Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late Miocene–Pliocene sequences of South America

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ABSTRACT

Fossil capybaras were long regarded as composed of numerous taxa, each one endemic to a particular area, a scenario completely different from the one shown by the living species. The interpretation of the record according to new criteria of ontogenetic change has demonstrated that they are useful for bio-correlation because their members have short biochrons with wide geographic distribution. The levels with capybaras of each locality would represent a short lapse within the bearing lithostratigraphic units. In turn, they would also represent short intervals within the temporal extension proposed for each Stage/Age or SALMA. All the late Miocene–Pliocene records of capybaras were analyzed and a chronological scheme was built mainly for Argentina, where records are most abundant. Numerical ages and mag-netostratigraphic studies contribute to correlate this scheme with the global time scale. The Chasicoan SALMA would be correlated with part of the Tortonian Stage/Age; the Huayquerian SALMA with the late Tortonian-Messinian, and it could even extend to the earliest Zanclean. The Montehermosan SALMA would be restricted to the Zanclean. The Chapadmalalan SALMA would be correlated with the late Zanclean-early Piacenzian.

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1. Introduction

The temporal calibration of the continental late Miocene–Pliocene lapse in South America is based mainly on mammal faunas from central Argentina. This interval has been subdivided into the Chasicoan, Huayquerian, Montehermosan, Chapadmalalan, and Marplatan South American land mammal Ages (SALMAs) and Stages/Ages (Cione and Tonni, 1995 and references therein). Limits between each of these units and their temporal extension, are still uncertain and controversial (compare Cione and Tonni, 1996, 2005; Verzi et al., 2008). Recently, a conspicuous group of mammals, the gigantic hydrochoerine rodents, has been considered as good biostratigraphic tools allowing a refreshing view of the correlations among lithostratigraphic units of this interval (Deschamps et al., 2009, 2012; Vucetich et al., 2013).

Hydrochoerids are members of the Superfamily Cavioidea (see below 2. List of analyzed taxa) and include the extinct car-diomyines, the hydrochoerines or capybaras, dolichotines, and the living rock cavies (Pérez and Vucetich, 2011). Other authors include all these taxa in the Family Caviidae (e.g. Rowe and Honeycutt, 2002; Woods and Kilpatrick, 2005; Pérez and Pol, 2012), but we prefer the use of two families until a cladistic analysis including more extinct taxa (e. gr. more cardiomyine species) are performed.

Living capybaras are represented by two species, *Hydrochoerus hydrochaeris* widely distributed in South America, and *H. isthmius*, restricted to the northwest of the Cordillera Oriental of Colombia (Moreira et al., 2012). Capybaras stand out for being the largest living rodents, for living in herds of up to 20 to 30 individuals gathering males and females of several generations, and for having semi-aquatic habits (Herrera, 2012 and references therein). Living capybaras are territorial and occupy areas from 6 to 16 Ha near water bodies which are quite stable in space for three or more years
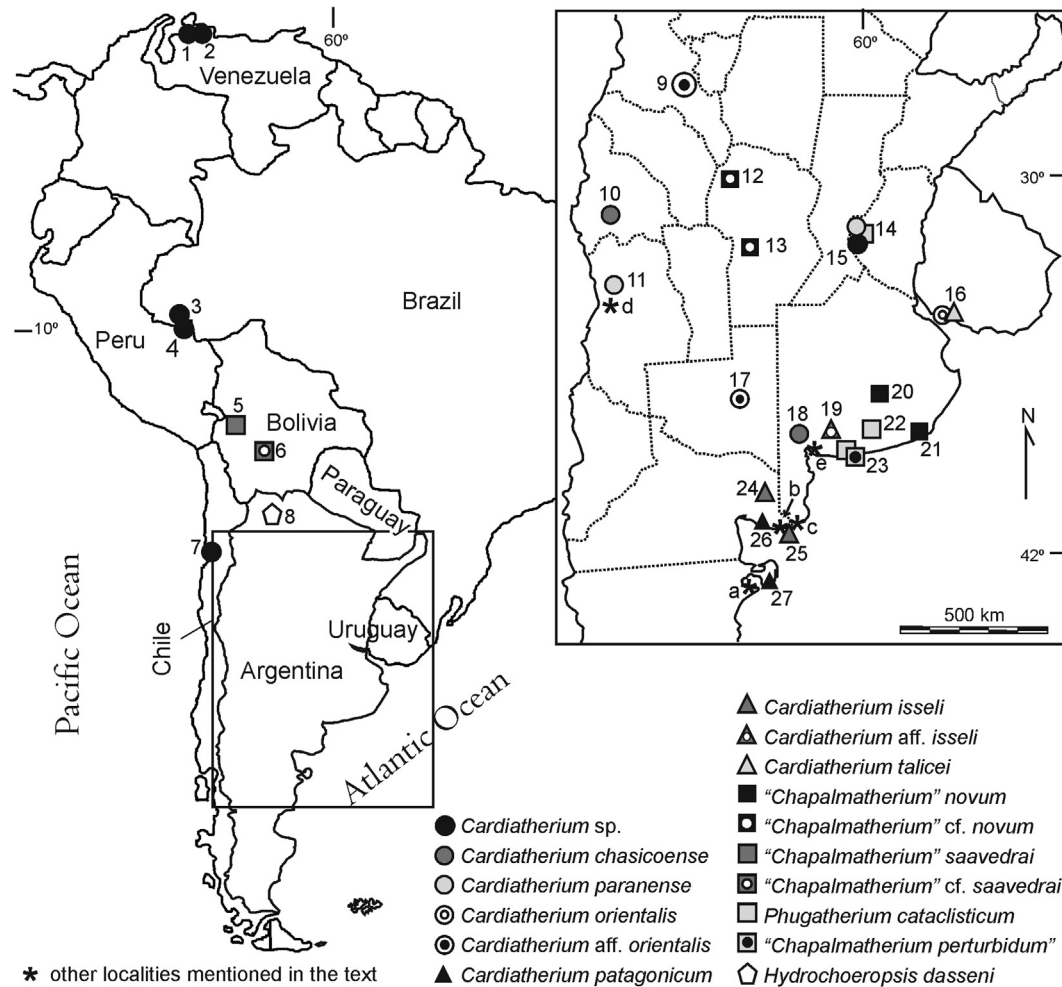
Fig. 1. Location map showing localities bearing Mio-Pliocene capybaras, and the recorded taxa. 1, Urumaco River; Venezuela; 2, San Gregorio, Venezuela; 3, Juruá River, Brazil; 4, Acre River, Perú; 5, Ayo Ayo, Bolivia; 6, Inchasi, Bolivia; 7, Bahía Inglesa, Chile; 8—15, 17—27, Argentina. 8, Uquía, Jujuy; 9, Andalhuala, Catamarca; 10, Albardón, San Juan; 11, Tupungato, Mendoza; 12, Cantera Tuclame (La Playa), Córdoba; 13, Cantera Maero (Las Caleras), Córdoba; 14, Paraná River cliffs, Paraná City, Entre Ríos; 15, La Juanita, Entre Ríos; 16, Barrancas de San Gregorio, Uruguay; 17, Laguna Chillhué and Laguna Guatraché, La Pampa; 18—22, Buenos Aires Province. 18, Arroyo Chasicó, 19, Sauce Grande River; 20, Calera Avellaneda; 21, Chapadmalal; 22, Quequén Salado River; 23, Farola Monte Hermoso; 24—26, Río Negro Province. 24, General Conesa; 25, Bahía Creek; 26, Balneario La Lobería; 27, Rincón Chico — La Pastosa (Chubut). a—e, other localities mentioned in the text. a, Punta Cracker; b, Balneario El Cóndor — Bahía Rosas; c, mouth of the Río Negro River; d, Huayquerías de San Carlos; e, Cantera Vialidad.

