

# A New Pliocene *Capybara* (Rodentia, Caviidae) from Northern South America (Guajira, Colombia), and its Implications for the Great American Biotic Interchange

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**Abstract** One of the most striking components of the modern assemblage of South American mammals is the semiaquatic capybara (Caviidae, Hydrochoerinae), the biggest rodent in the world. The large hydrochoerines are recorded from the middle Miocene to the present, mainly in high latitudes of South America. Although less known, they are also recorded in low latitudes of South America, and in Central and North America. We report the first record of capybaras from the late Pliocene of Colombia, found in deposits of the Ware Formation, Guajira Peninsula in northeastern Colombia. We analyze the phylogenetic position within Caviidae, the possible environmental

changes in the Guajira Peninsula, and the implications of this finding for the understanding of the Great American Biotic Interchange. The morphological and phylogenetic analyses indicate that the hydrochoerine of the Guajira Peninsula is a new species, *?Hydrochoeropsis wayuu*, and this genus is most closely related to *Phugatherium*. According to the latest phylogenetic results, this clade is the sister group of the lineage of the recent capybaras (*Neochoerus* and *Hydrochoerus*). *?Hydrochoeropsis wayuu* is the northernmost South American Pliocene hydrochoerine record and the nearest to the Panamanian bridge. The presence of this hydrochoerine, together with the fluvio-deltaic environment of the Ware Formation, suggests that during the late Pliocene, the environment that dominated the Guajira Peninsula was more humid and with permanent water bodies, in contrast with its modern desert habitats.

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## Introduction

The mammal assemblage that inhabits the Neotropics today (Neotropical region sensu lato; Morrone 2014) comprises about 30 % of the extant mammalian species of the world (Wilson and Reeder 2005; Patton 2015) including groups such as rodents (caviomorphs and sigmodontines), primates (platyrrhine monkeys), bats (e.g., phyllostomids), marsupials (e.g., opossums), and xenarthrans (armadillos, sloths, and anteaters) (Patterson and Costa 2012). This exceptional diversity of mammals and the multiple endemisms are the result of long periods of isolation of South America during most of the Cenozoic (Wilf et al. 2013), and the heterogeneity of the landscape and environments (e.g., tropical rain and dry forests, montane forests, highland grasslands, shrublands, savannas, and deserts; Solari et al. 2012) that

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characterize the Neotropical Region. This habitat heterogeneity is the outcome of sea transgressions, tectonic events with the subsequent elevation of the Andes, global climate change, and the rise of the Panamanian land bridge (Garzoine et al. 2008; Woodburne 2010; Farris et al. 2011; Bacon et al. 2015; Montes et al. 2015).

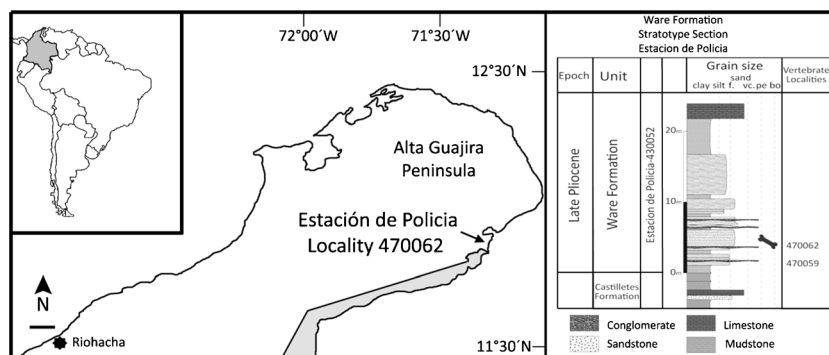
With the completion of the Isthmus of Panama and the development of environments favorable to migration, the isolation of South America ended, leading to the main phases of the Great American Biotic Interchange, or GABI (Woodburne 2010; Bacon et al. 2015, 2016; Carrillo et al. 2015). During this process many mammals native to South America, including marsupials, xenarthrans, platyrrhine monkeys, chiropters, and caviomorph rodents (porcupines, hutias, agoutis, pacas, capybaras, spiny rats), crossed to Central and North America (Webb 2006). Among the caviomorph lineages, porcupines and capybaras were the ones that reached the farthest north (Simpson 1928; Mones 1991; Morgan 2005; Morgan and Emslie 2010; Vucetich et al. 2015b).

Within the caviomorph rodents, one of the most striking groups is the capybaras (Hydrochoerinae) because of their large body size, gregarious social behavior, adaptation to a semiaquatic mode of life (Mares and Ojeda 1982; Woods 1984; Eisenberg and Redford 2000; Rowe and Honeycutt 2002; Ojasti 2011; Oliver and Sachser 2011; Moreira et al. 2013; García-Esponda and Candela 2016), and their ever-growing cheek teeth with derived and complex morphology (Vucetich et al. 2005, 2012, 2014, 2015a, b). The extant large hydrochoerines are represented by two gigantic semiaquatic species: *Hydrochoerus hydrochaeris*, distributed from Argentina to Colombia, and *H. isthmus*, in northwestern Colombia and Panama (Wilson and Reeder 2005). In contrast, their fossil record indicates that they were more diverse than today. The fossil record of hydrochoerines is abundant, particularly for the late Miocene of temperate South America. Fossil hydrochoerines include basal forms traditionally named as “cardiomyines” (middle Miocene – Pliocene) and a more derived clade, the capybaras, that includes numerous species of *Cardiatherium*,

*Hydrochoerus*, *Neochoerus*, and the largest hydrochoerines, *Phugatherium* and *Hydrochoeropsis* (Vucetich et al. 2005, 2014, 2015b; Deschamps et al. 2007, 2009, 2013; Vucetich and Pérez 2011; Pérez et al. 2014). The hydrochoerines are recorded from the middle Miocene to the present, mainly in high latitudes of South America (from Argentina including northern Patagonia, Uruguay, Chile, Bolivia; see Deschamps et al. 2013). Although less well known, they have also been recorded in low latitudes of South America (Urumaco and San Gregorio formations, Venezuela, Vucetich et al. 2010; Acre Region, Peru and Brazil, Frailey 1986; Sant’anna-Filho 1994; Pleistocene deposits of Soata, Colombia, Villarroel et al. 1996, 2001), the Caribbean (Grenada, Lesser Antilles, MacPhee et al. 2000), and Central and North America (Carranza-Castañeda and Miller 1988; Mones 1991; Morgan 2005).

The capybaras only occur near permanent water bodies such as marshes, estuaries, and along rivers and streams. Although both extant species of *Hydrochoerus* currently inhabit most of Colombia (Aldana-Dominguez et al. 2013), they are absent in the Guajira Peninsula of northeastern Colombia (Fig. 1), a region characterized by dry, open areas (Haffer 1967). Here, we report the first record of capybaras (Rodentia, Caviidae) from the late Pliocene of Colombia, found in deposits of the Ware Formation on the Guajira Peninsula (Moreno et al. 2015); we analyze the possible environmental changes in the Guajira Peninsula during this time, along with the implications of this discovery for our understanding of the Great American Biotic Interchange.

**Geological Settings** The recently described Ware Formation (Moreno et al. 2015) is an important geological unit of the Cocinetas Basin that crops out in the Department of Guajira, northeast Colombia (Fig. 1). The Ware Formation is dominated by detrital deposits of fluvial-deltaic origin with high fossil content. According to macroinvertebrate biostratigraphy and isotope chronostratigraphy, it is late Pliocene in age (Piacenzian stage ca. 3.6 to 2.5 Ma; Hendy et al. 2015;



**Fig. 1** Location and stratigraphic provenance of *?Hydrochoeropsis wayuu*, new species. On left, map of South America, Colombia (inset) and the Guajira Peninsula, indicating the place where the fossil was found. Shaded area points out the limit between Colombia and

Venezuela. Scale bar equals 1 km. On right, stratigraphic column of Estación de Policía Section, Ware Formation. Black bone shows the stratigraphic provenience of *?Hydrochoeropsis wayuu*

Moreno et al. 2015). The Ware Formation is correlated chronologically with the San Gregorio Formation in the Falcon Basin of Venezuela (Moreno et al. 2015). The vertebrate assemblage of the Ware Formation includes sharks and rays (Carcharhiniformes, Myliobatiformes, and Rajiformes); three orders of bony fish (Characiformes, Perciformes, and Siluriformes); reptiles, represented by Crocodylia and Testudines; and seven mammalian orders (Artiodactyla, Carnivora, Cingulata, Litopterna, Notoungulata, Pilosa, and Rodentia) (Forasiepi et al. 2014; Moreno et al. 2015; Moreno-Bernal et al. 2016; Amson et al. in press). The base of the Ware Formation, where the assemblage of mammals is recorded, was deposited in a fluvio-deltaic environment (Hendy et al. 2015; Moreno et al. 2015).

## Materials and Methods

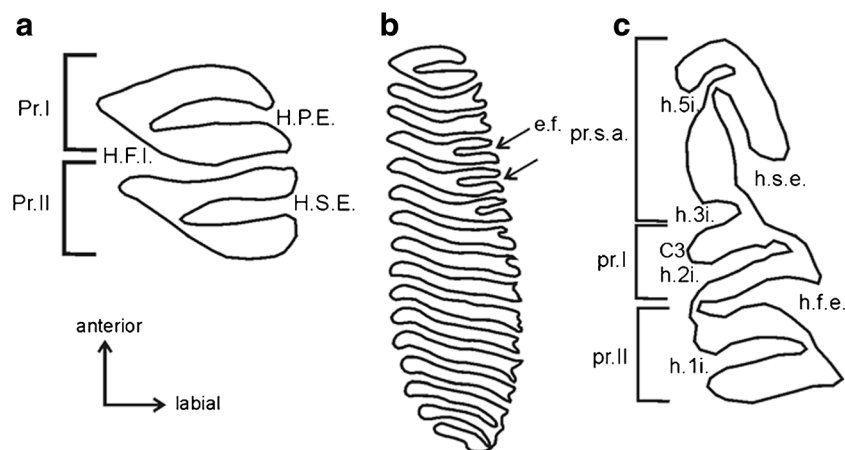
**Institutional abbreviations.** — **FMNH**, Field Museum of Natural History, Chicago. **MUN**, Mapuka Museum, Universidad del Norte, Barranquilla, Colombia. **STRI**, Smithsonian Tropical Research Institute, Panama.

**Dental nomenclature.** — Tooth terminology follows Vucetich et al. (2005) and is explained in Fig. 2.

**Dental abbreviations.** — **c3**, third internal column; **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; **h.sn.i.**, supernumerary internal flexid; **M1**, first upper molar; **M2**, second upper molar; **M3**, third upper molar; **p4**, fourth lower premolar; **P4**, fourth upper premolar; **pr.I/Pr.I**, prism I; **pr.II/Pr.II**, prism II; **pr.s.a.**, anterior secondary prism.

**Morphological Description** Description includes comparisons with other hydrochoerine species. Dental and skull measurements are in Tables 1 and 2.

**Phylogenetic Analysis** In order to test the phylogenetic position of the hydrochoerine of the Guajira Peninsula within Caviidae, we performed a cladistic analysis using the combined matrix of Madozzo-Jaén and Pérez (2016). Although *Kerodon* is the living sister group to *Hydrochoerus*, it was omitted from this analysis because it is the most basal lineage within Hydrochoerinae and beyond the scope of our study. The combined matrix (Online Resource 1) consists of 55 taxa of Cavoidea, 117 morphological characters (Online Resource 2), and 4014 characters from DNA sequences (12 s, cytb, TTH, GHR) obtained from GenBank. Some multistate characters of the morphological partition were considered as additive based on increasing degrees of similarity between the character states or in cases of interested homologies. This dataset was analyzed using equally weighted parsimony in TNT 1.1 (Goloboff et al. 2008a, b), and gaps were treated as missing data for DNA sequences. We used equally weighted parsimony to minimize the number of postulated evolutionary transformations. The heuristic search consisted of 1000 replicates of Wagner trees with random addition sequence of taxa, followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. After this procedure, a final round of TBR branch swapping was applied to find all most parsimonious trees (MPTs). Support values were calculated using Bremer indices, Bootstrap, and Jacking techniques. Unstable taxa in the set of MPTs were identified using IterPCR (Pol and Escapa 2009) to derive an informative reduced consensus.



**Fig. 2** Dental nomenclature in lower and upper teeth. **a** M1 or M2 (first or second upper molar); **b** M3 (third upper molar); **c** p4 (lower fourth premolar). Abbreviations: **C3**, third internal column; **e.f.**, external fissures; **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; **pr.I/Pr.I**, prism I; **pr.II/Pr.II**, prism II; **pr.s.a.**, anterior secondary prism

**Table 1** Dental measurements of *?Hydrochoeropsis wayuu*, new species (in millimeters). **AP**, antero-posterior length **AW**, anterior width; **HFI**, Fundamental internal flexus; **HPE**, primary external flexus; **HPEL**,HPE length; **HSE**, secondary external flexus; **HSEL**, HSE length; **Pr.I**, Prism I; **Pr.II**, Prism II; **PW**, posterior width. We incorporate new measurements, **LPr. I**, length of the Pr.I; **LPr.II**, length of Pr.II*?Hydrochoeropsis wayuu*

	Tooth	HPL/AW	HSEL/PW	AP	AW	PW	HPEL	HSEL	IPML (PI)	IPML (PII)	LPr.I	LPr.II
MUN STRI-12,846	M1	0,54	0,43	6,4	5,55	6,35	3	2,7	3,3	3,7	2,8	2,45
	M2	0,47	0,39	6,1	5,9	6,4	2,8	2,5	3,7	4	2,8	2,55
	M3			29,05								
MUN STRI-16,233	P4	0,54	0,4	13,6	8,4	9,15	4,5	3,7	4,5	7,3	7,1	5,2
	M1	0,47	0,36	10	9,6	10,3	4,5	3,7	5,65	6,7	5,3	4,2
	M2	0,46	0,38	9,6	10,2	10,5	4,7	4	5,6	7,05	5,05	
MUN STRI- 16,438	M1	0,41	0,33	8	7,8	7,95	3,2	2,65	5,2	5,9	4,05	3,45
	M2	0,5	0,36	7,9	8,0	8,5	4	3,1	5,3	5,8	4,6	4
MUN STRI- 37,602	p4			6<								

**Distribution Analysis** For analysis of the paleobiogeographic distribution, we used all occurrences of all Hydrochoerinae in the Paleobiology Database (PDBD; Alroy 2013), including numerous records of our own that we added to the PDBD. The data were downloaded from the PDBD on April 23, 2015, using the following parameters: taxa to include = Caviidae and Hydrochoeridae, time intervals = Neogene and Quaternary, region = North America and South America, include occurrences generically indeterminate = yes. All records of species and genus within Hydrochoerinae were grouped into five clades, *Caviodon*, *Cardiatherium*, *Hydrochoerus* + *Neochorus*, *Hydrochoeropsis*, and *Phugatherium*. The occurrences of every clade were mapped into four intervals, 10–5.3 Ma (late Miocene), 5.3 to 2.7 Ma (Pliocene), 2.7 to 0.01 Ma (Pleistocene), and younger than 10,000 years (Holocene). Within the *Hydrochoeropsis* clade, 14 occurrences were excluded from the analysis for being erroneous synonyms of species of the genus *Luantus* (*L. toldensis*, *L. propheticus*, and *L. minor*; belonging to the basal forms of Caviidae) with the genus *Hydrochoeropsis* (see Online Resource 4).

**Table 2** Skull measurements of *?Hydrochoeropsis wayuu*, new species. **PWIF**, posterior width of incisive foramen; **AZR**, rostral width at the anterior margin of the anterior root of the zygomatic arch; **OMS**, width between the anteriormost points of the scars marking the origin of the masseter superficialis muscle; **RWP4**, rostral width at the level of P4,

**Body Size Estimate** To estimate the body size of *?Hydrochoeropsis wayuu* we measured the femur length and diameter and used the allometric equations for rodents presented by Millien and Bovy (Millien and Bovy 2010).

## Results

### Systematic Paleontology

Rodentia Bowdich, 1821

Hystricognathi Tullberg, 1899

Cavioidea (Fisher von Waldheim, 1817) Kraglievich 1930

Caviidae Fisher von Waldheim, 1817

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

*Hydrochoeropsis* Kraglievich, 1930

*Type species.* — *Hydrochoeropsis dasseni* Kraglievich, 1930

*Referred species.* — *?Hydrochoeropsis wayuu*

measured at the alveolar margin of Pr.I; **PZR**, rostral width at the posterior margin of anterior root of the zygomatic arch; **RWM2**, rostral width at the level of M2, measured at the alveolar margin of Pr.II; **RL**, distance between posterior margin of the incisive foramen and P4; **P4-M1**, antero-posterior length from the P4 to the M1

*?Hydrochoeropsis wayuu*

Specimen	PWIF	AZR	OMS	RWP4	PZR	RWM2	RL	P4-M1	P4-M2	RWM2/ RWP4	PZR/ RWP4	AZR/ P4-M1	RWP4/ P4-M1	PZR/ P4-M1	RWM2/ P4-M1
MUN STRI-16,233	3,65	17,5	24,3	16	32,8	42,95	18,35	25,25	35,2	2,05	2,68	0,69	0,63	1,30	1,70
MUN STRI-16,438	3	21,4	26,9	18,9	31,4	39,1	13,9	25,6	33,1	1,66	2,07	0,84	0,74	1,23	1,53
MUN STRI-12,846	1,4	19,9	15,9	12,8	18,2	21,6	7,9	18,5	25,3	1,42	1,69	1,08	0,69	0,98	1,17

**Distribution and age.**—Uquíá Formation, Uquíá, Jujuy Province, late Pliocene (Reguero et al. 2007; see also Deschamps et al. 2013). Ware Formation, the Guajira Peninsula, northeast Colombia, Piacenzian (Hendy et al. 2015; Moreno et al. 2015).

### ?*Hydrochoeropsis wayuu*, New Species

**Holotype.**—MUN STRI-12,846, maxilla fragment with left and right M1–M3.

**Paratype.**—STRI-37,602, a left isolated p4 broken.

**Etymology.**—Named after the Wayúu, indigenous people of the Guajira Peninsula in whose territories the specimens were found.

**Referred material.**—MUN STRI-16,233, maxilla fragment with left and right P4–M2; MUN STRI-16,438, maxilla fragment with right M1–2; MUN STRI-34,315, a left femur.

**Diagnosis.**—Caviidae, diagnosed by the following unique combination of characters: euhipodont, and heart-shaped cheek teeth; p4 with three lobes and complex, and P4 with two lobes as in *Cardiatherium*, *Hydrochoerus*, *Nechoerus*, *Hydrochoeropsis dasseni*, and *Phugatherium*; H.F.I. completely crossing the tooth, differing from *Cardiatherium* in which the H.F.I. extends beyond the transverse midpoint of the crown but not splitting it; p4 with C3 as in *H. dasseni*, *Cardiatherium chasicoense*, and *Phugatherium*, and differing from *Hydrochoerus* and *Nechoerus* in which the h.2i. is behind the apex of the h.f.e.; h.2i and h.3i. equally deep as *H. dasseni*, but differing from *Hydrochoerus* and *Nechoerus* in which h.2i. is shallower than h.3i. and its apex is behind the h.f.e.; h.2i. and h.3i. are parallel as in *H. dasseni*, unlike *Phugatherium* in which they are convergent; h.5i. shallow, differing from *H. dasseni* in which the h.5i. is deeper; M3 composed of a first prism with H.P.E. and more than ten posterior laminar prisms, differing from that of *Cardiatherium*, which has fewer than ten posterior laminar prisms; external fissures present only in prisms two to five and shallow as in *H. dasseni*, unlike *Phugatherium* which has external fissures in all laminar prisms and very deep in prisms three to five, and *Hydrochoerus* and *Nechoerus*, in which these fissures are lacking or are ephemeral; the ventral root of the maxillary zygomatic arch arises posteriorly to the incisive foramen. The anterior portion of the palate is relatively flat as in *H. dasseni*.

### Description and Comparison

As in all hydrochoerines, the cheek teeth are euhipodont. The p4 is trilobed, the P4–M2 are bilobed, and the M3 is multilaminated with cement in the flexus/ids, and the enamel is interrupted along the labial wall of each lobe (or prism) of the upper molars (Mones 1991; Vucetich et al. 2005, 2014, 2015b; Deschamps et al. 2007; Pérez et al. 2014).

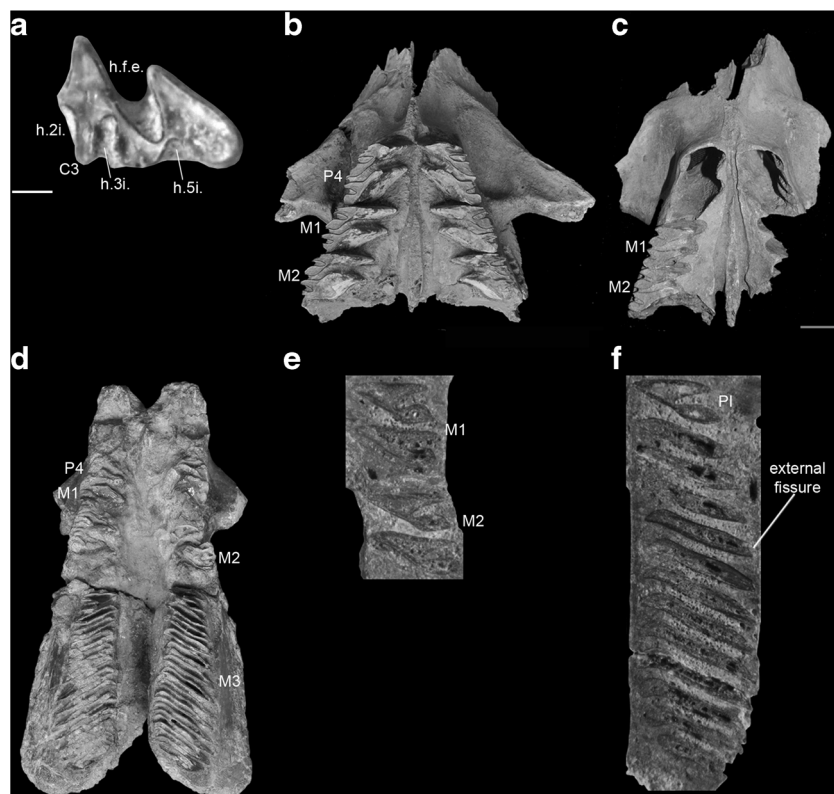
**Lower Premolar** The p4 is an isolated and broken left tooth that lacks its posterior prism (Fig. 3a). This premolar probably belongs to a young specimen because it is small (Table 1) and the enamel is not on the entire lingual wall of the tooth (as occurs in teeth of juvenile-adults of hydrochoerines); instead, it is slightly interrupted on the lingual wall of the C3 and of the pr.s.a. The pr.s.a. is smaller than the pr.I, and is oriented obliquely with the labial apex posteriorly directed (Fig. 3a). The h.5i. is wide and shallow (Fig. 3a), a condition that differs from *Phugatherium catacliticum*, *P. dichroplax*, *Hydrochoeropsis dasseni*, *Nechoerus*, and *Hydrochoerus*, in which the h.5i. is narrow and transversely deeper. Conversely, in *P. novum* (MMP 236, see Reig 1952; Vucetich et al. 2014) this fissure is even shallower than in MUN STRI-37,602, and *P. saavedrai* lacks the h.5i. The h.s.e. is deep and wider than in the other species of hydrochoerines. The pr.I is transversely longer than pr.s.a., and the labial apex is transversely oriented (Fig. 3a). It includes both fissures h.2i. and h.3i. giving rise to a long C3 (Fig. 3a). The fissures are transverse and deep (h.2i. slightly deeper than h.3i.), reaching up to 50 % of the lobe width (Fig. 3a) as in *P. novum* and *H. dasseni*. In the remaining species of *Phugatherium* (including *P. dichroplax*, see Vucetich et al. 2015b), these fissures are deeper. The C3 in *P. saavedrai* and *P. dichroplax* is drop-shaped, because the h.2i. and h.3i. are very long and strongly convergent. *Phugatherium catacliticum* differs from the other species in having a h.2i. that is much deeper than h.3i. In *Nechoerus* and *Hydrochoerus*, these fissures are also deep but the h.2i. is included in pr.II (some specimens of *Nechoerus* have the h.2i. between pr.I and pr.II.), not in pr.I as in *Phugatherium* and *H. dasseni*. The p4 differs from that of *Cardiatherium* in that h.2i. and h.3i. of this genus are shallower and h.5i., if present, is very shallow. In addition, an h.sn.i. (Vucetich et al. 2005) is frequent in *Cardiatherium*.

**Upper Cheek Teeth** The upper cheek teeth P4, M1, and M2 (Fig. 3b–c) are bilobed and the H.F.I. is completely open on the labial side, resembling the condition of *Phugatherium*, *Nechoerus*, and *Hydrochoerus* (although in these genera H.F.I. of P4 may be closed as individual variation), but contrasting with the labially closed H.F.I. in *Cardiatherium*. The P4 of the single specimen known of *H. dasseni* has the H.F.I. closed, whereas in M1 and M2 this flexus is opened (see Vucetich et al. 2015b).

Morphologically P4–M2 are similar, though they differ slightly in size (Table 1). MUN STRI-16,233 is the only specimen that preserves the P4 (Fig. 3b), whereas all specimens have the M1–2 (Fig. 3c).

The Pr.I of P4 has an anterior wall slightly anteriorly convex with its apex anteriorly directed. The posterior margin is elongated anterolingually-posterolabially (Fig. 3b), resembling the condition of *Hydrochoerus*. In the other taxa

**Fig. 3** ?*Hydrochoeropsis wayuu*, new species. **a** MUN STRI-37,602 (syntype) left fourth pre-molar; **b** MUN STRI-16,233 maxilla fragment with left and right P4-M2; **c** MUN STRI-16,438 maxilla fragment with right M1-M2; **d-f** STRI 12846, **d** maxilla fragment with left and right M1-M3, **e** M1-M2 detail, **f** M3 detail. Scale bar: 1 cm



(*Phugatherium*, *H. dasseni*, and *Nechoerus*) the Pr.I is more transverse. In Pr.II the lingual apex is anteriorly directed, the margin posterolingual and oblique is long, and the anterior margin is concave in its medial portion (Fig. 3b), resembling the condition of *Hydrochoerus*, and contrasting with those of the remaining hydrochoerines. The H.P.E. of the cheek teeth is relatively transverse and deep (Fig. 3b), as in *H. dasseni*, *Hydrochoerus*, and *Nechoerus*. In *P. novum* and *P. dichroplax*, the H.P.E. of P4 is posteriorly oriented. The H.S.E. is transversely shorter than H.P.E. (similar to *Hydrochoeropsis*) and slightly posteriorly oriented (Fig. 3b) as in *P. dichroplax* and *P. novum*. The H.F.I. is relatively wide and more obliquely oriented than in M1-M2. The lingual portion of the prisms (those without fissure) are more parallel, thus differing from *P. cataclisticum*, *P. novum*, and *P. dichroplax*, *Nechoerus*, and *Hydrochoerus*. The posterior portion of the anterior lobe placed between H.P.E. and H.F.I. is lanceolate-shaped and with a small tip at the labial end (Fig. 3b). This condition is similar to that of *P. dichroplax*, *Hydrochoerus*, *Nechoerus*, and *H. dasseni*, but in this last species (and in some specimens of *Hydrochoerus*) the tip end links both lobes.

The M1 and M2 are morphologically very similar to the P4, but differ in size (Table 1); the lobes are not as strongly directed forward, and the anterior margin of the Pr.I is straight as in other hydrochoerines (Fig. 3b-c).

The M3 is preserved only in specimen MUN STRI-12,846 (Fig. 3d,f) and, as in all hydrochoerines, has a first bilobed

prism that is followed by several laminar prisms. In the new specimen, the first lobe has the anterior margin slightly anteriorly convex (Fig. 3d,f). Moreover, the first lobe has the H.P.E. deep and slightly posteriorly oriented; the orientation of this fissure is variable between transverse and slightly posterior within the species. The posterior area of this lobe (Fig. 3d,f), delimited by the H.P.E. and the posterior margin, is lanceolate-shaped with the major apex transversely oriented, and a sharp labial end. This area is variable in the extension and orientation of their apices among hydrochoerines. The new specimen has the same condition as in *P. dichroplax* and *H. dasseni*, and contrasts with that of *Nechoerus* and *P. cataclisticum* in which labial end is not sharp. In *Hydrochoerus* the lanceolate area is posteriorly oblique and the labial end is strongly sharp, and in *P. novum* the minor apex is wider than in other species, giving a less lanceolate shape.

The hydrochoerine of the Guajira Peninsula has 13 posterior laminar prisms in the M3 (Fig. 3d,f). The presence of more than ten laminar prisms in this molar is a condition shared with *Phugatherium* (14 to 18), *H. dasseni* (13), *Hydrochoerus* (10–14), and *Nechoerus* (13–17), whereas *Cardiatherium* has fewer than ten (Vucetich et al. 2014, 2015b). The first eight laminar prisms have the lingual end posteriorly oriented and relatively sharp, while the last prisms have a rounded lingual end. The last two laminar prisms are transversely shorter and the lingual end is not posteriorly oriented. In the hydrochoerine of the Guajira Peninsula, a

shallow external fissure is present on the labial wall of the first five laminar prisms, resembling the condition of *H. dasseni*, whereas in *Phugatherium* these external fissures are present in all laminar prisms, some of them being very deep (3–6 in *P. catacliticum*, 3–4 in *P. saavedrai*, and 4–5 in *P. dichroplax*).

**Maxilla** Only three maxillary fragments represent the skull (MUN STRI-12,846, MUN STRI-16,233, and MUN STRI-16,438). In ventral view (Fig. 3b–c), the anterior margin of the maxillary palatal process is broken but preserves the posterior border of the incisive foramen, which is anteriorly concave (Fig. 3c). The area delimited between the incisive foramen and P4 is anterodorsally-posteroventrally oblique (as in other hydrochoerines), the anterolateral face is anteriorly concave, and its medial margin converges with its counterpart, forming the suture of both maxillae as a slight (Fig. 3c) or developed ridge (Fig. 3b). This ridge extends posteriorly, it narrows between the P4s, and at the level of M1 it widens up to the posterior contact with the palate (Fig. 3b–c). At both sides of the medial suture, there is a groove relatively deep and as wide as the ridge (Fig. 3b–c). The ventral surface of the maxilla, between the groove and the toothrow, is narrow at the level of P4 and becomes wider posteriorly, as in other hydrochoerines. The posterior margin of the maxillary palatal process is broken but the posterior border of the palatal foramen can be observed, and is posteriorly concave (Fig. 3b–c). These palatal foramina are located at the posterior end of the M2, the same position as in *Nechoerus* and *Hydrochoerus*. The dental series converges anteriorly, the area between right and left P4 is very narrow, and the lingual apices of the Pr.I of both premolars are very close (Fig. 3b–c). The rostrum measured at the level of the anterior zygomatic root and at the level of the P4 is considerably narrower than in *H. dasseni* and *Nechoerus*, and relatively similar to juvenile specimens of *P. novum* (Table 2).

The maxillary zygomatic process has preserved only the anterior root of the zygomatic arch, the anterior margin of which arises anterior to the P4, and posterior (or at the same level) to the incisive foramen (Fig. 3b–c). This condition resembles that of *Phugatherium*, *Hydrochoerus*, *Nechoerus*, and some species of *Cardiatherium*, but differs from that of *H. dasseni* in which the ventral root of the zygomatic arch arises anterior to the incisive foramen. The anterior root of the zygomatic arch is oblique anteromedially-dorsolaterally (only preserved in MUN STRI-16,233; Fig. 3b), resembling the condition of *P. novum*, and contrasting with that of *Hydrochoerus* and *Nechoerus* in which the anterior root is lateromedially straight and then it directs posteriorly. On the ventral surface of the zygomatic arch, there is a notch for the attachment of the m. masseter superficialis (Fig. 3b–c) that begins anterior to the P4 and extends posteriorly up to the posterior wall of P4. This notch is very large, occupies most of the surface of the anteroventral root of the zygomatic

process, and is oval-shaped (with its major axis oriented anteroposteriorly). This condition resembles that of *Phugatherium* and *H. dasseni* and differs from that of *Hydrochoerus* and *Nechoerus* in which the notch is anteroposteriorly shorter.

**Postcranium** Only one postcranial element, a complete and well-preserved left femur (Fig. 4), was found at the same locality and is tentatively assigned to the same species.

The femur is straight, but slightly medially concave in the proximal portion (Fig. 4). The maximum length (measured from the greater trochanter to the end of the distal head) and the maximum width of the diaphysis (measured from the medial margin to the neck) are shorter than in *Hydrochoerus* (Table 3).

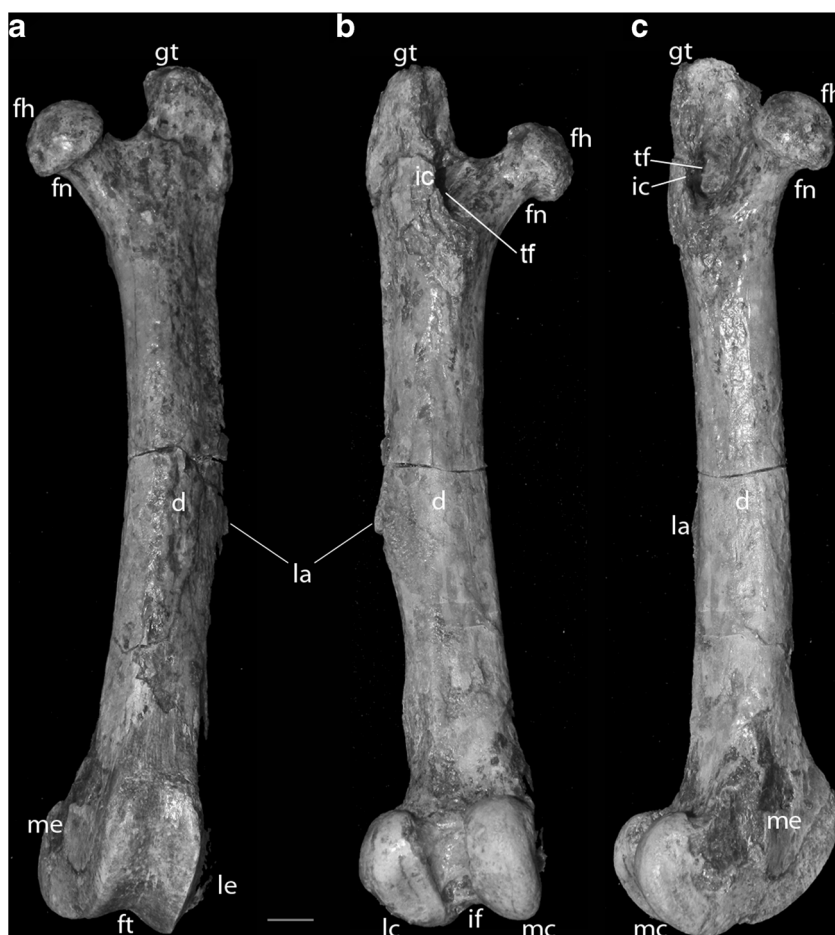
The proximal portion of the femur preserves the head, neck, greater trochanter, trochanteric fossa, and intertrochanteric crest (Fig. 4a–c). The femoral head is placed medially and the greater trochanter laterally in the proximal portion of the femur. The femoral head is hemispherical and has a distinct neck, which is proportionally larger than that of *Hydrochoerus* (Table 3). The dorsal surface between the head and the greater trochanter is dorsally concave (Fig. 4a–b), and wider than in *Hydrochoerus*. The medial margin of the greater trochanter is straight and vertical (Fig. 4a–b), contrasting with the condition of *Hydrochoerus* in which this margin is straight and oblique ventromedially-dorsolaterally. The greater trochanter in *?H. wayuu* has a dorsolateral surface that is dorsally convex and laterally slightly convex (Fig. 4a–b), resembling the condition of *Hydrochoerus*, but in this species the greater trochanter is more developed. In anterior view, the dorsolateral border of the greater trochanter forms a ridge that is developed up to the level of the femoral neck (Fig. 4a). In posterior view, ventral to the greater trochanter and medially opened is the trochanteric fossa, which is wide and ovoid-shaped with its major apex dorsoventrally oriented (Fig. 4b–c), similar to the trochanteric fossa of *Hydrochoerus*. This fossa is limited posterolaterally by the intertrochanteric crest, which is somewhat deteriorated in the femur of the *?H. wayuu* (Fig. 4b–c). Distal to the trochanteric crest is the linea aspera (Fig. 4a–c).

The distal portion of the femur consists of the following elements: medial and lateral condyles, trochlea, medial and lateral epicondyles, and intercondylar fossa (Fig. 4a–c). In anterior view, the trochlea is an anteroventrally concave fossa, dorsoventrally elongated, and delimited by the medial and lateral epicondyles (Fig. 4a). The dorsal margin of this fossa is dorsally convex and the medial and lateral epicondyles are laterally flat. The trochlea of the femur is wider than in *Hydrochoerus*. In posterior view, the medial and lateral condyles are strongly convex on the entire surface, and between them, the intercondylar fossa has a straight dorsal margin (Fig. 4b).

Between the proximal and distal portions, the diaphysis is slightly anteriorly and posteriorly convex (Fig. 4a–c). The

**Fig. 4** MUN STRI-34,315, left femur. **a** anterior view; **b** posterior view; **c** medial view.

Abbreviations: **d**, diaphysis; **fh**, femoral head; **fn**, femoral neck; **ft**, femoral trochlea; **gt**, greater trochanter; **ic**, intertrochanteric crest; **la**, linea aspera; **lc**, lateral condyle; **le**, lateral epicondyle; **mc**, medial condyle; **me**, medial epicondyle; **tf**, trochanteric fossa. Scale bar: 1 cm



linea aspera is on the lateral margin of the diaphysis and is dorsally extended up to the greater trochanter, but not in contact (Fig. 4a-c).

### Phylogenetic Analysis

The phylogenetic analysis resulted in 136 most parsimonious trees (MPTs) of 3244 steps. Caviidae shows a basal polytomy in the strict consensus (Fig. 5a), because the fragmentary fossil *Microcardiodon huemulensis* takes different positions within this clade in the MPTs. The alternative positions of this unstable taxon do not affect the monophyly of Hydrochoerinae. However, the strict consensus does not reflect the affinities between the three main clades of Caviidae. When the unstable

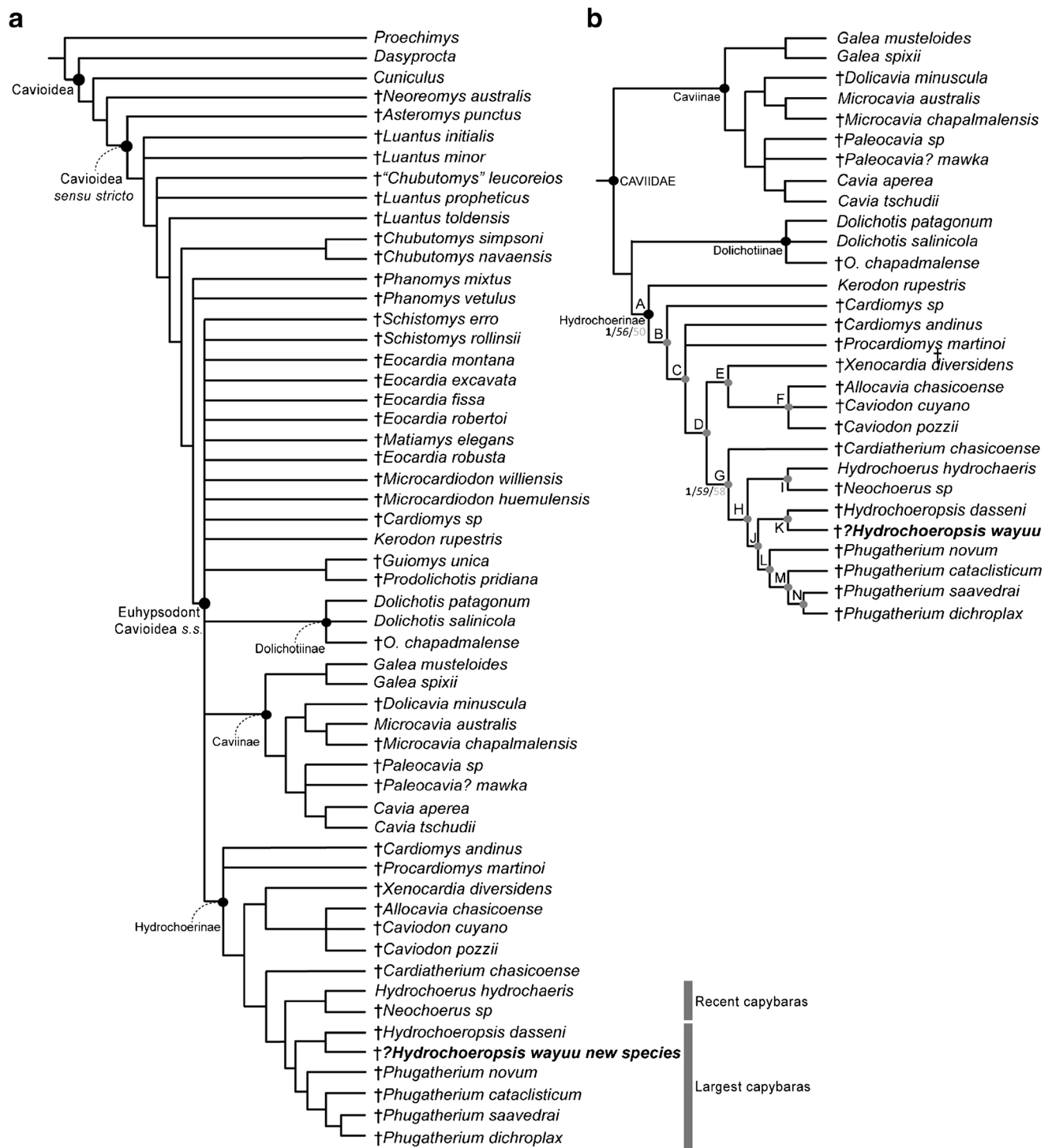
taxon is ignored from the MPTs (Pol and Escapa 2009), the reduced consensus retrieves as a monophyletic group Caviinae, Dolichotinae, and Hydrochoerinae, and these last two clades as sister groups (Fig. 5b).

*?Hydrochoeropsis wayuu* is the sister taxon of *H. dasseni* and nested among the largest hydrochoerines in all MPTs (Fig. 5b, node H). Only one unambiguous synapomorphy supports its position: h.2i. and h.3i. parallel to each other (character 83[0]). This clade is the sister group of *Phugatherium* (Fig. 5b, node I), which is supported by one unambiguous synapomorphy: first five laminar prisms of M3 with deep external fissures (c. 117[2]). The clade of the largest hydrochoerines (*Hydrochoeropsis* + *Phugatherium*; Fig. 5b, node G) is supported by two unambiguous synapomorphies:

**Table 3** Femoral measurements of *?Hydrochoeropsis wayuu*, new species and *Hydrochoeris hydrochaeris* (in millimeters)

	<i>?Hydrochoeropsis wayuu</i> MUN STRI-34,315	<i>Hydrochoeris hydrochaeris</i> FMNH P 60152
Proximo-distal length	173	210
Maximum width of diaphysis	21	27
Femoral head	18	30
Neck of femoral head	13,15	17
Relation: neck/ femoral head	0,52	0,72





**Fig. 5 a** Strict consensus of 136 most parsimonious trees (Length = 3244) resulting from the parsimony combined phylogenetic analysis of morphological and molecular dataset using TNT; **b** Caviidae with the monophyletic three main lineages: Caviinae, Hydrochoerinae,

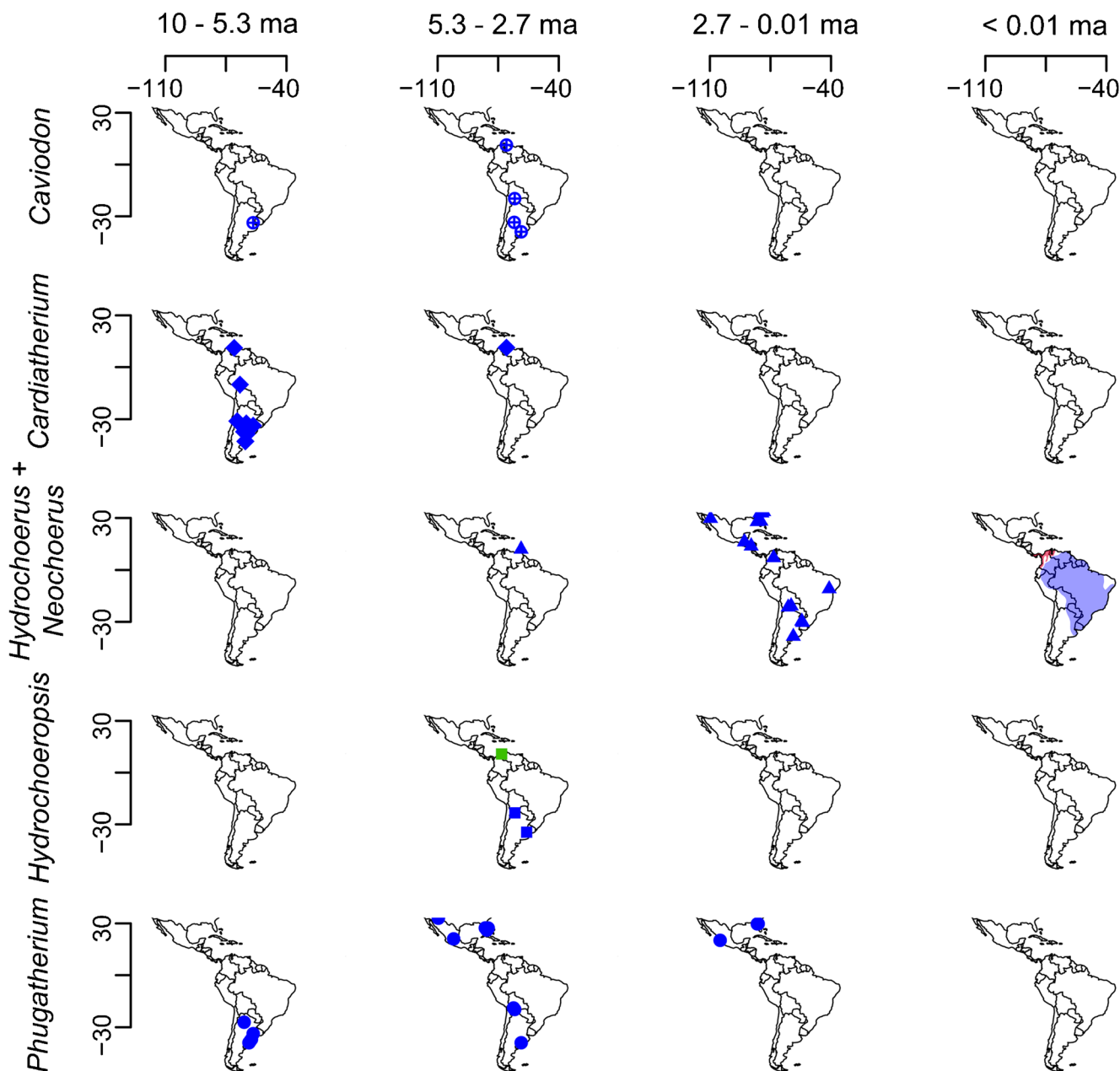
and Dolichotiinae in the reduced consensus ignoring the unstable and fragmentary fossil *Microcardiodon huemulensis*. The numbers in bold indicate Bremer indices, numbers in italics represent absolute Jackknife values, and numbers in gray represent GC Jackknife values

anteroposterior length of the upper diastema equal to or longer than the molariform series (c. 37[0]) (and h.2i. deeper than h.3i. (c. 82[0]). This clade is the sister group of *Neochoerus* and extant capybaras (*Hydrochoerus*).

The close affinities between *Hydrochoerus* and *Neochoerus* (Fig. 5b, node I) are supported by four unambiguous synapomorphies in all MPTs: posterior extension of the root of the lower incisors extending up to the level of the anterior lobe of

**Table 4** Body mass estimates for *?Hydrochoeropsis wayuu*. %PE : average absolute percent prediction error. Equation parameters according to Millien and Bovy (2010: Table 1)

Measurement (mm)	r ^ 2	Intercept	Slope	Standard error	% PE	Body mass (kg)	Mass - PE (kg)	Mass + PE (kg)
Femur length = 173	0.86	-1.964	2.825	0.240	48.59	23	12	34
Femur diameter = 21	0.84	0.903	2.635	0.257	47.45	24	13	35



**Fig. 6** Temporal and geographic distribution of the most derived hydrochoerines (†*Cardiatherium*, †*Phugatherium*, †*Hydrochoeropsis*, †*Neochoerus*, and *Hydrochoerus*) from the PBDB. The shaded areas correspond to the distribution of the two extant species *Hydrochoerus*

*hydrochaeris* (Blue) and *Hydrochoerus isthmius* (Red). Distribution of extant taxa taken from IUCN (International Union for Conservation of Nature) 2008. *?Hydrochoeropsis wayuu* is indicated by a green square

m1 (c. 20 [4]); h.2i. placed in pr.II of complex p4 (c. 79[1]), external fissure in pr.II of the complex m3 more than 75 % of transverse diameter (c. 105[1]), and very superficial or absent external fissures in the laminar prisms of M3 (c. 116 [0]).

The unambiguous synapomorphies that support the close relationships between the recent capybaras and the largest hydrochoerines (Fig. 5b, node H) include the transverse extension of H.F.I. and h.f.e. completely crossing the teeth (c. 99[3]) and more than ten laminar prisms in the M3 (c. 114[5]).

*Cardiatherium chasicoense* is the sister group of the more derived and largest hydrochoerines (Fig. 5b, node G) and this position is supported by seven unambiguous synapomorphies (Supporting Information S3).

### Body Size Estimate

According to the femoral measurements, *?H. wayuu* had a body mass of ~23–24 kg, with a margin of error ranging from 12 kg to 35 kg (Table 4). It is noteworthy that the femur (MUN-STRI 34315) does not belong to a young individual, as it has the distal and proximal epiphysis completely closed (Fig. 4).

### Discussion

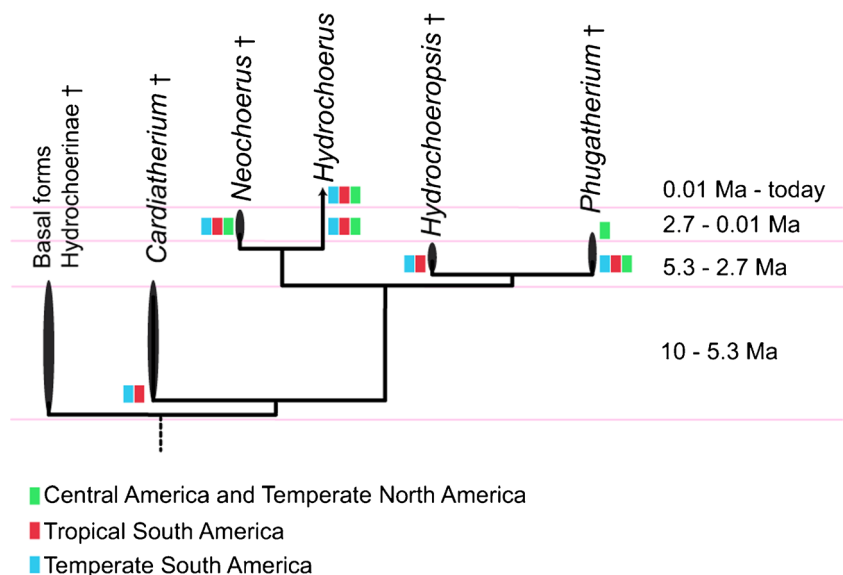
**Taxonomic status of *?Hydrochoeropsis wayuu*** According to the tooth morphology and the results of the phylogenetic analyses, the new hydrochoerine of the Ware Formation is tentatively assigned to the genus *Hydrochoeropsis*, because it is closely related to *H. dasseni* in all MPTs (see *Phylogenetic Analysis*). Here, we propose that the new specimen should be assigned to a new species for its unique combination of characters (see *Diagnosis*). However, we are cautious about its generic assignment because support values in the phylogenetic

analysis are low, and with only one extra step the relations between *Phugatherium*, *H. dasseni*, and *?H. wayuu* are unresolved (Fig. 5b). This is due mainly to the fragmentary nature of the remains, which limits information about the new species. *?Hydrochoeropsis wayuu* is undoubtedly a derived hydrochoerine because it shares seven synapomorphies with *Cardiatherium*, *Phugatherium*, *Hydrochoeropsis*, *Neochoerus*, and *Hydrochoerus* (Online Resource 3). Although the lower premolar (MUN STRI-37,602) is relatively juvenile (because of its small size) and lacks pr.II, it has some characters that separate it from the recent capybaras, *Hydrochoerus*, and the extinct *Neochoerus* (such as the presence of h.2i. in the pr.I), but resemble the condition of *H. dasseni* and *Phugatherium* (see *Phylogenetic Analysis*).

### Significance of Pliocene Capybaras in the Guajira Peninsula

The subfamily Hydrochoerinae is recorded from the middle Miocene in La Venta Colombia (Vucetich et al. 2015a) and in Patagonia (Vucetich and Pérez 2011). During the early late Miocene of temperate South America, the most basal genera of hydrochoerines (*Procardiomys*, *Cardiomys*, *Xenocardia*; Pérez et al. 2014; Vucetich et al. 2015a, b), and the derived *Cardiatherium chasicoense* (Deschamps et al. 2007, 2013) are recorded. From this time, the fossil record of hydrochoerines is abundant and relatively continuous, recording several species of *Caviodon* and *Cardiatherium* in the late Miocene (Rovereto 1914; Candela 2005; Vucetich et al. 2005, 2010; Deschamps et al. 2009, 2013). *Cardiatherium* is present during the late Miocene, mainly distributed in temperate South America, but is also recorded in tropical South America (Figs. 6,7; Online Resource 4 contains all the individual records used for this analysis). A few late Miocene specimens of *Phugatherium* (Fig. 6; Supporting Information S4) have been reported in Argentina (Bondesio

**Fig. 7** Summary of the temporal and geographic distribution of the most derived hydrochoerines (†*Cardiatherium*, †*Phugatherium*, †*Hydrochoeropsis*, †*Neochoerus*, and *Hydrochoerus*). Data from Fig. 6 and Supporting Information S4. Late Miocene records of *Phugatherium* are probably Pliocene and were excluded (Vucetich and Deschamps pers. comm.)



1975; Deschamps et al. 2013). However, these specimens are from the upper levels of the Ituzaingó Formation, and would correspond to the early Pliocene (Vucetich and Deschamps pers. comm.). The most derived capybara clade (*Phugatherium* + *Hydrochoeropsis* + *Neochoerus* + *Hydrochoerus*) is mostly known from high latitudes, and they have not been yet recorded in late Miocene sediments (Figs. 6, 7). Therefore, the lineage leading to them would have arisen within this time interval (Fig. 7). Because *Cardiatherium* is present in both temperate and tropical latitudes during the late Miocene, it is still uncertain whether the largest and recent hydrochoerine lineages originated in temperate South America and rapidly migrated toward tropical latitudes, or vice versa (Fig. 7).

Femoral body size estimates yielded a body mass of ~23–24 kg for *?H. wayuu*, comparable to the lesser capybara, *H. isthmus* (~28 kg) and smaller than *H. hydrochaeris* (35–65 kg). The two extant species differ in size and craniodental morphology (Aeschbach et al. in press). *Hydrochoerus hydrochaeris* shows intraspecific size and cranial shape differences across its geographical distribution, increasing in mass with increasing latitude (Mones and Ojasti 1986; Moreira et al. 2013; Aeschbach et al. in press). *?Hydrochoeropsis wayuu* is smaller than *Phugatherium* (Vucetich et al. 2014) and *Neochoerus*; for the latter, body mass estimates range from 110 kg (Vizcaíno et al. 2012) to ~200 kg (Ghizzoni 2014). The relatively small size of *?H. wayuu* suggests a higher body size disparity and geographical variation within the clade since the Pliocene.

During the Pliocene (5.3 to 2.7 Ma) the diversity of hydrochoerines decreased and their geographical range showed a dramatic change, with the first migration toward Central America and temperate North America (Figs. 6–7), during the GABI (Woodburne 2010). This initial dispersal across the Panamanian Isthmus could have been facilitated by the almost full emergence of the Isthmus by 10 Ma (Montes et al. 2015), and it is coetaneous with a significant wave of terrestrial dispersals across the Isthmus of many different clades at 6 Ma (Bacon et al. 2015). Despite the abundance of fossil mammals in North America and in temperate South America, the record from tropical South America is still scant and the information available to document the migration pathways is scarce (Carrillo et al. 2015). Nevertheless, given that the land connection occurs in the tropics, it is expected that many of the taxa that participated in the interchange or their close relatives inhabited tropical areas (Webb 1991).

The Pliocene record of hydrochoerines (the largest capybaras) consists of *Phugatherium*, which is recorded in southern South America (Deschamps et al. 2013; Vucetich et al. 2014, 2015b) and whose presence in the Pliocene of North America was recently corroborated with *P. dichroplax* (Vucetich et al. 2015b), and *H. dasseni* from the Uquía Formation (Kraglievich 1930). There is also one report from the late Pliocene to early Pleistocene of Grenada (Lesser

Antilles, MacPhee et al. 2000) that corresponds to *Hydrochoerus gaylordi*, but this occurrence is controversial and the specimen needs to be re-examined (see Vucetich et al. 2012). In northern South America, fragmentary remains from the Pliocene of the San Gregorio Formation (Venezuela) tentatively assigned to *Cardiatherium* also need to be re-examined (Vucetich et al. 2010, 2015b). These remains consist of small tooth fragments with the lobes still united, a diagnostic character of *Cardiatherium*, but also of young individuals of more derived hydrochoerines (Vucetich et al. 2014). Hence, taking into account the age of the fossil-bearing levels and the geographical proximity, these remains may represent juveniles of *?H. wayuu*. Additional caviomorphs from San Gregorio include the hydrochoerid *Cavidon*, the octodontid *Marisela gregoriana*, and the neopiblemid *Neopiblema* (Vucetich et al. 2010). Of these, neopiblemids (*Neopiblema* and *Phoberomys*) are also recorded in the late Miocene deposits of the Urumaco Formation (Sánchez-Villagra et al. 2003; Carrillo and Sánchez-Villagra 2015).

During the late Pliocene and Pleistocene (2.7 to 0.01 Ma) diversity of the Hydrochoerinae declined, with only two clades recorded, *Neochoerus/Hydrochoerus* and *Phugatherium*. While *Neochoerus/Hydrochoerus* were widely distributed in tropical and temperate South America, Central America, and North America, *Phugatherium* is restricted to temperate North America (Guanajuato, Mexico; Arizona, USA). The recent capybaras *Neochoerus* and *Hydrochoerus* are recorded in the Pleistocene of several localities of South America (Ameghino 1902; Soibelzon et al. 2005; Tonni et al. 2009; Kerber and Ribeiro 2012; Deschamps et al. 2013) and North America (Mones 1991). The validity of some species of *Neochoerus* and *Hydrochoerus* (e.g., *N. aesopi*, *H. gaylordi*) is controversial (see Mones 1991; Baskin and Thomas 2007; Morgan 2005, 2008; Vucetich et al. 2015b) and these need a more exhaustive revision. By the Holocene (10,000 b.p.), only one lineage of Hydrochoerinae is present (*Hydrochoerus*), and it is represented by the two extant species: *H. hydrochaeris* and *H. isthmus* (Figs. 6–7).

*?Hydrochoeropsis wayuu* from the Ware Formation in the Guajira Peninsula would be the northernmost hydrochoerine record from the Pliocene of South America, and the nearest one to the Panamanian bridge at 3.2 Ma (Moreno et al. 2015). By that time (late Pliocene) one of the largest capybaras, *P. dichroplax*, had already crossed the Isthmus as is evidenced by its record in Guanajuato (Mexico) and Arizona (USA) during the late early to early-late Blancan (Morgan 2008; Deschamps et al. 2013; Vucetich et al. 2015b). Vucetich et al. (2015b) indicated that oldest record of *P. dichroplax* in the late Pliocene of North America (Guanajuato, Mexico; 3.6 Ma) suggesting that this lineage was present in northern South America before 3.6 Ma. The presence of *?Hydrochoeropsis wayuu* in Guajira corroborates that the lineage of the largest capybaras inhabited the low latitudes of South America during the GABI.

Today *Hydrochoerus* does not inhabit the Guajira Peninsula, an extremely dry landscape that has a prolonged dry season (~11 months), is dominated by xerophytic vegetation, and lacks large rivers or year-round bodies of fresh water. Capybaras, which depend on water physiologically and for refuge (Herrera 2012) require habitats close to water bodies including marshes, estuaries, swamps, and the banks of rivers and streams. This suggests that major changes in the landscape occurred, leading to the extreme aridification of the region over the past 2.5–3 Ma.

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