Protohydrochoerinae” (then including  
208 *Protohydrochoerus* and *Chapalmatherium*, both junior synonyms of *Phugatherium*) and  
209 *Hydrochoeropsis* Kraglievich, 1930 (Fig. 4.8; see revision in Vucetich et al., 2014b).

210 The analysis of the molariforms, in the context of the South American species,  
211 suggests that the specimens on which “*N.* *dichroplax*” is based would not pertain to the  
212 genus *Neochoerus*, but to *Phugatherium*. The main characters on which this statement is  
213 based are: 1) the deep h.2i. and h.3i. in pr.I of p4 defining a conspicuous and  
214 transversally long C3 (in *Neochoerus* the h.3i. is opposite or posterior to h.f.e.; see Figs.  
215 2, 3.2, 3.8), and 2) the M3 with external fissures (Figs. 2, 4) in all (or almost all) the  
216 prisms like in all the species of South American *Phugatherium*. In *Hydrochoeropsis*  
217 these fissures are present only in the anterior prisms (2 to 6; Fig. 4.8). They are  
218 exceptional and very shallow in *Neochoerus* (Fig. 4.9), and absent in *Hydrochoerus*  
219 (Fig. 4.10). Mones (1975, 1980) considered that these fissures appeared several times  
220 among fossil capybaras, but new analyses showed that they are conspicuous only in the  
221 species of *Phugatherium* and in *Hydrochoeropsis*. These fissures are present already in

222 the late Miocene *Cardiatherium* (Fig. 1) as a smooth continuous wave along the  
223 external face of the M3. However, *Cardiatherium* is very different from the other  
224 capybaras because the prisms are still united (Mones, 1991; Vucetich et al., 2005;  
225 Deschamps et al., 2013).

226 The m3 with a deep h.s.e. of pr.IIb (Fig. 3.9) is intermediate between  
227 *Phugatherium* (Figs. 3.3–4, 3.6–7) and *Neochoerus* (Fig. 3.8) and was interpreted by  
228 Mones (1980) as more closely related to the latter. But as there is a gradual deepening  
229 of the fissures in the evolution of capybaras (Vucetich et al., 2005; Vieytes and  
230 Deschamps, 2007), this could be a character state more derived than in the other species  
231 of *Phugatherium*. This tooth is unknown in *Hydrochoeropsis*.

232 The mandible has longer diastema and symphysis than in *Neochoerus* (Mones,  
233 1980). In *Phugatherium* the diastema is longer than p4-m3, except for *P. saavedrai* in  
234 which it is approximately equal in length (Hoffstetter et al., 1984). But the holotype of  
235 *P. saavedrai* is small, and the relatively short symphysis could be a juvenile character as  
236 seen in modern capybaras (pers. ob.). In *Neochoerus* the diastema is much shorter than  
237 p4-m3. In *P. dichroplax*, the posterior margin of the symphysis area has a dorsal  
238 entrance not seen in *Neochoerus*, but present in *P. novum* and *P. cataclisticum* (Mones,  
239 1980, Plate 1, 5). The mandible is unknown in *Hydrochoeropsis*.

240 *Phugatherium dichroplax* differs from the other species of the genus in the  
241 configuration of the p4 (Figs. 3.1–2), with the h.2i. deeper than h.3i. (up to 75% of the  
242 tooth) determining a drop-shaped C3 (column of pr. II). This is clearly observed in  
243 specimens F: AM 107689 (Figs. 3.1–2; p4 AP=1.88 cm) and F: AM 107686 (=SAF 9-  
244 19 in Mones, 1980). In *P. novum* (Fig. 3.6) these fissures are sub equal in depth, and a  
245 little shallower than in *P. dichroplax*. In *P. cataclisticum*, the h.3i. is slightly shorter  
246 than h.2i. which turns forwards, and the secondary anterior prism (pr.s.a., Fig. 2) is very

247 different as a whole (Fig. 3.7). In *P. saavedrai* (Fig. 3.4) these fissures and the drop-  
248 shaped C3 are similar to those of *P. dichroplax*, but the margins of the prism are less  
249 divergent. This specimen can be a juvenile according to its size (Deschamps et al.,  
250 2013).

251 The pr. IIb of m3 is Y shaped (Fig. 3.9), with a marked external fissure (h.s.e.),  
252 which reaches up to 50% of the width of the tooth. It differs from the South American  
253 species of *Phugatherium*, in which the h.s.e. is very shallow (Fig. 3.11), or short (Fig.  
254 3.10). It is also different from that of *Neochoerus* (Fig. 3.8) in which pr.IIb is V shaped  
255 because the h.s.e. reaches almost the labial side.

256 The M3 has 16 prisms depressed on the labial side, and in some specimens, with  
257 marked external fissures up to 33% of the width of the tooth in prisms 4 and 5 (Fig. 4.1-  
258 4). This is observed in specimens F: AM 107680) and F: AM 107695 (Fig. 4.2). The  
259 number of prisms in *Phugatherium* varies between 11 and 18 depending at least  
260 partially on the age of the specimen, because they increase with age (Vucetich et al.  
261 2014b). In *P. catacliticum* (Fig. 4.7) these fissures are very deep in prisms 4 to 6. In *P.*  
262 *novum* (Fig. 4.6) all fissures are shallow, and in *P. saavedrai* (Fig. 4.5), they are deeper  
263 in 3 and 4.

264 The characters that define *P. dichroplax* (the typical shape of p4, m3 and M3)  
265 are also present in "*N.* *cordobai*. Hence, we follow Mones (1984, 1991) considering  
266 this species a junior synonym of *P. dichroplax*. The characters described and figured of  
267 *Neochoerus* sp. (Carranza-Castañeda and Miller, 1988) from the same site as *P.*  
268 *cordobai* do not permit a precise determination. However the presence of two species in  
269 a single locality would be an exception in the capybaras record. Recently, it was  
270 proposed that the different morphs found in each locality actually represent individuals  
271 of different ontogenetic stages of a population or successive populations, rather than a

272 multiplicity of coeval species in different stages of evolution (Deschamps et al., 2007,  
273 2013; Vucetich et al., 2014a,b).

#### 274 ***Phylogenetic analysis***

275 In order to test the phylogenetic position of *P. dichroplax* nov. comb. within  
276 Caviidae, a cladistics analysis was performed using the combined matrix of Vucetich et  
277 al. (2014a) with identical methodology (Supplementary Information Online 1). We  
278 included *P. dichroplax* nov. comb. and added four new morphological characters  
279 (Supplementary Information Online 2), resulting a combined matrix of 4406 characters  
280 and 52 taxa (Supplementary Information Online 3).

281 The parsimony analysis resulted in 4116 most parsimonious trees (MPTs) of  
282 3182 steps and *P. dichroplax* nov. comb. is depicted in all MPTs nested within  
283 *Phugatherium*. The reduced consensus (ignoring the alternative positions of four  
284 unstable taxa; Supplementary Information Online 1) retrieves the three major living  
285 lineages of Caviidae: Caviinae, Hydrochoerinae and Dolichotinae.

286 *Phugatherium* (node A, Fig. 5) forms a monophyletic group and the  
287 synapomorphies of the genus are: first five laminar prisms of M3 with deep external  
288 fissures (character 97[2]). *P. novum* is the most basal species of this genus (node A, Fig.  
289 5). The node of *P. catacliticum* and more derived species (node B, Fig. 5) is supported  
290 by only one unambiguous synapomorphy: h.t.i. in m2 crossing the prism but not  
291 splitting (character 43[1]). The close relationship between *P. dichroplax* nov. comb. and  
292 *P. saavedrai* (node C, Fig. 5) is the long C3 (character 92[2]). In addition,  
293 *Hydrochoeropsis* is basal to *Phugatherium* and this clade is the sister group of the node  
294 formed by *Hydrochoerus* and *Nechoerus* (Fig. 5).

295

#### 296 **DISCUSSION**

297           The genus *Phugatherium* was known so far only in the Pliocene of southern  
298 South America, with the species *P. catacliticum* from the Monte Hermoso Formation  
299 (between 5 and 4.5 Ma), *P. novum* from the Chapadmalal Formation (4 to 3.3 Ma) and  
300 Calera Avellaneda, and the northernmost record *P. saavedrai* from the Umala  
301 Formation, Bolivia (see details in Deschamps et al., 2013; Vucetich et al., 2014a).  
302 Moreno-Bernal et al. (2013) reported the genus “*Chapalmatherium*” from the Castilletes  
303 Formation, northern Colombia, but the assignment could not be verified because no  
304 illustrations or descriptions were provided. As well, an isolated and fragmented  
305 specimen found in Pliocene sediments of Venezuela was tentatively assigned to  
306 *Cardiatherium* (Vucetich et al., 2010), but it is a very small specimen and could be a  
307 juvenile of a more derived capybara.

308           The species newly referred to *Phugatherium*, *P. dichroplax*, was so far  
309 considered to be restricted to the early Late Blancan (3.0-2.2 Ma), but in this paper its  
310 biochron is substantially extended. On the one hand the reassignment of “*Neochoerus*”  
311 *cordobai* (Mexico) as a junior synonym of *P. dichroplax* extends the biochron back to  
312 the late Early Blancan (<3.6 Ma). On the other hand, the recognition of *P. dichroplax* in  
313 Inglis-1A (TRO 564) extends it up to the Latest Blancan (2.2-1.8 Ma). Another  
314 capybara is already mentioned for this locality, *Hydrochoerus holmesi* (e.g., Morgan,  
315 2005), but this report could not be corroborated. If it were so, this will represent an  
316 exceptional case among hydrochoerids with two different species living together in  
317 sympatry. Besides, this new assignment greatly enlarges the geographical distribution of  
318 the genus, and extends its biochron into the Early Pleistocene (Fig. 1).

319           The taxonomical reassignment of the North American materials originally  
320 described as *Neochoerus dichroplax* has several implications in the understanding of  
321 which groups participated in the northward dispersal of South American mammals

322 during the GABI. From a biogeographical standpoint it corroborates that *Phugatherium*  
323 must have been living in northern South America at least before 3.6 Ma, when it is  
324 recorded in Guanajuato, Mexico (Carranza-Castañeda and Miller, 2004). The presence  
325 of this lineage in North America proves that two main lineages of capybaras entered  
326 across the Panama land bridge. One of them is the lineage of *Phugatherium*. This is the  
327 first mention of a Pliocene South American lineage of capybaras crossing the  
328 Panamanian bridge. *Phugatherium* is recorded in Mexico at 3.6 Ma (Carranza-  
329 Castañeda and Miller, 2004) reaching Florida and Arizona, their northernmost record, at  
330 about 2.7 Ma (Morgan, 2005). The other lineage is that of *Nechoerus-Hydrochoerus*.  
331 The differentiation between both genera is made on the basis of characters of the skull  
332 (see diagnosis of *Hydrochoerus* in Mones, 1991) and the extent of the masseteric ridge  
333 on the lateral side of the mandible (sensu Ahearn and Lance, 1980). Hence, the  
334 identification of fragmentary material or exclusively teeth has not been well supported  
335 yet. This issue will be discussed in a future work, but it must be taken into account  
336 when making inferences about the age of their records, since it is possible that some  
337 assignments are not correct. This lineage is certainly represented in the Pleistocene with  
338 *N. aesopi*, *N. pinckneyi* and *H. holmesi*. The Pliocene records of the two latter must be  
339 revised both taxonomically and stratigraphically. If the presence of both *Nechoerus*  
340 and *Hydrochoerus* in North America is confirmed there would be three capybara  
341 lineages involved in the GABI.

342         The genus *Nechoerus* is first recorded in South America in the Pleistocene,  
343 although in accordance with phylogenetic analysis (Vucetich et al., 2014a), its  
344 differentiation from the Pliocene *Phugatherium* would be older. The lineage  
345 *Nechoerus-Hydrochoerus* would have been restricted to Neotropical South America in  
346 the Pliocene, where the fossil record is very scanty and Pliocene hydrochoerines have

347 not been well studied yet. If this is correct, it could explain the presence of *N. pinckneyi*  
348 in Pliocene sediments of temperate North America (Sanders, 2002: 101-102; Morgan,  
349 2008: 122; Woodburne, 2010: 250).

350         Based on the previous taxonomic assignments it had been proposed that  
351 *Nechoerus* could have originated in Central America (Woodburne et al., 2006;  
352 Woodburne, 2010) because it was recorded since the Pliocene, whereas in South  
353 America, only since the middle Pleistocene. The assignment of the species “*dichroplax*”  
354 to *Phugatherium* weakens this statement because the records of *Phugatherium* in South  
355 America are about two My older. Moreover, even if the assignments of the Pliocene  
356 North American records of *Nechoerus* is confirmed, this would not prove a North  
357 American origin because the dichotomy from the *Phugatherium* lineage is older than the  
358 Pliocene (Vucetich et al., 2014a; see above). No capybaras have been recorded in North  
359 America previous to the Pliocene, whereas in South America they are recorded since the  
360 late Miocene (Pérez and Pol, 2012; Deschamps et al., 2007 and literature therein). This  
361 would be in accordance with Webb (1985: 375-376) who suggested that this  
362 discrepancy in the record would be an artifact.

363         Modern capybaras inhabit areas around ponds, lakes, rivers, marshes and  
364 swamps, using water primarily as refuge but also for basic physiological requirements  
365 as temperature regulation (Nowak and Paradiso, 1983, Herrera, 2012). In South  
366 America, all of the lithological units bearing capybaras have been interpreted as  
367 deposited in water-related settings, mostly fluvial deposits, but also karstic landscapes  
368 or travertine deposits formed by hydrothermal processes (Deschamps et al., 2013).  
369 Accordingly, in North America *Phugatherium dichroplax* nov. comb. was found in  
370 water-related sediments. The sediments that yielded the capybaras from Guanajuato are  
371 horizontal deposits of flood plains (Carranza-Castañeda and Miller, 1988). The

372 composite stratigraphic section in the 111 Ranch area, Arizona, consists of fluvial and  
373 lacustrine sediments (Morgan and White, 2005). The Florida sites Macasphalt Shell Pit  
374 and Kissimmee River were formed by accumulations from freshwater and nearshore  
375 settings in a shallow marine depositional environment; and Haile 15A consists of  
376 undifferentiated sands and clays filling a karst fissure developed in marine Eocene  
377 limestone (Morgan, 2005). This suggests that *P. dichroplax* nov. comb. had ecological  
378 requirements similar to modern capybaras. Hence, the dispersal route from South  
379 America through the Panamanian bridge to central Mexico, and temperate North  
380 America during the Pliocene must have been scattered with permanent water bodies.

381

#### 382 **ACKNOWLEDGEMENTS**

383 We thank J. Meng and J. Flynn (AMNH, USA), M. Reguero (MLP), A.G. Kramarz  
384 (MACN) who gently allowed the study of materials under their care. G. Morgan and A.  
385 Mones made thoughtful comments that helped improving the manuscript. This paper  
386 was partially supported by Grants of Agencia Nacional de Promoción Científica y  
387 Tecnológica PICT 2012-1483 (MGV) and PICT 2010-2613 (MEP), and Universidad  
388 Nacional de La Plata N11-674.

389

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548

### 549 **Captions for figures**

550 Fig. 1. Stratigraphic chart with the record of extinct capybaras, and the Global, North  
551 and South American stages/ages. Scales based on the International Stratigraphic  
552 chart (2013), Deschamps et al. (2013), Verzi and Quintana (2005), and Morgan  
553 (2008). **1**, Guanajuato, Mexico; **2**, 111 Ranch, Arizona; **3**, Kissimmee River,  
554 Florida; **4**, Macaspalt Shell Pit, Florida; **5**, Inglis -1A, Citrus County, Florida.

555 Fig. 2. Tooth nomenclature in left lower and upper teeth. **1**, p4 MMP 236; **2**, M1 MLP  
556 15-231a; **3**, MLP 15-231a (reversed); pr.s.a., anterior secondary prism; pr.I,  
557 prism I; pr.II, prism II; h.1i., internal fifth fissure; h.2i. internal second fissure;  
558 h.3i., internal third fissure; h.5i., internal fifth fissure; h.f.e., external  
559 fundamental fissure; h.s.e., external secondary fissure; H.F.I., internal  
560 fundamental fissure; H.P.E., external primary fissure; H.S.E., external secondary  
561 fissure.

562 Fig. 3. Lower cheek teeth. **1-2**, *Phugatherium dichroplax*, F: AM 107689, right p4-m1  
563 and detail of p4; **3**, *P. catacliticum* P-14282 (holotype of *Chapalmatherium*  
564 *irenense*), R p4-m3; **4**, *P. saavedrai* MNHN AYO 226, R p4-m3; **5**,  
565 *Hydrochoeropsis dasseni* MACN 5302a right p4; **6**, *P. novum* MMP 236 right  
566 p4-m3; **7**, *P. catacliticum* MLP 15-232a right p4-m3; **8**, *Nechoerus* sp. MMH  
567 08-04-02, right p4-m3. Scale equals 2 cm.

568 Fig. 4. Upper cheek teeth. **1-3**, *Phugatherium dichroplax*. **1**, F: AM 107694, left M1-  
569 M2; **2**, F: AM 107695, right M3 (reversed); **3**, F: AM 107691, left M2-M3, **4**,  
570 detail of part of M3; **5-10**, left M3. **5**, *P. saavedrai*, MNHN AYO 193; **6**, *P.*

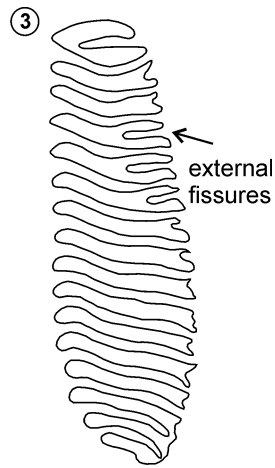
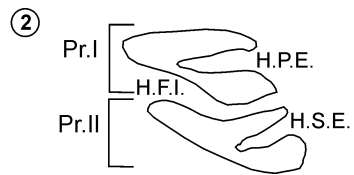
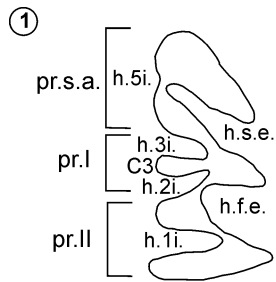
571 *novum*, Fcs 92-V-15-2; **7**, *P. catacliticum*, MLP 15-232a (reversed); **8**,  
572 *Hydrochoeropsis dasseni* MACN 5302; **9**, *Nechoerus sulcidens*; **10**,  
573 *Hydrochoerus hydrochaeris* (both taken from Mones, 1991). Scale equals 2 cm.

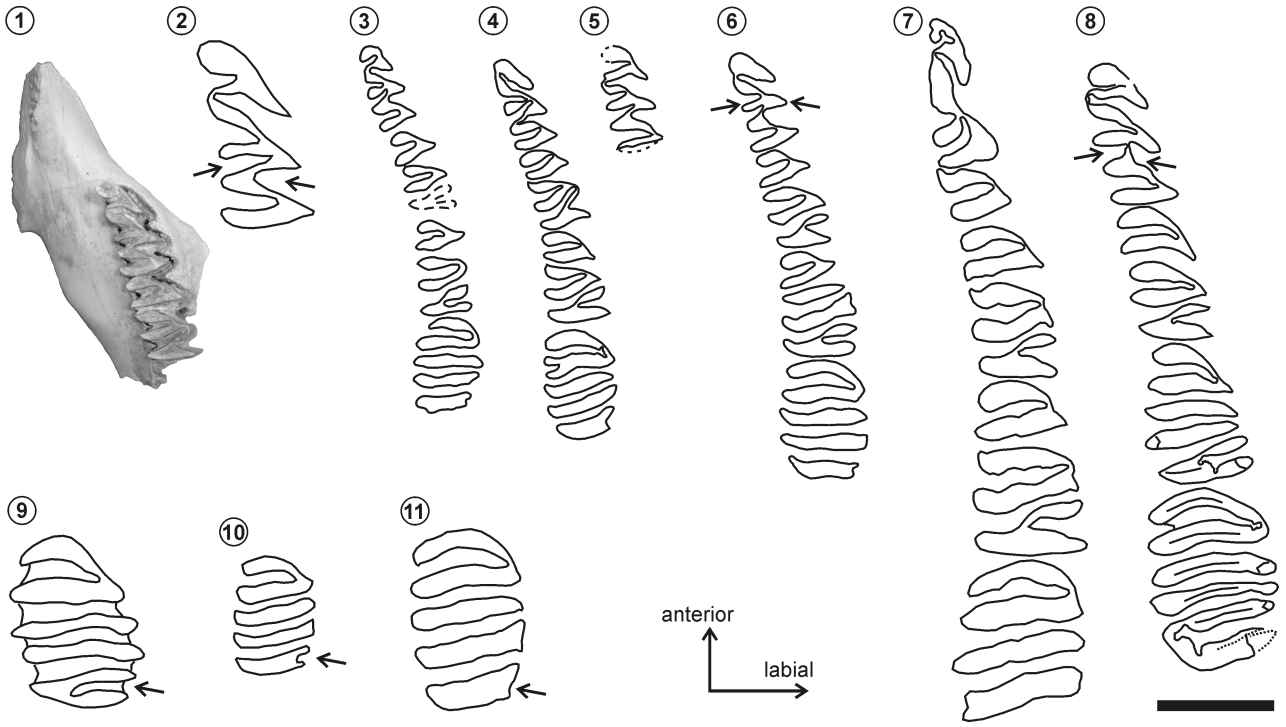
574 Fig. 5. Reduced strict consensus tree ignoring *Allocavia*, *M. huemulensis*, *C. andinus*  
575 and *Xenocardia* from the 4116 MPTs obtained in the combined phylogenetic  
576 analysis.

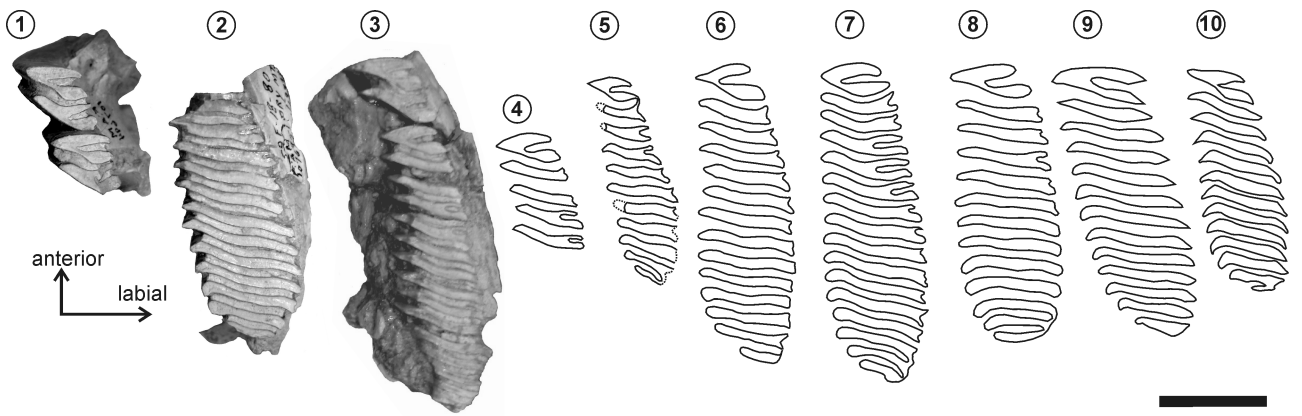
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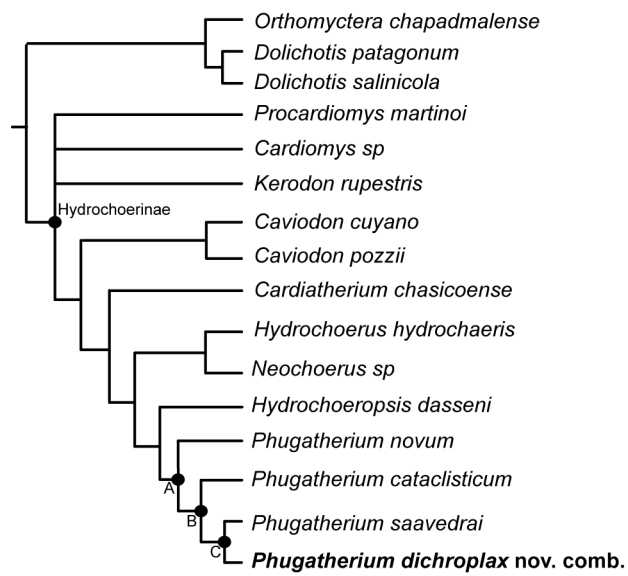


Ma	Epoch	Global scale Stage/Age	South American Stage/Age	North American Stage/Age	Localities with "N." <i>dichroplax</i>	Southern South American capybaras		
1 2 3 4 5 6 7 8 9	Pleistocene	Late	"Ionian"	Lujanian	Rancholabrean	⑤ ③ ④ ② ①  <i>Phugatherium dichroplax</i>	<i>Neochoerus</i>  <i>Hydrochoeropsis</i>  <i>P. saavedrai</i>  <i>P. cataclisticum</i> <i>P. novum</i>  <i>Cardiatherium</i>  <i>Phugatherium</i>	
			Bonaerian	Irvingtonian				
		Early	Calabrian	Ensenadan	Early Late   Late			
	Gelasian		Sanandresian					
	Pliocene	Late	Piacenzian	Marplatense	Vorohuean			Early
				Barrancalobian	Blancan			
		Early		Zanclean	Chapadmalalan			?
	Late Miocene		Messinian	Huayquerian	Hemphillian			
		Tortonian	Chasicoan					







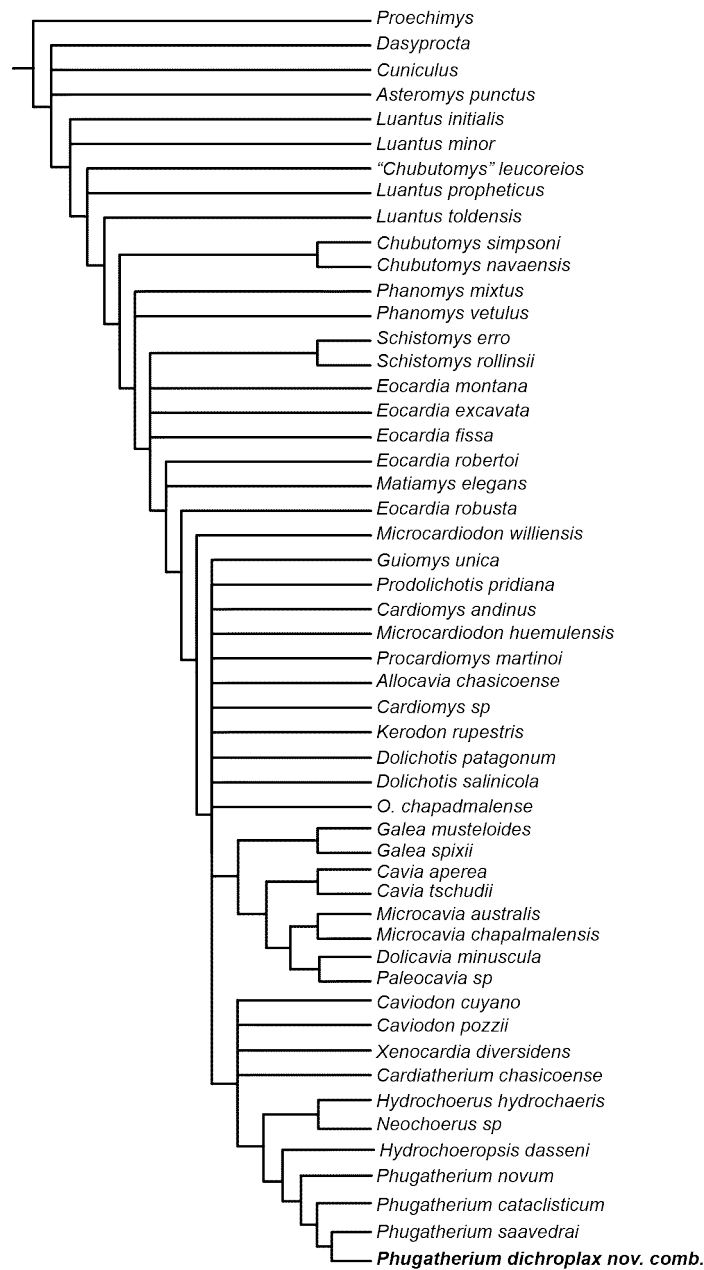


## Supplementary Information 1: Phylogenetic Analysis

The combined dataset (modified of Vucetich et al., 2014) consists in 103 morphological characters (Supplementary Information Online 2) concatenated with the DNA sequences of the four genes (*I2s*, *Cytb*, *Ghr*, and *Tth*), scoring fossil taxa with missing entries for the DNA partitions. This dataset contained a total of 52 taxa and a total of 4303 characters. The combined matrix (Supplementary Information Online 3) was analyzed using equally weighted parsimony in TNT 1.1 (Goloboff et al. 2008a, b), treating gaps as missing data. The heuristic search consisted in 1000 replicates of a Wagner tree followed by TBR branch swapping, collapsing zero-length branches under strictest criterion. Some morphological characters were treated as ordered (Supplementary Information Online 2).

The support values were calculated using Bootstrap and Jackknife resampling techniques and Bremer indices in TNT. Unstable taxa in the set of the most parsimonious trees (MPTs) were identified using IterPCR (Pol and Escapa, 2009) to derive an informative reduced consensus.

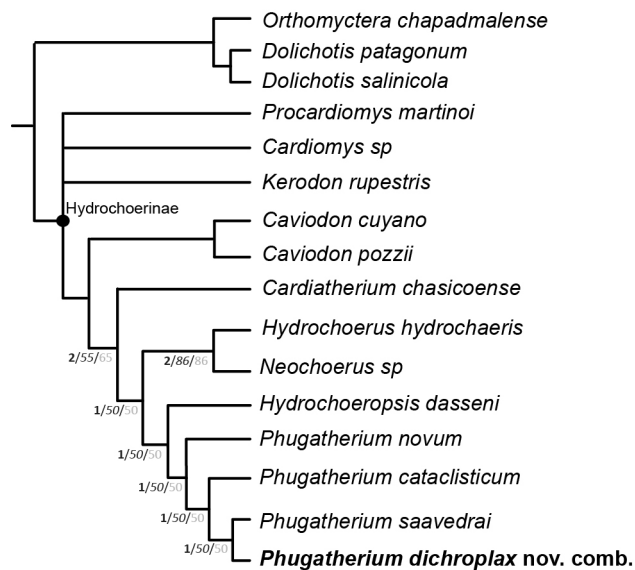
The combined analysis resulted in a total of 4116 MPTs of 3182 steps and the strict consensus of all trees was calculated (Fig. S1.1). This consensus shows as monophyletic the subfamilies Caviinae and Hydrochoerinae, while the other taxa of the crown group form a basal polytomy due to the unstable fragmentary fossil taxa: *Allocavia chasicoense* Pascual 1962, *Microcardiodon huemulensis* (Kraglievich 1930), *Cardiomys andinus* Kraglievich 1930, and *Xenocardia diversidens* Pascual and Bondesio 1963.



**Figure S1.1.** Strict consensus tree including all taxa of the combined phylogenetic analysis

When the alternative positions of the unstable fragmentary fossil taxa are ignored, the reduced consensus tree reveals that all MPTs have a common topology that resolves the interrelationships of the three major lineages of Caviidae: Caviinae, Dolichotinae, and Hydrochoerinae (Fig. S1.2).

The nodal support of the combined analysis was evaluated using Bremer support (Bremer 1994), bootstrap (Felsenstein 1985), and jackknife (Farris et al. 1996). The nodal support values were calculated in the reduced consensus trees ignoring the unstable taxa (*Allocavia*, *M. huemulensis*, *C. andinus* and *Xenocardia*). Bremer support values were calculated using the TNT script BREMER.RUN included in the TNT software package (Goloboff et al. 2008a,b). For both resampling techniques (bootstrap and jackknife) we performed 1000 replicates and a heuristic tree search. The support values are low for most nodes (within the crown group) in the reduced consensus with Bremer support values of 1 and only a few nodes with frequency values above 50% in the Jackknife and Bootstrap analyses (Fig. S1.2).



**Figure S1.2.** Reduced strict consensus tree ignoring *Allocavia*, *M. huemulensis*, *C. andinus* and *Xenocardia* from the 24708 MPTs obtained in the combined phylogenetic analysis. The numbers in bold indicate Bremer indices, numbers in italics represent absolute jackknife values, and numbers in grey represent absolute bootstrap values.



## References

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## Supplementary Information 2: Morphological Character List

Characters with an asterisk (\*) are considered "ordered"

1. Mental foramen: absent (0); present (1).
2. Location of the mental foramen on the anterior region of the dentary: close to the dorsal margin of the dentary and opening dorsolaterally (0); at the dorsoventral midpoint of the lateral surface of the dentary and opening laterally (1).
3. Position of the mandibular foramen: behind the retromolar fossa (0); below the m3 (1).
4. Posteroventral projection of the posterior end of the mandibular symphysis: absent (0); present (1).
5. Development of posteroventral projection of the posterior end of the mandibular symphysis in lateral view: well developed, forming an elongate peg exposed in lateral view (0); moderately developed, only a low bulge projects ventrally and is marginally exposed in lateral view (1).
6. Labial edge of the condyle that is the insertion point of *m. masseter posterior*, in posterior view: projecting laterally with respect to wall of the dentary, forming small knob (0); lacking a distinct knob, continuous with lateral wall of the dentary (1).
7. Medial edge of the condyle that is the insertion point of *m. pterygoideus externus*, in posterior view: projecting medially forming a shelf that overhangs the medial surface of the dentary (0); poorly developed projecting medially forming a small knob with respect to medial wall of the dentary (1).
8. Shape of the post-condylar process, in lateral view: squared-off, forming approximately a 90° angle (0); rounded (1).
9. Length of the post-condylar process: equal or longer than the anteroposterior length of the condyle (0); shorter than anteroposterior length of the condyle (1).
10. Height of the coronoid process compared to the position of the condyle: located at the same dorsoventral level as the condyle (0); located more ventrally than the condyle (1).
11. \*Anterior margin of the coronoid process: convex (0); straight (1); concave (2).