(Herrera, 2012: 196). They are also characterized by their ever growing cheek teeth, with a particularly complicated occlusal design that changes through life. In birth season, different ages and sizes may be found within the group, reflected in different sizes and cheek teeth occlusal morphologies. This diversity in size and dental morphology is quite outstanding in the paleontological record, and was traditionally interpreted as a result of high taxonomic diversity, which in turn complicated or even prevented comparisons among mammal assemblages from different localities. Vucetich et al. (2005, 2012, 2013) and Deschamps et al. (2007) proposed a new taxonomic arrangement based on dental ontogeny and using as analogous the structure of modern populations. These authors stated that the record of each capybara bearing unit represents the structure of a population with individuals of different generations rather than a succession of species with different evolutionary stage as classically proposed. The taxonomical improvement allowed establishing patterns of spatial and temporal distributions of species that permits their use in biocorrelations (Deschamps et al., 2012).

The aim of this paper is to refine the biochronological scheme of the late Miocene—Pliocene based on the reinterpretation of the

record of capybaras. This analysis includes the reassessment of correlations made between several South American capybara-bearing lithostratigraphic units with the Argentine chronological scale.

2. Methodology

The taxonomic criterion followed in this paper is based on the study of the materials found in four localities: Paraná River cliffs, Rincón Chico (Península Valdés), Laguna Chillhué, and Arroyo Chasicó (Fig. 1. 14, 27, 17, 18; Fig. 2) made by Vucetich et al. (2005, 2012, 2013) and Deschamps et al. (2007). According to this taxonomical proposal, the working hypothesis is that the large amount of individuals of different sizes would represent juveniles and adults within one population or successive populations. In capybaras, increasing size (age) implies a morphological change in the dental pattern with deepening of fissures that eventually end with the separation of prisms, within a particular pattern for each species.

All the bearing units are fluvial deposits in which the levels with capybara remains are stratigraphically constrained. According to
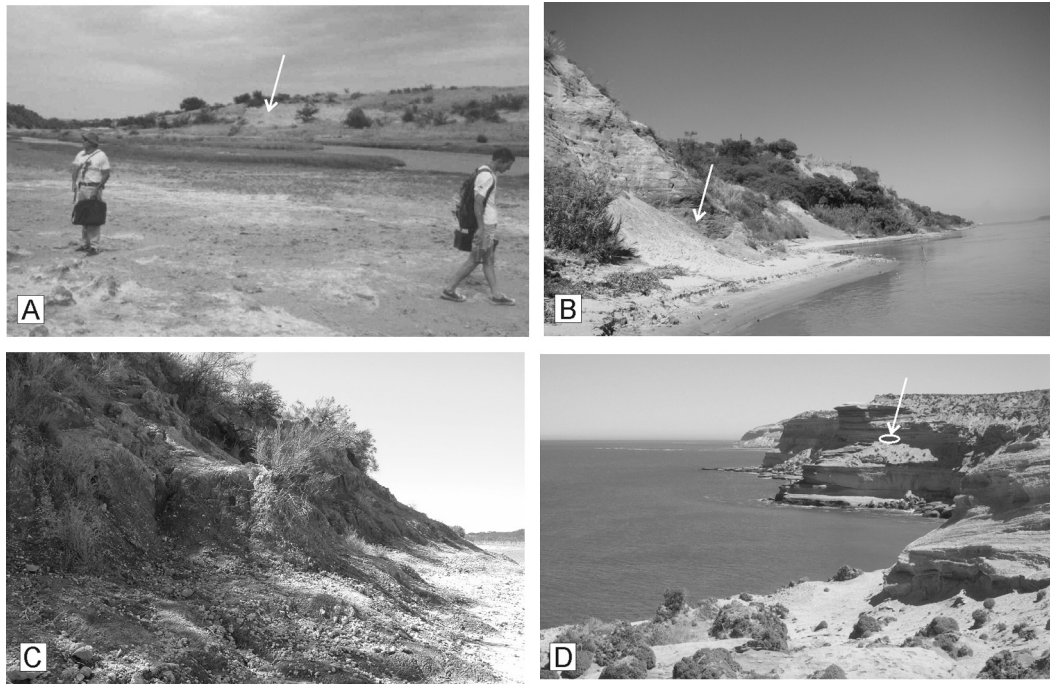
Fig. 2. View of some of the exposures with Miocene–Pliocene capybaras. A, Arroyo Chasicó Formation at Bajada de los Toros; B, "conglomerado osífero" of the Ituzaingó Formation, Paraná River cliffs at Toma Vieja; C, Cerro Azul Formation exposed at Laguna Chillhué; D, upper levels of the Puerto Madryn Formation at Rincón Chico.

Behrensmeyer (1988), in fluvial environments remains would come mainly from the floodplain, although it may not be discarded their incorporation directly into the channels. Channel-fills offer a sample of organic remains from the immediate vicinity of an abandoned channel. Individual sedimentary units within channel fills may sample shorter time intervals than other fluvial environments (Behrensmeyer and Hook, 1992). These authors suggest values of 10^2–10^4 yr for the deposition of these levels.

Taphonomic analyses performed in La Pastosa (Scasso et al., 2012), and Farola Monte Hermoso (Tomassini, 2012) determined that the capybaras assemblages from these localities were established during short intervals. Sedimentological features of the bearing levels and taphonomic attributes of the remains collected in Arroyo Chasicó and Laguna Chillhué would also support the deposition of these materials in short lapses. These intervals would be within the time resolution proposed by Behrensmeyer and Hook (1992) and they would represent the record of true ecological successions.

In addition, in spite of being less informative from a paleobiological standpoint, scanty or isolated remains of capybaras from other Argentine and South American localities were also examined and discussed since they provide useful data for biocorrelation.

Despite the definition of the Cerro Azul Formation sensu Folguera and Zárate (2009) is accepted, the classical names of lithostratigraphic units (Arroyo Chasicó, Saldungaray and Irene formations) are kept in the list and description of materials in order to facilitate comparison with previous literature.

Institutional abbreviations. Argentina: CORD-PZ, Museo de Paleontología, Universidad Nacional de Córdoba; GHUNLPam Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa; IMUSJ, Instituto y Museo, Universidad Nacional de San Juan; MACN, Museo Argentino de Ciencias Naturales; MD-MH, Museo Darwin, Monte Hermoso Collection, Punta Alta, Buenos Aires; MLP, Museo de La Plata; MMP, Museo Municipal de Mar del Plata; MMH, Museo Municipal de Monte Hermoso. AMNH, American Museum of Natural History, New York, USA; DGM, Divisão de Geologia e Mineralogia do Departamento Nacional de Produção

Mineral, Rio de Janeiro, Brazil; LACM, Natural History Museum of Los Angeles County, USA; MNHN Bol, Museo Nacional de Historia Natural, La Paz, Bolivia; MNHN (Paris), Muséum national d'Histoire naturelle, Paris, France; MPC, Museo Paleontológico de Caldera, Chile; SPV-FHC, Sección Paleontología Vertebrados, Departamento de Paleontología, Facultad de Humanidades y Ciencias, Montevideo, Uruguay; UNEFM-VF, Universidad Nacional Experimental Francisco de Miranda, Vertebrate Paleontology Collection, Coro, Venezuela.

Dental anatomical abbreviations. p-m/P-M, lower cheek teeth and upper cheek teeth (premolars, molars); pr.I-II/Pr.I-II, prisms of lower/upper cheek teeth. Other abbreviations explained in the text.

List of analyzed taxa. Updated taxonomy follows Vucetich et al. (2005, 2012, 2013) and Deschamps et al. (2007). The * indicates taxonomic status proposed in this paper. The geographic and stratigraphic provenance of each species is included.

Order Rodentia Bowdich, 1821
Superfamily Cavioidea (Gray, 1821) Kraglievich, 1930
Family Hydrochoeridae (Gray, 1825) Gill, 1872
Subfamily Hydrochoerinae (Gray, 1825) Weber, 1928

Cardiatherium chasicoense (Pascual and Bondesio, 1968). Fig. 3A. Arroyo Chasicó Formation, Las Barrancas Member (Fidalgo et al., 1978) or Lithofacies association 3 (sensu Zárate et al., 2007), Arroyo Chasicó, Buenos Aires Province. Loma de las Tapias Formation, Albardón Member, Albardón, San Juan Province (Deschamps et al., 2009).

Cardiatherium paranense (Ameghino, 1883). Fig. 3B,C. "Conglomerado osífero" of the Ituzaingó Formation, Paraná River cliffs, Entre Ríos. Río de los Pozos Formation, Tupungato, Mendoza Province (Vucetich et al., 2013).

Cardiatherium orientalis (Francis and Mones, 1965a). Fig. 3D,E. San Pedro Member (or Kiyú Lithofacies) of the Camacho Formation (see discussion in Perea and Martínez, 2005), or the base of the Raigón Formation (Bossi and Navarro, 1991); Barrancas de San Gregorio, San José, Uruguay. Member A of the Madre de Dios
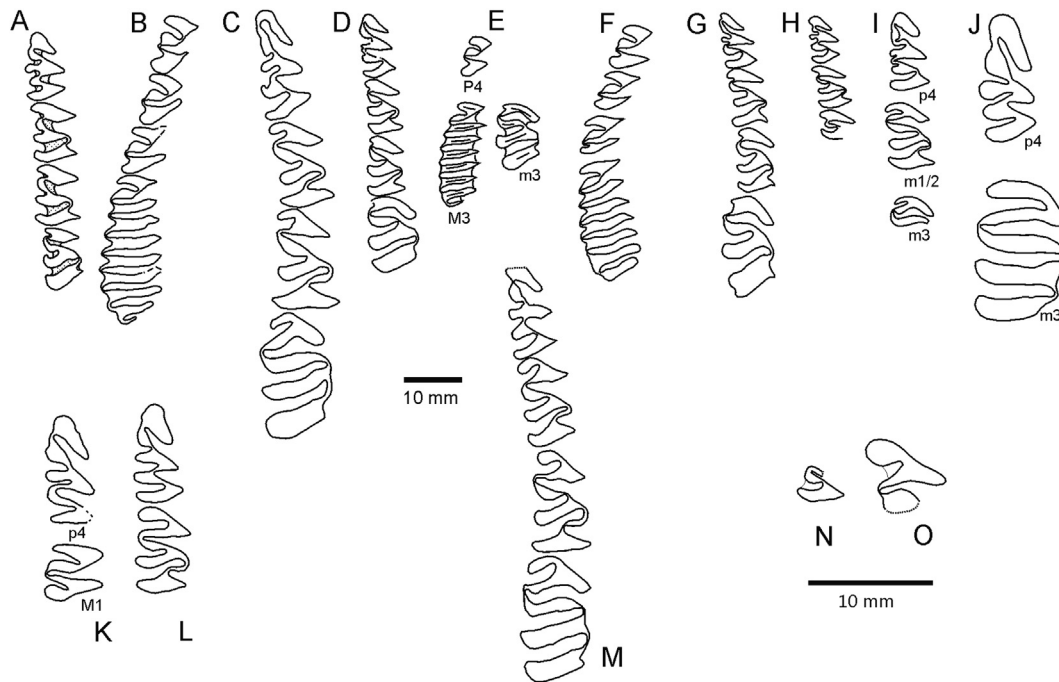
Fig. 3. Dental series of Miocene capybaras in occlusal view. A, *Cardiatherium chasicoense*, MMP 300-M (holotype), R p4-m3; B–C, *Cardiatherium paranense*. B, MLP 87-XI-1-27 (holotype of *Anatochoerus inusitatus*) R P4-M3; C, MLP 40-XI-15-1 (holotype), R p4-m3; D-E, *Cardiatherium orientalis*. D, SPV-FHC 27-XI-64-20 (holotype of *Kiyutherium orientalis*), R p4-m3; E, LACM 117511, R P4, LACM 117515, L M3 (reversed), LACM 117510, R m3; F-G, *Cardiatherium* aff. *orientalis*. F, GHUNLPam 14452, R P4-M3; G, GHUNLPam 27389, L p4-m3 (reversed); H, *Cardiatherium rosendoi*, MLP 29-X-8-26, L p4-m2 (reversed); I, *Cardiatherium patagonicum*, MPEF 740/9, R p4, MPEF 740/24, R m1 or m2, and MPEF 740/7, fragment of L m3 (reversed); J, *Cardiatherium isseli*, MACN-P 6354, R p4 and left m3 (reversed); K-L, *Cardiatherium* aff. *isseli*. K, MLP 60-VI-14-15, R p4 and L M1 (reversed); L, MLP 57-VII-23-1, R p4-m1 (reversed); M, *Cardiatherium talicei*, SPV-FHC-10-VIII-63-1, L p4-m3 (reversed); N, AMNH 55831 L p4? and DGM 537, pr.I of a L p4 (both reversed). Anterior to the top; L, left; R, right.

Formation (Campbell et al., 2006), Localities LACM 4611 and 5158, Acre River, Peru (Frailey, 1986).

Cardiatherium aff. *orientalis*. Fig. 3F,G. Cerro Azul Formation, Laguna Chillhué and Laguna Guatraché, La Pampa Province (Vucetich et al., 2013, and references therein).

Cardiatherium rosendoi (Bondesio, 1985). Fig. 3H. Andalhuala Formation, Corral Quemado, Catamarca Province.

Cardiatherium patagonicum Vucetich et al., 2005. Fig. 3I. Puerto Madryn Formation, Rincón Chico and La Pastosa (Dozo et al., 2010), Chubut Province. Río Negro Formation, "capa d" of Angulo and Casamiquela (1982) between 2 and 5 m at the base of the profile (19 m high), Bahía Creek, Río Negro Province.

Cardiatherium isseli Rovereto, 1914. Fig. 3J. Río Negro Formation, General Conesa (46 m deep), Río Negro Province. * = *Cardiatherium* aff. *isseli* in Pascual and Bondesio (1985), Balneario La Lobería, upper levels of the Río Negro Formation, Río Negro Province. See 4.1.2. for the status of this species.

Cardiatherium aff. *isseli* (as *Chapalmatherium* sp. in Furque, 1967, 1973). Fig. 3K,L. Saldungaray Formation, Dique Paso Piedras, Buenos Aires Province.

Cardiatherium talicei Francis and Mones, 1965b. Fig. 3M. Raigón Formation, San José Member, Barrancas de San Gregorio, San José, Uruguay (see discussion in Bossi et al., 2009).

cf. *Cardiatherium*. Bahía Inglesa Formation, Bahía Inglesa, Tercera Región, Chile (Gutstein et al., 2007).

*cf. *Cardiatherium* (as Hydrochoeridae indet. in Sant'Anna, 1994). Fig. 3N,O. Solimões Formation, Museu (Loc. 06), Cachoeira da Pedreira (Loc. 07), and Lago Grande (Loc. 25), Río Juruá, Estado do Acre, Brazil.

Cardiatherium sp. Urumaco Formation (Middle? and Upper members), Urumaco River (as *Kiyutherium* in Linares, 2004), and Vergel Member of the San Gregorio Formation (Vucetich et al., 2010), Falcón State, Venezuela.

Phugatherium cataclisticum Ameghino, 1887. Fig. 4A,B. Monte Hermoso Formation, Farola Monte Hermoso, Buenos Aires Province.

"*Chapalmatherium perturbidum*" (Rovereto, 1914). Fig. 4C–G. Monte Hermoso Formation, Farola Monte Hermoso, Buenos Aires Province. Irene Formation, Paso del Indio Rico, Quequén Salado River, Buenos Aires Province (Deschamps et al., 2012). See 4.1.3. for the status of this species.

"*Chapalmatherium*" *novum* (Ameghino, 1908). Fig. 4H–J. Chapadmalal Formation, Barrancas de Chapadmalal, Buenos Aires Province (see Reig, 1952). El Polvorín Formation, Calera Avellaneda, Olavarría, Buenos Aires Province (Prado et al., 1998; Zurita et al., 2012).

* "*Chapalmatherium*" cf. *novum* (as *Cardiatherium* sp. in Bondesio and Pascual, 1981). Fig. 4K. Calcáreos Las Playas, Cantera Tuclame, Córdoba Province.

* "*Chapalmatherium*" cf. *novum* (as *Cardiatherium* aff. *talicei* in Tauber, 2000). Fig. 4L. Cantera Maero, Las Caleras, Córdoba Province.

"*Chapalmatherium*" *saavedrai* Hoffstetter et al., 1984. Fig. 4M,N. Umala Formation, Ayo Ayo, Aroma Province Bolivia.

"*Chapalmatherium*" cf. *saavedrai*. Fig. 4O. Inchasi beds, Comunidad Inchasi, Linares Province, Bolivia (Anaya and MacFadden, 1995).

Hydrochoeropsis dasseni Kraglievich, 1930. Fig. 4P,Q. Uquía Formation, Uquía, Jujuy Province.

3. Regional geological framework of Argentine late Miocene–Pliocene deposits

The Late Miocene–Pliocene continental record of Argentina, geographically distributed across a heterogenous region involving several different geological provinces and morphostructural units, comprises thick (several km) sedimentary sequences that fill mountain basins along the Andes together with very extensive and relatively thin (100–300 m thick on average) mantles across the
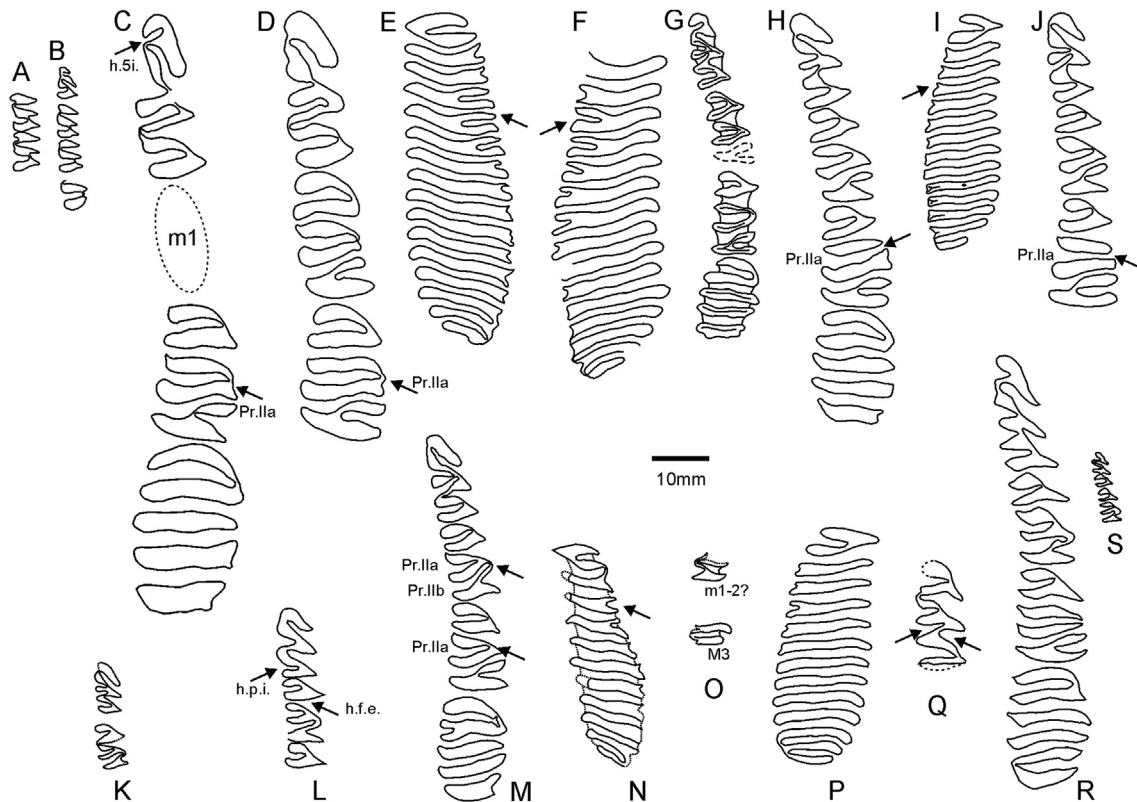
Fig. 4. Dental series of Pliocene capybaras in occlusal view. A–B, *Phugatherium cataclisticum*. A, MLP 61-IV-7-1 (holotype), L m1–m2 (reversed); B, MLP 61-IV-8-1, L p4-m2 and fragment of m3 (reversed); C–F, "*Chapalmatherium perturbidum*". C, MD-01-03, R p4, m2–3; D-E, MLP 15–231a–b. D, R p4-m2; E, L M3 (reversed); F, MLP 57-VII-23-2, R M3; G, *Chapalmatherium irenense*, P-14282 (holotype), R p4-m3; H-J, "*Chapalmatherium*" *novum*. H, MMP 236-S, R p4-m3; I-J, FCS 92-V-15/1. I, R M3; J, R p4-m2; K-L, "*Chapalmatherium*" cf. *novum*. K, MMP 774, L p4-m1 (reversed); L, CORD-PZ 4090, L p4-m1 and fragment of m2 (reversed); M–N, "*Chapalmatherium*" *saavedrai*. M, MNHN AYO 226, R p4-m3; N, MNHN AYO 193, L M3; O, "*Chapalmatherium*" cf. *saavedrai*, MNHN Bol. V-00338, fragments of L m1 and M3; P-Q, *Hydrochoeropsis dasseni*, MACN 5302, P, R M3; Q, R p4; R–S, *Hydrochoerus hydrochaeris*, R, adult R p4-m3; S, juvenile R p4-m1. Anterior to the top. h.5i., fifth internal fissure; h.f.e., external fundamental fissure; h.p.i., internal primary fissure; Pr.IIa,b, second prism a,b; L, left; R, right.

eastern lowlands. The deposits crop out at numerous localities of the Andes Cordillera and its piedmont, the Pampean ranges, the Paraná River cliffs, as well as other sites of Entre Ríos and Corrientes provinces, and also the southern Pampas and northern Patagonia. In addition, drilling information indicates the presence of Neogene deposits that are covered by Quaternary deposits and fill several tectonic sedimentary basins of central and northern Argentina (Folguera and Zárate, 2009 and references therein).

The accumulation of late Miocene–Pliocene continental deposits in central and eastern Argentina occurred after the regression of the so-called Paranense sea documented by transgressive facies (Paraná Formation), and regressive facies (Entre Ríos Formation), sensu Chebli et al. (1999) in northeastern Argentina. Further south (Northeastern Patagonia) these marine deposits have been grouped into other lithostratigraphic units (e.g. Barranca Final Formation in the Colorado tectonic basin; Zambrano, 1972). Hence, Neogene continental sequences overlie either the Miocene marine deposits at the sedimentary basins (e.g. Salado, Colorado, Macachín tectonic basins, among others) or a Precenozoic basement (Precambrian to Mesozoic) on block areas (e.g. San Rafael, Positivo Bonaerense, La Pampa central blocks, among others; Folguera and Zárate, 2009, 2011).

From a tectonic viewpoint, the Neogene continental record that crop out in the Andes Cordillera, the southern Pampean plain and northern Patagonia are interpreted as sinorogenic deposits related to several diachronic episodes of Andean tectonic uplift during the late Miocene–Pliocene (Ramos, 1999; Folguera and Zárate, 2011). Hence, at a regional scale, the sedimentary sequences of the Andean mountain basins and the piedmont represent proximal

sinorogenic facies with a variable lithology associated to the migration of the orogenic front (Ramos, 1999); in turn, the Pampean and northeastern Patagonian sequences correspond to distal sinorogenic deposits that also document the Andean tectonic dynamic (Folguera and Zárate, 2009, 2011). The Andean foreland was fragmented and stabilized between 36° and 40° S (southern Pampas and northern Patagonia) around 6 (?) Ma resulting in the migration of sedimentary depocenters from the southern Pampas to northern Patagonia and the southeast part of the so called Pampa interserrana of Buenos Aires province (Folguera and Zárate, 2009, 2011). In this context, the deposits of the type locality of the Huayquerian Stage-Age corresponds to proximal sinorogenic facies (Huayquerias Formation, Mendoza) while the deposits of the type localities of the Chasicoan, Montehermosan, and Chapadmalalan faunal assemblages represent distal sinorogenic facies. Recently, Folguera and Zárate (2009) and Montalvo et al. (2012) proposed an evolutionary, regional geological model to explain the geographical distribution and antiquity of the faunal associations found in different exposures of the Late Miocene–Pliocene deposits, among which are the bearing levels of *Cardiatherium chasicoense*, *C.* aff. *orientalis*, *Cardiatherium* aff. *isseli*, "*Chapalmatherium perturbidum*" and "*Chapalmatherium*" *novum*.

4. The fossil record and correlations

Capybaras are first recorded in the late Miocene Chasicoan Stage/Age, and exhibit a good record through the Huayquerian, Montehermosan and Chapadmalalan ages. They are not recorded in

Ma	Epoch	Global scale Stage/Age	South American Stage/Age	Arroyo Chasicó	San Juan	Entre Ríos	Mendoza	La Pampa	Catamarca	Península Valdés	Río Negro	Monte Hermoso	Quequén Salado	Ayo Ayo Bolivia	Chapadmalal	Olavarría	Jujuy	Capybaras
3	Pliocene	Gelasian	Marplatan (Sanandresian / Vorohuean / Barrancalobian)											(10) 2.89	(11) 3.35 Chapadmalal Fm.	?	Uquía Fm.	Hydrochoeropsis dasseni
		Piacenzian							Corral Quemado Fm.					?	El Polvorín Fm.	?		"Chapalmatherium" novum
4		Zanclean	Chapadmalalan								(9) 4.41			Umala Fm.		?		"Ch." saavedrai
			Montehermosan							Puerto Madryn Fm.		Monte Hermoso Fm.	Irene Fm.				?	Phugatherium cataclisticum / "Chapalmatherium perturbidum"
5	late Miocene	Messinian	Huayquerian				(4) 5.8	(1) 5.28 *	(7) 5.22					(10) 5.348				Cardiatherium isseli
6									(6) 6.02		Río Negro Fm.		?					Cardiatherium patagonicum
7					(2) 7.0 ± 0.9	"Conglomerado osífero"	(3) ca. 7.2 Río de los Pozos Fm.	Cerro Azul Fm.	Andalhuala Fm. (5) 7.14									Cardiatherium aff. orientalis / Cardiatherium "rosendoi"
8		Tortonian	Chasicoan	Arroyo Chasicó Fm. Lithofacies Assoc 3	Loma de las Tapias Fm.		(3) ca. 8.7											Cardiatherium paranense
9				(1) 9.23 ± 0.09					Chiquimil Fm. (7) 9.14		(8) 9.41							Cardiatherium chasicoense

Fig. 5. Stratigraphic chart with correlation of units bearing capybaras with Global and South American stages/ages. (1) Schultz et al., 2006; Zárate et al., 2007; (2) Bercowsky et al., 1986; Serafini et al., 1985; (3) Irigoyen et al., 2002; (4) Marshall et al., 1986; (5) Latorre et al., 1997; (6) Marshall and Patterson, 1981; (7) Bossi and Muruaga, 2009; (8) Zinsmeister et al., 1981; (9) Alberdi et al., 1997; (10) Marshall et al., 1992; (11) Schultz et al., 1998. * This formation sensu Folguera and Zárate (2009), exposed at Cantera Vialidad, near Bahía Blanca.

the Marplatan, except for *Hydrochoeropsis dasseni* Kraglievich, 1930, from the Uquía Formation (Reguero et al., 2007), which is discussed below (4.1.5.). The remaining hydrochoerid records are Pleistocene-Holocene in age. A polarity is observed from the Chasicoan species to those of the Chapadmalalan because of the deepening of flexids and the separation of prisms of cheek teeth, although among the Huayquerian species, the relationships are not clear yet.

On the basis of the evolutionary stage of capybaras, together with geological evidences and numerical ages, a chronological scheme is proposed (Fig. 5) in order to allow refinement of bio-correlations, first within Argentina and then with the rest of South America. In each geographical section, capybaras are listed from oldest to youngest.

4.1. Argentina

4.1.1. Chasicoan

Cardiatherium chasicoense (Fig. 3A) is the oldest species of capybaras. The numerous remains only found at the outcrops of the Arroyo Chasicó Formation in the Bajada de los Toros site (Deschamps et al., 2007, Figs. 1.18 and 2A), come from mudstones and sandy siltstones (lithofacies 3) accumulated in generally low energy conditions of sedimentation in a fluvial swampy environment; the 3 m thick deposits lie unconformably on lithofacies

associations 2 and 1 (Zárate et al., 2007). On the basis of numerical ages of "escorias" (impact glass) from the base of the Arroyo Chasicó Formation (Schultz et al., 2006), and magnetostratigraphy, Zárate et al. (2007) proposed that the lithofacies associations 1 and 2 of the Arroyo Chasicó Formation would have been deposited between 9.43 Ma and 9.07 Ma—hence, the capybara bearing deposits of lithofacies association 3 is younger than 9.02 Ma—, and that the whole sedimentation of the formation could have extended up to 8.7 Ma (see Cione et al., 2000; Cione and Tonni, 2005).

The single specimen of this species (IMUSJ 537) found out of the type area comes from the Albardón Member of the Loma de las Tapias Formation at Albardón (Deschamps et al., 2009, Fig. 1.10). The unit reported as an alluvial fan with development of a braided river system (Contreras et al., 2001) was dated in 7 ± 0.9 Ma (Bercowsky et al., 1986; Serafini et al., 1985). Taking into account that it was found below the dated tuff, in the Assemblage A (Contreras and Barraldo, 2011), and the upper unconstrained limit of the Arroyo Chasicó Formation (Zárate et al., 2007), the most parsimonious option is to consider that the Chasicoan Land Mammal Age could have extended up to near 8 Ma (Fig. 5).

Candela et al. (2012) reported cf. *Cardiatherium* sp. represented by two isolated teeth found at the upper levels of the late Miocene marine deposits of the Paraná Formation that underlies the Ituzaingó Formation (see below). A "pre-Huayquerian" age is

attributed to the remains (Candela et al., 2012) on the basis of their similarity with *C. chasicoense*. At La Juanita (Fig 1.15) the unit begins with whitish to yellowish sandy levels, alternating with greenish clays, strongly bioturbated. Upwards, the level which yielded the capybaras remains includes sediments of heterogenous grain-size showing normal gradation. The genesis of the fossiliferous level corresponds to a littoral marine environment containing a storm deposit with mixture of marine and continental fauna. Terrestrial vertebrates would be the contribution of streams or rivers to the marine environment from the backshore or nearby inlands (Candela et al., 2012).

4.1.2. Huayquerian

Cardiatherium paranense (Fig. 3B,C) reported from the "conglomerado osífero" (Fig. 1.14) of the Ituzaingó Formation, is the best represented species in number of specimens. An update of the systematics (Vucetich et al., 2012, 2013) regards a single species for the bearing unit. The areal extension of the "conglomerado osífero" (also known as "Mesopotamiense"; Figs. 1.14 and 2C) that yielded the remains of *Cardiatherium paranense* is very restricted (Herbst, 2000). It is interpreted as a fluvial deposit with paleochannels (Cione et al., 2000). All the continental vertebrates are disarticulated, very fragmented, and display different degrees of preservation and abrasion due to transport (Delupi de Bianchini and Bianchini, 1971; Cione et al., 2000). Although no detailed taphonomic analyses have been performed yet, Cione et al. (2000) stated that the marine vertebrates found in these levels would have been reworked from the underlying Paraná Formation, but the continental remains would have been transported from a nearby area. The "conglomerado osífero", considered late Miocene upon its fossil vertebrates, would encompass a short interval according to the reinterpretation of the capybaras content.

The specimen found in the Río de los Pozos Formation (Fig. 1.11) published as *Kiyutherium* cf. *orientalis* (or *K.* aff. *orientalis*; see Yrigoyen, 1993a,b) and also as *Procardiatherium* sp. (Irigoyen et al., 2000; but see Yrigoyen, 1993a for a history of this specimen) is a juvenile of *C. paranense* (Vucetich et al., 2013). It comes from gray-yellowish massive sands with bioturbation interpreted to record deposition from unconfined and channelized flows in a semiarid setting (Yrigoyen, 1993a,b; Irigoyen et al., 2002). According to Irigoyen et al. (2002) as the underlying Tobas Angostura was dated in 8.64 + 0.17 Ma, the deposition of the Río de los Pozos Formation would have began ~8.7 Ma and would have extended up to ca. 7.2 Ma. The specimen was found 70 m above the contact with Tobas Angostura and indicates a Huayquerian age for these levels.

Cardiatherium aff. *orientalis* (Fig. 3F,G) was found in the Cerro Azul Formation exposed at Laguna Guatraché and Laguna Chillhué, La Pampa (Fig. 1.17, 2D; Pascual and Bondesio, 1982; Montalvo et al., 1995; Rocha and Montalvo, 1999; Vucetich et al., 2005, 2013). Remains from Laguna Chillhué were recovered from the same levels where Verzi et al. (2008) defined the Biozone of *Chasichimys scagliai*. In the biochronologic sequence established by Verzi et al. (2008) this biozone was assigned to the Huayquerian older than 6 Ma (see also Deschamps et al., 2007). Originally the deposits were interpreted as lacustrine (Goin et al., 2000), but recent studies suggest also the occurrence of fluvial facies at Laguna Chillhué (MAZ, personal observation). In these deposits, materials are disarticulated, being often isolated remains including isolated teeth. Generally they show little or no evidence of abrasion ruling out strong transport.

A single remain (MLP 29-X-8-26; Fig. 3H) from Corral Quemado, Catamarca (Fig. 1.9), was referred to a different species of the genus, *C. rosendoi* (originally *Kiyutherium rosendoi* Bondesio, 1985). Preliminary studies of this remain (MGV and CMD personal observation) suggest that the occlusal morphology of the m1–2 is similar to

that of the species found in the Cerro Azul Formation. If this is confirmed, the correct name for the species from the Cerro Azul Formation would be *C. rosendoi*. But more materials including skull remains of the latter are necessary to elucidate the taxonomical status of these species. Recent revisions indicate that *C. rosendoi* comes from the Andalhualá Formation (Bonini et al., 2012). The lower part of this unit is a gravelly braided river deposit and the upper part (1000 m thick) consists of floodplain sandy facies with channelized bodies (Bossi et al., 2001). A tuff in the basal levels was dated in 7.14 Ma (Latorre et al., 1997), above which Huayquerian fauna was reported (Nasif et al., 2009). Two other numerical ages of 6.02 (Marshall and Patterson, 1981) and 5.22 Ma (Bossi and Muruaga, 2009) were reported for this formation in the nearby areas (Fig. 5).

Cardiatherium patagonicum (Fig. 3I) was described for numerous specimens found in the upper levels of the Puerto Madryn Formation at Rincón Chico and La Pastosa (Península Valdés; Fig. 1.27; Vucetich et al., 2005; Dozo et al., 2010). The bearing levels were interpreted as coarse-grained channel-fill deposits (Scasso et al., 2001, 2012). The remains accumulated in areas close to the tidal-fluvial channels (Facies 2, 3 and 4) are considered as a coeval, autochthonous assemblage, without weathering evidence, and with scarce abrasion (Scasso et al., 2012). Afterward, either before or after burial, the lateral migration of the channel eroded the deposits incorporating the remains. Redeposition would have occurred in the nearby areas, since there is no evidence of strong transport. Hence, these remains may be interpreted as reelaborated (sensu Fernández-López, 2000).

Cardiatherium patagonicum is also represented by one cheek tooth (MJG 22-IV-1976) found in the lower levels of the Río Negro Formation ("capa d"; Angulo and Casamiquela, 1982:36) at Bahía Creek, Río Negro (Fig. 1.26) which allows to correlate it with the Puerto Madryn Formation. The deepening of the flexids (Fig. 3I) suggests this species is more derived than the rest of the Huayquerian species, although with the same pattern. Vucetich et al. (2005) stated this could be explained either by its geographical distribution—it is the southern most species of the family—or because it is younger than the others. The available numerical ages of the Puerto Madryn and Río Negro formations come from near areas. Zinsmeister et al. (1981) dated through ^{40}K–^{39}Ar three glass concentrations of a tuff from the upper level of the marine "Rionegrense" of Punta Cracker (Golfo Nuevo, Fig. 1a) that yielded a mean age of 9.41 Ma (Tortonian). Palynological and malacological studies support a late Miocene age for the marine levels of the Puerto Madryn Formation (Martínez and del Río, 2002; Del Río, 2004; Palazzesi and Barreda, 2004). As *C. patagonicum* was found above the marine levels of the Puerto Madryn and Río Negro formations (Scasso et al., 2012; see also Zavala and Freije, 2001), its age may be interpreted as younger than 9.41 Ma (Fig. 5). In view of its evolutionary stage, we propose that the bearing levels should be much younger, probably representing a late Huayquerian.

Cardiatherium isseli (Fig. 3J) was described on mandibular remains found in a 46 m deep water-well made in the Río Negro Formation, between General Conesa and Río Colorado (Rovereto, 1914, Fig. 1.24). Another mandible (MLP 97-VIII-1-1, cast of MJG 12-II-1977 currently lost, as well as the associated skull material) found in the Río Negro Formation at Balneario La Lobería (Río Negro; Fig. 1.25) is also assigned to this species. It was found in a block fallen from the upper levels of the cliff, originally referred to *Cardiatherium* aff. *isseli* (Angulo and Casamiquela, 1982; Pascual and Bondesio, 1985).

Thus, two species *C. patagonicum* and *C. isseli*, come from the lower and the upper levels respectively of the Río Negro Formation, described as a mostly fluvial unit (Andreis, 1965). Later, the unit was divided into a lower (Rl, eolian), middle (Rm, marine), and upper

(Ru, eolian) members along a section between Balneario El Cóndor and Bahía Rosas (Fig. 1b) by Zavala and Freije (2001). Although these authors assign an eolian origin, they report wet interdune facies extensively developed especially in Ru2–3 sequences (3 m thick of massive or finely laminated reddish mudstone), which could have been suitable for capybaras. Numerous ichnites of mammals and birds have been recorded in Ru2–3 levels together with fish and freshwater bivalves. These authors correlate the change to an eolian depositional environment of the Upper Member with the sudden fall of the sea level of the Messinian. Zavala and Freije (2001) suggest that the Upper Member may range from the late Miocene to the Pliocene, according to the fossil content and to a date of 4.41 ± 0.5 Ma obtained at a tuff of the upper member above the fossiliferous levels (Alberdi et al., 1997, Fig. 1c), southwest of the mouth of the Negro River (Fig. 5). In view of the evolutionary stage of *C. isseli*, we interpret that the bearing level should not be younger than the late Miocene, probably a late Huayquerian.

A remain found in the Saldungaray Formation (MLP 60-VI-14-15, Furque, 1967, 1973, Fig. 3K) exposed at the Sauce Grande River near Bahía Blanca (Fig. 1.19) was originally referred to *Chapalmatherium* sp., a genus characteristic of the Pliocene (see below). Hence, the bearing sediments were also considered of this age. Here we refer this remain, together with the unpublished MLP 57-VII-23-1 (Fig. 3L), to *Cardiatherium* aff. *isseli* and thus, estimate the bearing levels as late Miocene (Messinian) in age. These levels are composed of brown-reddish silt and loessoid silt (Zavala and Navarro, 1993).

Other Huayquerian faunas have been dated in different localities which support the correlation of these faunas with the Messinian Stage/Age of the global scale. The upper part of the Huayquerías Formation (Huayquerías del Este, Mendoza Province; Fig. 1d), where the Huayquerian SALMA was established, was dated by Marshall et al. (1986) with an average age of 5.8 ± 0.1 Ma obtained from a tuff layer (Fig. 5). Schultz et al. (2006) obtained numerical ages of 5.28 ± 0.04 Ma in the middle levels of Cantera Vialidad (southern Buenos Aires Province near Bahía Blanca; Fig. 1e). A few remains of Huayquerian fauna, including the ctenomyine rodent *Xenodontomys* sp., were exhumed from these and the overlying levels. Thus, the numerical ages (Schultz et al., 2006) together with geological (Folguera and Zárate, 2009; Montalvo et al., 2012), and paleoclimatic evidence (Verzi et al., 2008) support the extension of the Huayquerian up to *circa* the Miocene–Pliocene boundary.

4.1.3. Montehermosan

In the Monte Hermoso Formation at its type locality Farola Monte Hermoso (Fig. 1.23) two morphotypes of capybaras are recorded: a very small one identified as *Phugatherium cataclisticum* (Fig. 4A,B) of juvenile specimens exclusive of this unit (Ameghino, 1887, 1889), and a large one "*Chapalmatherium perturbidum*" (Rovereto, 1914; Prado et al., 1998, Fig. 4C,D), with peculiar dental features. These two morphs have been considered as juveniles and adults of a single species (Deschamps et al., 2012; Vucetich et al., 2012; MGV and CMD personal observation). If these two species are indeed synonymous as suggested in Deschamps et al. (2012) (see below), the remains recovered from the Monte Hermoso Formation would represent a single or successive populations as in the previous cases.

This unit was interpreted as deposited by a meandering fluvial system, with sub environments (channel and floodplain) genetically related without differences of significant discontinuities (Zavala, 1993; Zavala and Navarro, 1993).

The fauna from the Monte Hermoso Formation includes taxa more derived than their Huayquerian relatives (e.g. the ctenomyine rodents *Actenomys* vs. *Xenodontomys* respectively, see Verzi, 2008; Tomassini, 2012), and consequently is interpreted as younger, and

thus, younger than the Miocene–Pliocene boundary (see above). The upper boundary could be no younger than the base of the Chapadmalalan (see below). Consequently, the Montehermosan should be considered early Pliocene in age (Deschamps et al., 2012; Tomassini et al., 2013), representing part of the Zanclean Age of the global scale (Fig. 5).

Remains of a large capybara assigned to *Chapalmatherium irenense* (Reig, 1958, Fig. 4F,G) were found in the Irene Formation exposed at the banks of the Quequén Salado River (Fig. 1.22). The Irene Formation was informally described by Reig (1955) near the village of Irene, and then by Kraglievich (1960) as reddish silts and sandy silts, with calcareous concretions, and few fragments of "escorias" and "tierras cocidas" (impactites, sensu Folguera and Zárate, 2009). Deschamps et al. (2012) synonymized this species with "*Chapalmatherium*" *perturbidum* (or adult specimens of *Phugatherium cataclisticum*), and thus, correlated the bearing levels with the Monte Hermoso Formation, not with the Chapadmalal Formation as did Prado et al. (1998) (Fig. 5). This is supported by other rodent taxa (e.g. the species of the echimyid rodent *Eumysops*; Olivares, 2009; