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THE FIRST CAPYBARAS (RODENTIA, CAVIIDAE, HYDROCHOERINAE) INVOLVED IN THE GREAT AMERICAN BIOTIC INTERCHANGE

LOS PRIMEROS CARPINCHOS (RODENTIA, CAVIIDAE, HYDROCHOERINAE) PARTICIPANTES DEL GRAN INTERCAMBIO BIÓTICO AMERICANO

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

Keywords: Capybaras. Pliocene. North America. GABI

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

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

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

Capybaras are a unique group of rodents, with ever-growing cheek teeth that increase in size and change in occlusal morphology through life. The change is caused partly by generation of structures after birth and by their allometric growth (Vucetich et al., 2005, 2014a; Deschamps et al., 2007, 2009). These characteristics caused some confusion when interpreting the fossil record, and led to regard them as taxonomically highly diverse. Small species with simple dental morphology where considered as primitive, and large species with complicated cheek teeth, as derived. In the past ten years Vucetich et al. (2005) began the revision of the late Miocene –Pliocene South American capybaras and stated that in each locality small specimens were juveniles of the species represented by large specimens. This new taxonomic paradigm led to a reduction of nominal taxa and a better comprehension of the species limits (Vucetich et al., 2005, 2014a, b; Deschamps et al., 2007, 2009). They also made the first phylogenetic analyses that helped to understand their relationships, resulting in the Pleistocene clade *Neochoerus*-*Hydrochoerus* the sister group of the Pliocene *Phugatherium* (Pérez et al, 2014; Vucetich et al., 2014a). All this new knowledge showed that extinct species had short stratigraphic ranges (Fig. 1) (partly because of their physiological requirements) and relatively wide geographic distributions, establishing them useful as biostratigraphic tools (Deschamps et al., 2013).

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

MATERIALS AND METHODS

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

They were compared with *Phugatherium cataclisticum* Ameghino, 1887 from the early Pliocene Monte Hermoso Formation, Argentina, *P. novum* (Ameghino, 1908) from the early late Pliocene Chapadmalal Formation, Argentina, *Hydrochoeropsis dasseni* Kraglievich, 1930 from the late Pliocene Uquía Formation, Argentina, *Neochoerus* sp. (MMH 08-04-02 and UNSGH 645) from the Pleistocene of southern Buenos Aires Province, Argentina, and illustrations of *Phugatherium saavedrai* (Hoffstetter, Villarroel and Rodrigo, 1984) from the Pliocene Umala Formation, Bolivia, and *Neochoerus cordobai* Carranza-Castañeda and Miller, 1988 from the late Pliocene of San Miguel de Allende, Guanajuato, Mexico.

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

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

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

TAXONOMICAL BACKGROUND

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

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

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

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

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Superfamily CAVIOIDEA (Fischer, 1817) Kraglievich, 1930

Family CAVIIDAE Fischer, 1817

Subfamily HYDROCHOERINAE (Gray, 1825) Gill, 1872: Weber, 1928 sensu Kraglievich, 1930

Genus ***Phugatherium*** Ameghino, 1887

Type species. *Phugatherium cataclisticum* Ameghino, 1887; fixed by monotypy. Montehermosan, early Pliocene, Argentina.

Included species. *P. cataclisticum*, *P. novum*, *P. saavedrai*, *P. dichroplax*

Additions to the diagnosis (see Vucetich et al., 2014a). The p4 (Fig. 1) with C3 well defined by deep h.2i. and h.3i. at least reaching 50% of the width of the tooth, equal in depth or h.3i. deeper; both within the pr.I (ahead the h.f.e.).

Distribution. Montehermosan-Chapadmalalan (Zanclean-early Piacenzian) of South America, and late Early-latest Blancan (Piacenzian- Gelasian) of North America (Fig. 1).

Phugatherium dichroplax nov.comb.

Figures 3.1-2, 3.9, 4.1-3

Neochoerus dichroplax Ahearn and Lance, 1980

Neochoerus lancei Mones, 1980

Neochoerus cordobai Carranza-Castañeda and Miller, 1988 (=*Neochoerus* sp. nov. A Carranza-Castañeda, Ferrusquía-Villafranca and Miller, 1981)

Neochoerus sp. nov. B Carranza-Castañeda, Ferrusquía-Villafranca and Miller, 1981 (=*Neochoerus* sp. Carranza-Castañeda and Miller, 1988)

Holotype. F: AM 107691, left M2-M3.

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

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

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

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

Relationships of Phugatherium dichroplax

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

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

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

The analysis of the molariforms, in the context of the South American species, suggests that the specimens on which *"N". dichroplax* is based would not pertain to the genus *Neochoerus*, but to *Phugatherium*. The main characters on which this statement is based are: 1) the deep h.2i. and h.3i. in pr.I of p4 defining a conspicuous and transversally long C3 (in *Neochoerus* the h.3i. is opposite or posterior to h.f.e.; see Figs. 2, 3.2, 3.8), and 2) the M3 with external fissures (Figs. 2, 4) in all (or almost all) the prisms like in all the species of South American *Phugatherium*. In *Hydrochoeropsis* these fissures are present only in the anterior prisms (2 to 6; Fig. 4.8). They are exceptional and very shallow in *Neochoerus* (Fig. 4.9), and absent in *Hydrochoerus* (Fig. 4.10). Mones (1975, 1980) considered that these fissures appeared several times among fossil capybaras, but new analyses showed that they are conspicuous only in the species of *Phugatherium* and in *Hydrochoeropsis.* These fissures are present already in the late Miocene *Cardiatherium* (Fig. 1) as a smooth continuous wave along the external face of the M3. However, *Cardiatherium* is very different from the other capybaras because the prisms are still united (Mones, 1991; Vucetich et al., 2005; Deschamps et al., 2013).

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

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

Phugatherium dichroplax differs from the other species of the genus in the configuration of the p4 (Figs. 3.1–2), with the h.2i. deeper than h.3i. (up to 75% of the tooth) determining a drop-shaped C3 (column of pr. II). This is clearly observed in specimens F: AM 107689 (Figs. 3.1–2; p4 AP=1.88 cm) and F: AM 107686 (=SAF 9-19 in Mones, 1980). In *P. novum* (Fig. 3.6) these fissures are sub equal in depth, and a little shallower than in *P. dichroplax*. In *P. cataclisticum*, the h.3i. is slightly shorter than h.2i. which turns forwards, and the secondary anterior prism (pr.s.a., Fig. 2) is very different as a whole (Fig. 3.7). In *P. saavedrai* (Fig. 3.4) these fissures and the drop-shaped C3 are similar to those of *P. dichroplax*, but the margins of the prism are less divergent. This specimen can be a juvenile according to its size (Deschamps et al., 2013).

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

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

The characters that define *P. dichroplax* (the typical shape of p4, m3 and M3) are also present in "*N*". *cordobai*. Hence, we follow Mones (1984, 1991) considering this species a junior synonym of *P. dichroplax*. The characters described and figured of *Neochoerus* sp. (Carranza-Castañeda and Miller, 1988) from the same site as *P. cordobai* do not permit a precise determination. However the presence of two species in a single locality would be an exception in the capybaras record. Recently, it was proposed that the different morphs found in each locality actually represent individuals of different ontogenetic stages of a population or successive populations, rather than a multiplicity of coeval species in different stages of evolution (Deschamps et al., 2007, 2013; Vucetich et al., 2014a,b).

Phylogenetic analysis

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

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

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

DISCUSSION

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

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

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

The genus *Neochoerus* is first recorded in South America in the Pleistocene, although in accordance with phylogenetic analysis (Vucetich et al., 2014a), its differentiation from the Pliocene *Phugatherium* would be older. The lineage *Neocheorus-Hydrochoerus* would have been restricted to Neotropical South America in the Pliocene, where the fossil record is very scanty and Pliocene hydrochoerines have not been well studied yet. If this is correct, it could explain the presence of *N. pinckneyi* in Pliocene sediments of temperate North America (Sanders, 2002: 101-102; Morgan, 2008: 122; Woodburne, 2010: 250).

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

Modern capybaras inhabit areas around ponds, lakes, rivers, marshes and swamps, using water primarily as refuge but also for basic physiological requirements as temperature regulation (Nowak and Paradiso, 1983, Herrera, 2012). In South America, all of the lithological units bearing capybaras have been interpreted as deposited in water-related settings, mostly fluvial deposits, but also karstic landscapes or travertine deposits formed by hydrothermal processes (Deschamps et al., 2013). Accordingly, in North America *Phugatherium dichroplax* nov. comb. was found in water-related sediments. The sediments that yielded the capybaras from Guanajuato are horizontal deposits of flood plains (Carranza-Castañeda and Miller, 1988). The composite stratigraphic section in the 111 Ranch area, Arizona, consists of fluvial and lacustrine sediments (Morgan and White, 2005). The Florida sites Macasphalt Shell Pit and Kissimmee River were formed by accumulations from freshwater and nearshore settings in a shallow marine depositional environment; and Haile 15A consists of undifferentiated sands and clays filling a karst fissure developed in marine Eocene limestone (Morgan, 2005). This suggests that *P. dichroplax* nov. comb. had ecological requirements similar to modern capybaras. Hence, the dispersal route from South America through the Panamanian bridge to central Mexico, and temperate North America during the Pliocene must have been scattered with permanent water bodies.

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Captions for figures

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

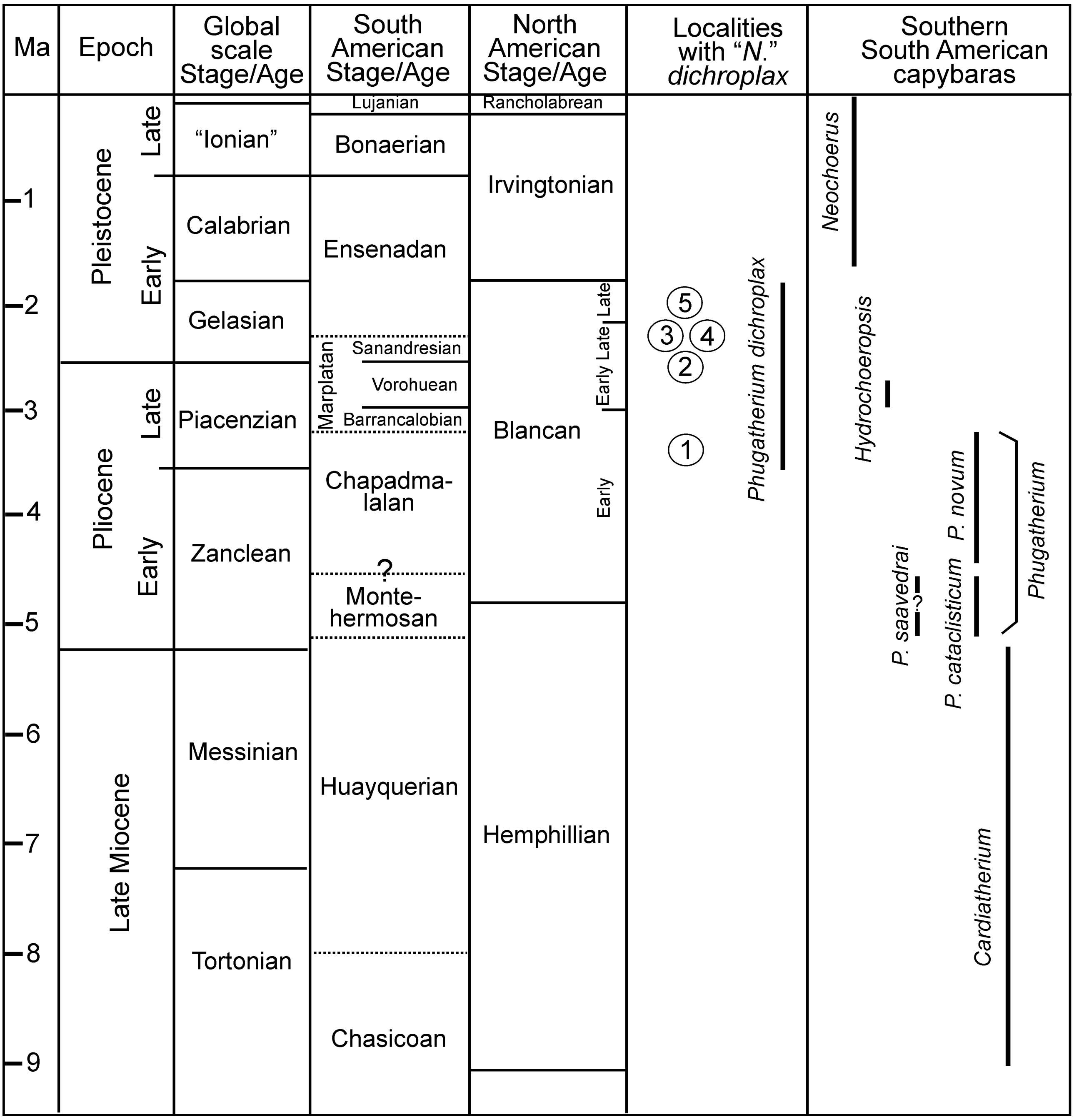
Fig. 2. Tooth nomenclature in left lower and upper teeth. **1**, p4 MMP 236; **2**, M1 MLP 15-231a; **3**, MLP 15-231a (reversed); pr.s.a., anterior secondary prism; pr.I, prism I; pr.II, prism II; h.1i., internal fifth fissure; h.2i. internal second fissure; h.3i., internal third fissure; h.5i., internal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

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

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

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

Fig. 5. Reduced strict consensus tree ignoring *Allocavia, M. huemulensis, C. andinus* and *Xenocardia* from the 4116 MPTs obtained in the combined phylogenetic analysis.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Epoch
Global scale Stage/Age
South American Stage/Age
North American Stage/Age
Localities with "N." dichroplax
Southern South American capybaras
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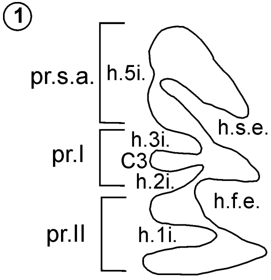
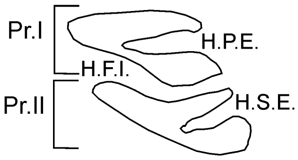
3
4
5
6
7
8
9
Pleistocene
Late
Early
Pliocene
Late
Early
Late Miocene
"Ionian"
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Lujanian
Bonaerian
Ensenadan
Marplatan
Sanandresian
Vorohuean
Barrancalobian
Chapadmalalan
?
Montehermosan
Huayquerian
Chasicoan
Rancholabrean
Irvingtonian
Blancan
Late
Early Late
Early
Hemphillian
⑤
③
④
②
①
Phugatherium dichroplax
Neochoerus
Hydrochoeropsis
P. saavedrai
?
P. cataclisticum
P. novum
Phugatherium
Cardiatherium

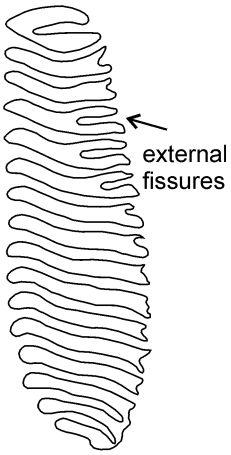
①

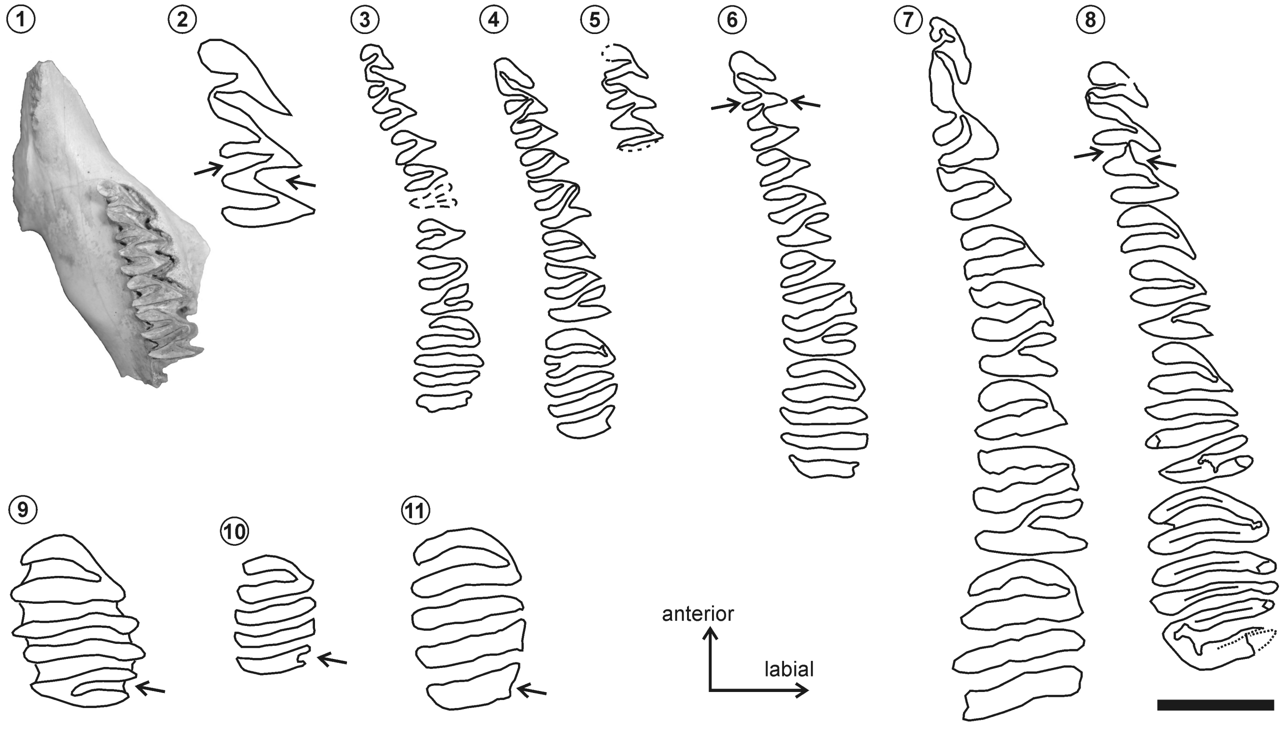

pr.s.a.
h.5i.
h.s.e.
pr.I
h.3i.
C3
h.2i.
h.f.e.
pr.II
h.1i.

②


Pr.I
H.P.E.
H.F.I.
Pr.II
H.S.E.

③


external
fissures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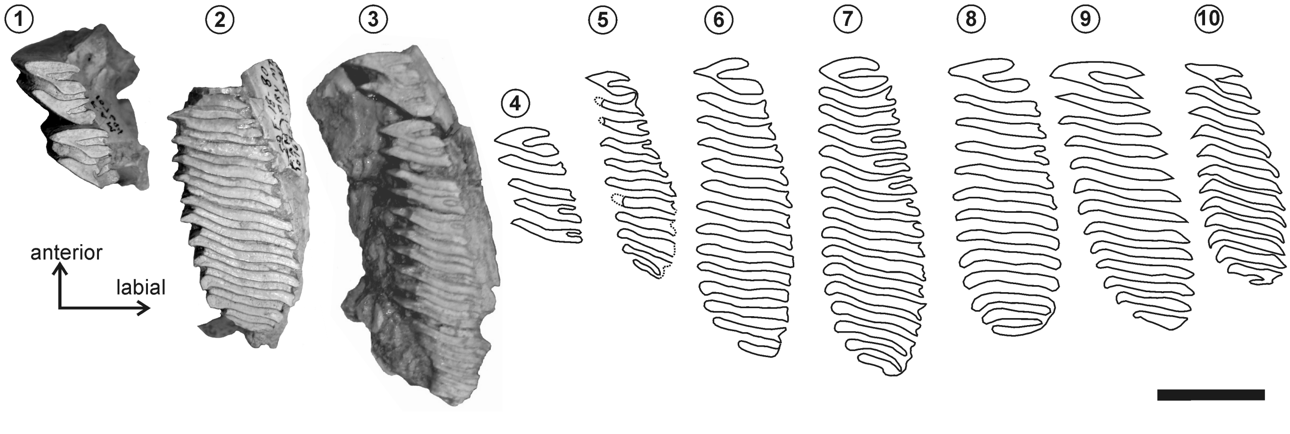
labial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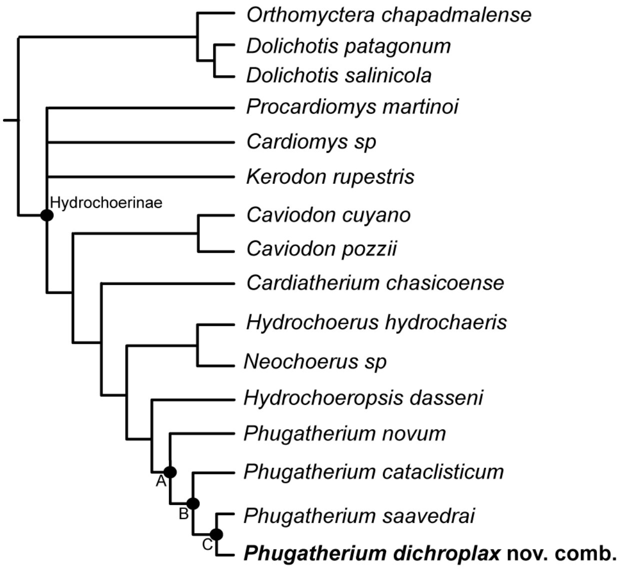
Orthomyctera chapadmalense
Dolichotis patagonum
Dolichotis salinicola
Procardiomys martinoi
Cardiomys sp
Kerodon rupestris
Hydrochoerinae
Caviodon cuyano
Caviodon pozzii
Cardiatherium chasicoense
Hydrochoerus hydrochaeris
Neochoerus sp
Hydrochoeropsis dasseni
Phugatherium novum
A
Phugatherium cataclisticum
B
Phugatherium saavedrai
C
Phugatherium dichroplax nov. comb.

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 (*12s*, *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.

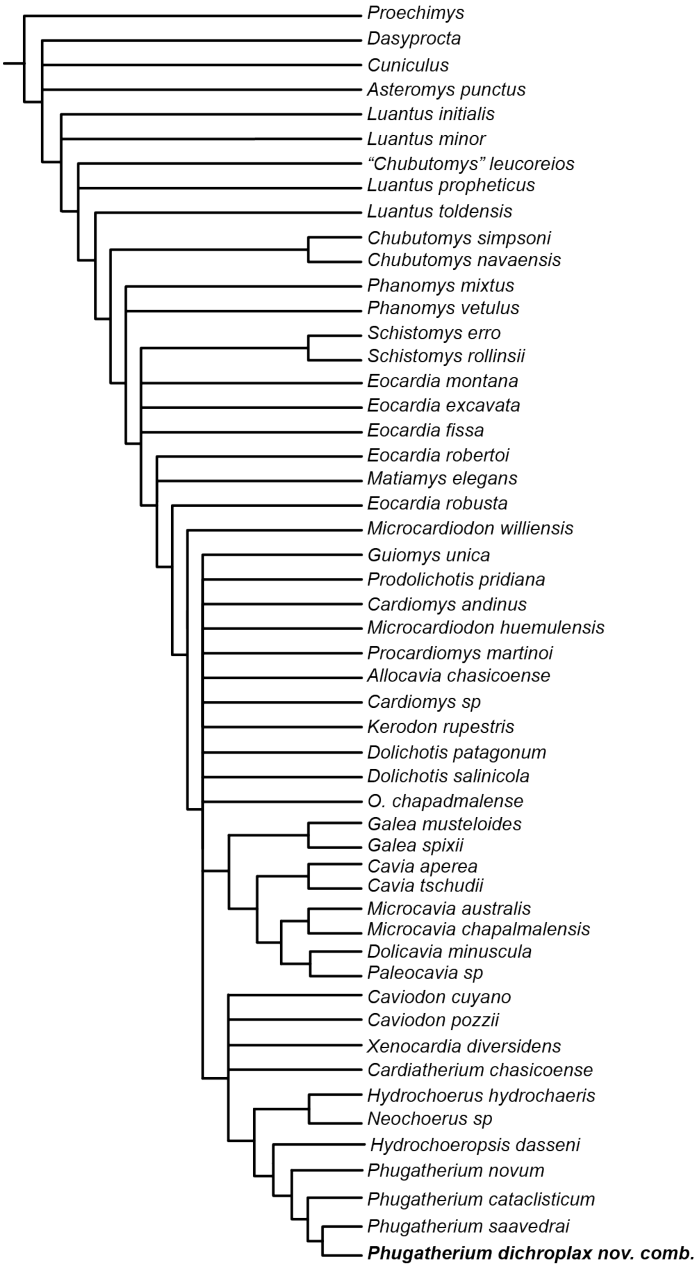

Figure S1.1. Strict consensus tree including all taxa of the combined phylogenetic analysis

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).

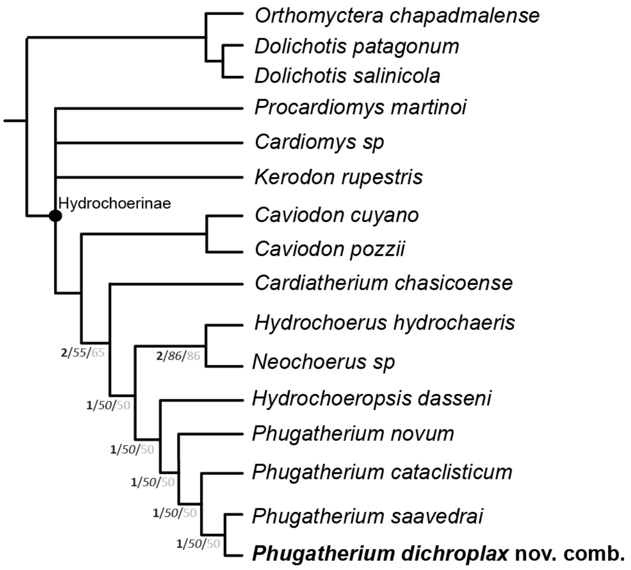

Figure S1.2. Reduced strict consensus tree ignoring *Allocavia, M. huemulensis, C. andinus* and *Xenocardia* from the 24708 MPTs obtained in the combined phylogenetic analysis. The numbers in bold indicate Bremer indices, numbers in italics represent absolute jackknife values, and numbers in grey represent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

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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 massteric 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 hyopflexus/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 then 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 distema: 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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mxr 100;
nstates num;
xread
'12 cytb tth ghr'
4406 52

&[num]
Proechimys  0?011000000000000000000000?000????0?000?0???0??0?00?0000000?0
Cuniculus   1000?101100210103001001110?100????0?000?0???0??0?[0 1]0?00000
Dasyprocta  1000?111012201010000000000?100????0?000?0???0??0?00?000101100
Asteromys_punctus   10111???????????100110?120?11000??1??00?0???0??0?0??0
Chubutomys_simpsoni ????????????????????1??????211[0 1][0 1]?????00?0???0
Chubutomys_leucoreios   10111???????????110111?110?21100??1??10?0???0??0
Chubutomys_navaensis    10?11???????????120111?1?0?210[0 1][0 1]??1??00?0
Luantus_initialis   ????????????????????????????11100210100?0???0??0?00?1
Luantus_minor   ????????????????1101?1???0?21100????100?0???0??0????110?
Luantus_propheticus 10111???????????110111?210?2110[0 1]0110110?0???0??0
Luantus_toldensis   ???????????????????????????211[0 1][0 1]0110110?0???0
Phanomys_mixtus ????????????????2?0??????0?211[0 1][0 1]0110110?0???0??0
Phanomys_vetulus    ???????????????????????????211[0 1][0 1]0110110?0???0
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Eocardia_excavata   10110???????????220011?220?311110120110?0???0??0?00?
Eocardia_robusta    10111???????????320111?2210311110120200?0???1?10?00?
Eocardia_robertoi   ???????????????????????????311??012021???????????00?
Schistomys_erro 101110?1101100??2200111220?311110121110?0???0??0?00?22001
Schistomys_rollinsii    ???????????????????????????31???01?111??????????
Matiamys_elegans    ???????????????????????????311??01?021???????????00?
Guiomys_unica   101?????????????121212?3210311110131200?0???1?10?00?2301
Microcardiodon_williensis   1[0 1]1?????????????220101?1210311?1??11?0??0
Orthomyctera_chapadmalense  1110?1011022001?22220213211311110121210?0???0
D.patagonum 1110?1111020002222220?13211311110121210?0???0??0?00?231122111
D.salinicola    1110?1111020002222220??3211311110121210?0???0??0?00?2311
Prodolichotis_pridiana  1010?11[0 1]01120[0 1]1222[1 2]21223210311110131
Allocavia_chasicoense   ???????????????????????????31???01?1?1??????????
Paleocavia  11111???????21??312212?3111311212111200?0???1?10?01?2311?21?1
Dolicavia_minuscula 111111111?1?211031220?03110311110131200?0???1?00?01?
Microcavia_chapalmalensis   11?110?110002012320202?103112101?1200?0???1
M.australis 111110011010202242220203100311210121200?0???1?10?01?231012101
Cavia_tschudii  11110?001010202221220223110311311111100?0???1?20?01?2211
C.aperea    101100001110202220220203110311311111100?0???1?20?01?221132111
G.musteloides   111110011010012210220223010311210121200?0???1?10?11023111
G.spixii    111101[0 1]11011112211220223210311210121200?0???1?10?11023111
K.rupestris 1110?00001?120124122020320?31111014120[0 1]00???1100?11023010
Cardiomys_chasico   1110?????????????02202?321[0 1]311110141300?0???1??0
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H.hydrochaeris  11110111101220224122021320?310120141601312[1 2]0114111113
Cardiatherium_chasicoense   11?1011?????????212202?310?310120141401110001
Phugatherium_cataclisticum  1110?1????????223122?21320?310120141601311101
Phugatherium_saavedrai  ?????????????????122?2?3?0?31012014?6013111011411
Neochoerus_ 1111011??01?2?2?4122021320?3101201416013112111411111340013??1
Xenocardia_diversidens  ???????????????????????????310??21?140??????????
Caviodon_pozzii 111?????????????40220??311031011014140120???1020?110230?
Caviodon_cuyano ?????????????????02????3???31011014140120???1020?11023012
Procardiomys_martinoi   1110????????????3???0????1?31111014130100???1100
Cardiomys_andinus   ????????????????????????????31111????0100???1100????
Microcardiodon_huemulensis  ????????????????????????????31111????00?0???1
Hydrochoeropsis_dasseni ????????????????????????31012014160?????????????
Phugaterium_dichroplax  11?0?????????????3122????0?3101201416013111011411

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C.aperea         CAGCCTTTTTATTAGCTGTCTGCAGGATTATACATGACAAAATCCCTACACCGG?T
M.australis      TGGCCTTTTTATTAGTTGTCTGCAGAATTATACATGCAAAAATCCCTATACCGG?T
G.musteloides    TAGCCTTTTTATTAGTTATTTGTAAACTTATACATGCAAGTATCATCACACCGG?T
G.spixii         TAGCCTTTTTATTAGCTATTTGTAAACTTATACATGCAAGCATCCCCACACCAG?T
D.patagonum      CAGCTTTTTTATTAGTTGTCTGCAAAATTATACATGCAAGAGTCATCACACCAG?T
D.salinicola     TGGCTTTTTTATTAGTTATTTGCAGAATTATACATGCAAGAGTCATCGAACCGG?T
H.hydrochaeris   ???????????????????????????????????GCAAGAGTCATCGCCCCGG?T
K.rupestris      TGGCTTTTTTATTAGTTATTTGCAGAATTATACATGCGAGAGTCATCATACCAG?T
Dasyprocta       TGGCCTTTTTATTAGTTAAATGTAAAATTATACATGCAAGACTCCTCTCCCCGGGT
Cuniculus        TAGCCTTTTTATTAGTTGTTCGCAAAATTATACATGCAAGAATCACCATGCCAG?T

&[dna]
Proechimys      ATG?CCAACGTACGAAAATCCCACCCTCTAATCAAAATCATTAACCACTCTTTCATT
K.rupestris     ATGACCCACATGCGAAAATCACACCCACTAATCAAAATTATCAACCATTCACTCATC
H.hydrochaeris  ATGACCCACCTACGAAAATCACACCCACTAATCAAAATCATCAACCACTCATTCATT
C.aperea        ATGACCCACCTACGAAAATCACACCCACTCATCAAAATCATTAACCACTCCCTAATC
D.patagonum     ATGACCCACATACGAAAATCACACCCACTAATCAAAATTATCAACCACTCATTCATC
Cuniculus       ATGACCCACATACGCAAGTCCCACCCGCTAATTAAAATTATAAACCACTCATTCATT
D.salinicola    ATGACCCACATACGAAAATCACACCCACTAATCAAAATCATCAACCACTCATTCATC
G.musteloides   ATGACCCACATACGAAAATCTCATCCACTCATTAAAATTATTAATCACTCATTCATT
G.spixii        ATGACCCACATTCGAAAAACACATCCCCTTATCAAAATCATTAACCACTCATTTATT
Dasyprocta      ATGACTCACCTACGAAAATCACACCCACTAATCAAAATTATTAACCACTCTTTCATT
M.australis     ???????????????CAATCACACCCACT?ATT???ATTAT?AATCACTCGCTCAT


&[dna]
Proechimys       CATTCTTTAACGTCCCTACTATAGAACACTGA?TGTACACTGGGTGACATACAAGT
H.hydrochaeris   GATTCTTTAAAATCCCTGTTATAGAATACGGA?TGTACATTAGGTGGCATGGAAGT
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K.rupestris      GATTCTTTAAAGTCCCTGGTATAGAATGCAGA?TGTACATTAGGTGGCATGGAAG
G.musteloides    GATTCTTTAAAGTCCCTGTTATAGGATGCAGA?TGTACACTAAATGGCAATGAAG
G.spixii         GATTCTTTAAAGTCCCTGTTATAGGATGCAGA?TGTACACTAGATGGCATGGAAG
D.patagonum      GATTCTTTGAAGTCCCTATTATAGAAYGCAGA?TGTACATTAGGTGGCATGGAAG
D.salinicola     GATTCCTCTAAGTCCCTCTTATAGAATGTAGA?TGTGCATTAGGTGGCATGGAAG
M.australis      GATTCTTTAAAGTCCCTGCTATAGAATGCAGA?TGTACATTAGGTGGCATGAAAG
C.aperea         GATTCTTTAAAGTCCCTGTTATAAAATGCAGA?TGTACATTGGGTG?????????
Dasyprocta       GATTCTTTCACATCCCTGGTATAGAACGCAGA?TGTACATTAGATGGCATGGAAG
Cuniculus        GATTCTTTAAAGGCC??GTTTTAGAATGCAGAATGTACATTAGGTGGCATGGAAA


&[dna]
Proechimys      CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTGTGATGAAAAGATTGAAG
D.patagonum     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
D.salinicola    CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
K.rupestris     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
H.hydrochaeris  CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
C.aperea        CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
M.australis     CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGAAG
G.musteloides   CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACTCTGATGAAAAGATTGGAG
G.spixii        CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGAATCTGATGAAAAGATTGGAG
Cuniculus       CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACCCTGATGAAAAGATTGAAG
Dasyprocta      CTCTTGGGTTGAATTTATTGAGCTAGATATTGATGACCCTGATGAAAAGATTGAAG

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ccode    +  10 12 14 16.19 21.23 27 52 91 96 *;

ho 100000;
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