(Continued)

12. Dorsal end of the coronoid process: pointed and posterodorsally projected (0); pointed and dorsally projected (1); blunt (2).
13. \*Dorsoventral position of the mandibular notch: located above the occlusal surface of the dental series (0); located at the same height as the occlusal surface of the dental series (1); located ventral to the occlusal surface of the dental series (2).
14. Shape of the mandibular notch: concave (0); almost straight (1).
15. \*Dorsoventral position of the anterior most point of the lunar notch: low, located ventral to the dorsoventral midpoint of the dentary (between the ventral edge of the dentary and the condyle) (0); located at the approximate dorsoventral midpoint of the dentary (1); high, located above the dorsoventral midpoint of the dentary (2).
16. Posterior extension of the angular process: level with the post-condylar process (0); ending anterior to the post-condylar process (1); ending posterior to the post-condylar process (2).
- 17 \*Posterior extension of the root of the lower incisors: extending up to the level of m3 (0); extending up to the level of the posterior lobe of m2 (1); extending up to the level of the anterior lobe of m2 (2); extending up to the level of the posterior lobe of m1 (3); extending up to the level of the anterior lobe of m1 (4).
- 18 \*Location of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* with respect to the toothrow: between p4 and m1 (0); below m1 (1); between m1 and m2 (2).
- 19 \*Notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: connected to the masseteric crest (0); isolated, located between the masseteric crest and the horizontal crest (1); connected to the horizontal crest (2).
- 20 \*Development of the masseteric crest: well developed, forming a shelf that projects laterally with respect to the lateral surface of the dentary (0); forming a well-developed ridge that fails to project with respect to the lateral surface of the dentary (1); absent or poorly developed as a thin and low ridge (2).
21. Shape of the lateral crest (*sensu* Woods, 1972): straight, projecting anteroventrally from the base of the coronoid process (0); curved, deflecting anteroventrally from the base of the coronoid process (1).
22. \*Anterior origin of the masseteric crest with respect to the toothrow: below m1 (0); below m2 (1); below m3 or posteriorly to m3 (2).

(Continued)

23 \*Posterior extension of the horizontal crest, in lateral view: extending up to the anterior margin of the mandibular condyle (0); approximately ending at the anteroposterior midpoint of the mandibular condyle (1); extending up to the posterior margin of the mandibular condyle (2).

24 \*Development of the horizontal crest: absent or extremely reduced (0); present as a low and broad ridge (1); present as a conspicuous crest, forming a laterally projected shelf but lacking a dorsal fossa (2); well developed, forming a laterally projected shelf and bearing a fossa on its dorsal surface (3).

25. Depth of the fossa located dorsal to the horizontal crest with respect to the dorsoventral depth of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: notch deeper than fossa (0); fossa deeper than notch (1); notch and fossa equal in depth (2).

26. Alveolar protuberances (ventral outgrowth of the base of some molariform alveoli that projects ventrally from the ventral surface of the dentary): absent (0); present (1).

27. Development of alveolar protuberances: present as a small but distinct convexity on the ventral margin of the dentary (0); present as well-developed bulge on the ventral margin of the dentary (1).

28. \*Degree of hypsodonty: slightly hypsodont, having the root and the anteroposterior length of the occlusal surface longer than the height of the crown (0); mesodont, having the root and the anteroposterior length of the occlusal surface approximately equal to the height of the crown (1); protohypsodont, having the root and the anteroposterior length of the occlusal surface less than half the height of the crown (2); euhypsodont, lacking roots (3).

29. Developments of lobes in m1-m2: incipient lobes (0); developed lobes (1).

30. Constriction of the apex in each lobe of the m1-m2: absent (0); present (1).

31. Shape of the anterior lobe of m1-m2: triangular (0); heart-shaped (1); lanceolate (leaf-shaped) (2); laminar (3).

32. Shape of the posterior lobe of m1-m2: triangular (0); heart-shaped (1); complex heart-shaped (2).

33. Shape of the anterior lobe of M1-M2: heart-shaped (0); laminar (1); lanceolate (leaf-shaped) (2).

34. Shape of the posterior lobe of M1-M2: triangular (0); heart-shaped (1).

(Continued)

35. Lobes in p4: two incipient lobes (0); two well-developed lobes, but lacking an anterior projection (1); two well-developed lobes and one incipient anterior projection that is not separated from the anterior lobe by an interprismatic furrow (2); two well-developed lobes and one developed anterior projection separated from the anterior lobe by a well-developed interprismatic furrow (3); three lobes (4).

36. Number of lobes in P4: one (0); two (1).

37. Number of lobes in M3: one (0); two lobes with an incipient posterior projection (1); two lobes with a developed posterior projection (2); 3-4 with posterior projection (3); 5-6 with posterior projection (4); 7-10 with posterior projection (5); more than 10 lobes.

38. Longitudinal furrow opposite to hypoflexus/id: absent (0); present (1).

39. h.s.i. in m1-m2: absent (0); present (1).

40. Depth of h.s.i. in m1-m2: shallow (0); less than 50% (1); approximately half of the prisms (50%) (2); more than 50% of the prism but not splitting (3).

41. h.t.i. in m1-m2: absent (0); present (1).

42. Depth of h.t.i. in m1: up to 50% of the prism (0); crossing the prism but not splitting (1); crossing and dividing the prism (2).

43. Depth of h.t.i. in m2: up to 50% of the prism (0); crossing the prism but not splitting (1); crossing and dividing the prism (2).

44. Depth of h.s.i. respect to h.t.i. m1: equally deep (0); h.s.i. shallower than h.t.i. (1).

45. h.p.i. in m1-m2: absent (0); present (1).

46. Depth of h.s.i. respect to h.p.i. m1: equally deep (0); h.s.i. shallower than h.p.i. (1).

47. Depth of h.p.i. in m1-m2: shallow (0); up to 25% (1); up to 50% (2); reaching the labial end (3); dividing the prism (4).

48. h.s.e. in m1-m2: absent (0); present (0).

49. Depth of h.s.e. in m1-m2: shallow, not surpassing the labial end of the h.p.i. (0); up to 50% of the width of the tooth (1).

50. H.P.E. in M1-M2: absent (0); present (1).

51. H.S.E. in M1-M2: absent (0); present (0).

52. Depth of H.P.E. respect to H.S.E.: equally deep (0); H.P.E. deeper than H.S.E. (1); H.S.E. deeper than H.P.E. (2).

(Continued)

53. \*Transverse extension of the hypoflexus/id: transversely shorter than half of the width of the crown (0); extending from the margin up to the transverse midpoint of the crown (1); extending beyond the transverse midpoint of the crown (2); crossing completely the tooth (3).
54. Shape of the hypoflexus/id in occlusal view: very narrow and short (0); V-shaped (1); narrow and very long (2); funnel shaped (3); canal shaped (4); V-shaped with blunt end (5).
55. Transverse dentine crest on the occlusal surface, located at the middle of each molar lobe: absent (0); present (1).
56. Length of p4-m1 with respect to the length of the m2-m3 (Wood and Patterson, 1959): p4-m1 shorter than m2-m3 (0); p4-m1 approximately equal to m2-m3 (1).
57. Relative size of lower molars:  $m1 < m2 > m3$  (0);  $m1 < m2 < m3$  (1);  $m1 = m2 < m3$  (2);  $m1 = m2 = m3$  (3).
58. Relative size of the upper molars:  $P4 < M1 < M2$  (0);  $P4 > M1 < M2$  (1);  $P4 > M1 = M2$  (2);  $P4 > M1 > M2$  (3).
59. Replacement of deciduous premolar: unreplaced (0); with replacement (1).
60. Type of replacement: postnatal replacement (0); prenatal replacement (1).
61. Orientation of left and right molar series: parallel to each other (0); anteriorly convergent (1).
62. Cement in late ontogenetic stages: absent (0); present (1).
63. Cement in young-adult ontogenetic stages: absent (0); present (1).
64. Cement in juvenile ontogenetic stages: absent (0); present (1).
65. Distribution of enamel in molars: covering the entire crown (0); interrupted at the base of the lingual wall (1); interrupted at the base and the corner of the lingual wall (2); interrupted at the base and in two strips (3); interrupted along the entire labial wall of the upper molars (lingual of the lower molars) except for the flexus/ids opposite to the hypoflexus/id (4); interrupted along the entire lingual wall and anterolingual and posterolingual walls (5).
66. Fossettes/ids in late ontogenetic stages: present (0); absent (1).
67. Fossettes/ids in young-adult ontogenetic stages: present (0); absent (1).
68. Fossettes/ids in juvenile ontogenetic stages: present (0); absent (1).
69. Mesofossettid in young-adult stages: present (0); absent (1).

(Continued)

70. Length of the upper diastema: equal or longer than the molariform series (0); shorter than molariform series (1).
71. Apex of mesopterygoid fossa with respect to M2: level with M2 (0); apex in front of M2 (1). (Quintana 1998: character 2).
72. Shape of the apex of mesopterygoid fossa: acuminate (0); curved (1); plane (2).
73. Margens of the mesopterygoid fossa: convergent (0); subparallel (1).
74. Articulation of nasals with respect to premaxillae: nasals articulate with premaxillae throughout their length (0); anterior half of nasals do not articulate with premaxillae (1). (Quintana 1998: character 6)
75. Shape of frontals: not convex (0); convex (1); markedly convex posteriorly (2). (Quintana, 1998: character 15)
76. Interorbital width: longer or equal to braincase (0); shorter than braincase (1). (Quintana 1998: character 14).
77. Length of incisive foramina: long, <50% (0); short, >50% (1).
78. Palatal concavity: plane (0); only anterior portion concave (1); concave (2). (Quintana 1998: character 24)
79. Position of upper incisors: orthodont (0); inclined (1). (Quintana 1998: character 35)
80. Enamel of upper and lower incisors: uncolored (0); with color (1). (Quintana 1998: character 36)
81. Position of the boundary between the mastoid and paraoccipital processes: at the same level or above the external auditory meatus (0); beneath the external auditory meatus (1). (Ubilla et al. 1999: character 15)
82. Length of ulna bone with respect to length of skull: ulna less or same than skull (0); ulna greater than skull (1). (Quintana 1998)
83. Length of shin bone with respect to length of skull: shin bone less than skull (0); shinbone greater than skull (1). (Quintana 1998)
84. Length of radius with respect to length of humerus: radius less than humerus (0); radius greater than humerus (1). (Quintana 1998)
85. Area between temporal fossae: plane interposed (fossae do not merge on the middle line) (0); sagittal crest (1).

(Continued)

86. Development of the temporal fossae: shallow (0); deep (1).
87. Orientation of the posterior projection of the posterior lobe of M3: antero-posterior (0); transverse (1).
88. Length of the lower diastema: equal or shorter than molariform series (0); longer than the molariform series (1).
89. Dorsal margin of the lower diastema: oblique (0); subplane (1)
90. Ventral margin of the lower diastema: oblique (0); subplane (1)
91. C3: absent (0); present (1). **New character**
92. C3 development: normal (0); long (1). **New character**
93. \*External fissures in prisms of M3: ephemeral or absent (0); present (1). **New character**
94. p4: simple (0); complex (1). **New character**
95. m3: simple (0); complex (1). **New character**
96. Transversal extension of the external fissure in complex m3: up to 75% (0); more than 75% (1).
97. First five laminar prisms in M3 when have more than 10 laminar prisms: ephemeral or absent (0); shallow (1); deep (2). **New character**
98. h.5i. in complex p4: absent (0); shallow (1); deep (2). **New character**
99. h.2i.: shallow (0); deep (1). **New character**
100. h.3i.: shallow (0); deep (1). **New character**
101. depth of h.2i. respect to h.3i.: h2.i deeper h.3i (0); equally deep (1); h2.i shallower h.3i (2). **New character**
102. Location of h.2i. in complex p4: PrI (0); Pr.II (1). **New character**
103. Orientation of h.2i. and h.3i.: parallel (0); convergent (1). **New character**



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1 mxr 100;
2 nstates num;
3 xread
4 '12 cytb tth ghr'
5 4406 52
6
7 &[num]
8 Proechimys 0?0110000000000000000000000?000????0?000?0???0??0?00?0000000?0
9 Cuniculus 1000?101100210103001001110?100????0?000?0???0??0?[0 1]0?00000
10 Dasyprocta 1000?111012201010000000000?100????0?000?0???0??0?00?000101100
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12 Chubutomys_simpsoni ?????????????????????1??????211[0 1][0 1]?????00?0???0
13 Chubutomys_leucoreios 10111????????????110111?110?21100??1??10?0???0??0?
14 Chubutomys_navaensis 10?11????????????120111?1?0?210[0 1][0 1]??1??00?0
15 Luantus_initialis ?????????????????????????????????111002110100?0???0??0?00?1
16 Luantus_minor ?????????????????????1101?1??0?21100????100?0???0??0????110??
17 Luantus_propheticus 10111????????????110111?210?2110[0 1]0110110?0???0??0?
18 Luantus_toldensis ?????????????????????????????????211[0 1][0 1]0110110?0???0
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20 Phanomys_vetulus ?????????????????????????????????211[0 1][0 1]0110110?0???0
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22 Eocardia_montana 101101???11210??12001102211311110120100?0???1?[0 1]0?
23 Eocardia_excavata 10110????????????220011?220?311110120110?0???0??0?00??
24 Eocardia_robusta 10111????????????320111?2210311110120200?0???1?10?00??
25 Eocardia_robertoi ?????????????????????????????????311??012021????????????00??
26 Schistomys_erro 101110?1101100??2200111220?311110121110?0???0??0?00?22001
27 Schistomys_rollinsii ?????????????????????????????????31????01?111????????????
28 Matiamys_elegans ?????????????????????????????????311??01?021????????????00??
29 Guiomys_unica 101????????????????121212?3210311110131200?0???1?10?00?23012
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31 Orthomyctera_chapadmalense 1110?1011022001?22220213211311110121210?0???0
32 D.patagonum 1110?111102000222220?13211311110121210?0???0??0?00?231122111
33 D.salinicola 1110?111102000222220??3211311110121210?0???0??0?00?23112
34 Prodolichotis_pridiana 1010?11[0 1]01120[0 1]1222[1 2]212232103111101312
35 Allocavia_chasicoense ?????????????????????????????????31????01?1?1????????????
36 Paleocavia 11111??????21??312212?3111311212111200?0???1?10?01?2311?21?1
37 Dolicavia_minuscula 111111111?1?211031220?03110311110131200?0???1?00?01??
38 Microcavia_chapalmalensis 11?110?11000201232020202?103112101?1200?0???1
39 M.australis 111110011010202242220203100311210121200?0???1?10?01?231012101
40 Cavia_tschudii 11110?001010202221220223110311311111100?0???1?20?01?2211?
41 C.aperea 101100001110202220220203110311311111100?0???1?20?01?221132111
42 G.musteloides 111110011010012210220223010311210121200?0???1?10?11023111
43 G.spixii 111101[0 1]11011112211220223210311210121200?0???1?10?11023111
44 K.rupestris 1110?00001?120124122020320?31111014120[0 1]00???1100?11023010
45 Cardiomys_chasico 1110????????????????02202?321[0 1]311110141300?0???1?0?
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46 Phugatherium\_novum 1110????????????31220??320?31012014160131121114111113  
47 H.hydrochaeris 11110111101220224122021320?310120141601312[1 2]0114111113  
48 Cardiatherium\_chasicoense 11?1011????????212202?310?310120141401110001  
49 Phugatherium\_cataclisticum 1110?1????????223122?21320?310120141601311101  
50 Phugatherium\_saavedrai ?????????????????122?2?3?0?31012014?6013111011411  
51 Neochoerus\_ 1111011?01?2?2?4122021320?3101201416013112111411111340013??1  
52 Xenocardia\_diversidens ?????????????????????????????310??21?140?????????  
53 Caviodon\_pozzii 111????????????40220??311031011014140120???1020?110230??  
54 Caviodon\_cuyano ?????????????????02????3???31011014140120???1020?11023012  
55 Procardiomyx\_martinoi 1110????????????3???0????1?31111014130100???1100?  
56 Cardiomyx\_andinus ?????????????????????????????31111????0100???1100?????  
57 Microcardiodon\_huemulensis ?????????????????????????????31111????00?0?????  
58 Hydrochoeropsis\_dasseni ?????????????????????????????31012014160??????????  
59 Phugatherium\_dichroplax 11?0????????????3122?????0?3101201416013111011411  
60  
61 &[dna]  
62 Proechimys ?????????????????????????????????????GCAAGAGTCATCACTCCTG?1  
63 C.aperea CAGCCTTTTTATTAGCTGTCTGCAGGATTATACATGACAAAATCCCTACACCGG?1  
64 M.australis TGGCCTTTTTATTAGTTGTCTGCAGAATTATACATGCAAAAATCCCTATACCGG?1  
65 G.musteloides TAGCCTTTTTATTAGTTATTTGTAACTTATACATGCAAGTATCATCACACCGG?1  
66 G.spixii TAGCCTTTTTATTAGCTATTTGTAACTTATACATGCAAGCATCCCCACACAG?1  
67 D.patagonum CAGCTTTTTATTAGTTGTCTGCAAAATTATACATGCAAGAGTCATCACACAG?1  
68 D.salinicola TGGCCTTTTTATTAGTTATTTGCAGAATTATACATGCAAGAGTCATCGAACCGG?1  
69 H.hydrochaeris ?????????????????????????????????????GCAAGAGTCATCGCCCCGG?1  
70 K.rupestris TGGCCTTTTTATTAGTTATTTGCAGAATTATACATGCGAGAGTCATCATACAG?1  
71 Dasypsecta TGGCCTTTTTATTAGTTAAATGTAAATTATACATGCAAGACTCCTCTCCCCGGG?1  
72 Cuniculus TAGCCTTTTTATTAGTTGTTGCAAAATTATACATGCAAGAATCACCATGCCAG?1  
73  
74 &[dna]  
75 Proechimys ATG?CCAACGTACGAAAATCCCACCTCTAATCAAATCATTAACTCTTTTCAT  
76 K.rupestris ATGACCCACATGCGAAAATCACACCCACTAATCAAATTATCAACCATTCACTCATC  
77 H.hydrochaeris ATGACCCACCTACGAAAATCACACCCACTAATCAAATCATCAACCATTCACTCATC  
78 C.aperea ATGACCCACCTACGAAAATCACACCCACTCATCAAATCATTAACTCCCTAATC  
79 D.patagonum ATGACCCACATACGAAAATCACACCCACTAATCAAATTATCAACCATTCACTCATC  
80 Cuniculus ATGACCCACATACGCAAGTCCCACCCGCTAATTAATTAATTAACCATTCACTCATC  
81 D.salinicola ATGACCCACATACGAAAATCACACCCACTAATCAAATCATCAACCATTCACTCATC  
82 G.musteloides ATGACCCACATACGAAAATCTCATCCACTCATTAATTAATTAACCATTCACTCATC  
83 G.spixii ATGACCCACATTGCAAAAACACATCCCCTTATCAAATCATTAACTCATTTAT  
84 Dasypsecta ATGACTCACCTACGAAAATCACACCCACTAATCAAATTATTAACCATTCTTTTCAT  
85 M.australis ?????????????????CAATCACACCCACT?ATT??ATTAT?AATCACTCGCTCAT?  
86  
87  
88 &[dna]  
89 Proechimys CATTCTTTAACGTCCCTACTATAGAACACTGA?TGTACTGGGTGACATACAAGT  
90 H.hydrochaeris GATTCTTTAAAATCCCTGTTATAGAATACGGA?TGTACATTAGGTGGCATGGAAGT

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91 K.rupestris      GATTCTTTAAAGTCCCTGGTATAGAATGCAGA?TGTACATTAGGTGGCATGGAAGT
92 G.musteloides   GATTCTTTAAAGTCCCTGTTATAGGATGCAGA?TGTACACTAAATGGCAATGAAGT
93 G.spixii        GATTCTTTAAAGTCCCTGTTATAGGATGCAGA?TGTACACTAGATGGCATGGAAGT
94 D.patagonum     GATTCTTTGAAGTCCCTATTATAGAAYGCAGA?TGTACATTAGGTGGCATGGAAGT
95 D.salinicola    GATTCCTCTAAGTCCCTCTTATAGAATGTAGA?TGTGCATTAGGTGGCATGGAAGT
96 M.australis     GATTCTTTAAAGTCCCTGCTATAGAATGCAGA?TGTACATTAGGTGGCATGAAAGC
97 C.aperea       GATTCTTTAAAGTCCCTGTTATAAAATGCAGA?TGTACATTGGGTG?????????
98 Dasyprocta     GATTCTTTCACATCCCTGGTATAGAACGCAGA?TGTACATTAGATGGCATGGAAGT
99 Cuniculus      GATTCTTTAAAGGCC??GTTTTAGAATGCAGAATGTACATTAGGTGGCATGGAAA?
100
101
102 &[dna]
103 Proechimys     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTGTGATGAAAAGATTGAAGC
104 D.patagonum     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
105 D.salinicola    CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
106 K.rupestris     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
107 H.hydrochaeris CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
108 C.aperea       CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
109 M.australis     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAGC
110 G.musteloides   CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGGAGC
111 G.spixii        CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGAATCTGATGAAAAGATTGGAGC
112 Cuniculus      CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACCCTGATGAAAAGATTGAAGC
113 Dasyprocta     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACCCTGATGAAAAGATTGAAGC
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118 ccode      + 10 12 14 16.19 21.23 27 52 91 96 *;
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120 ho 100000;
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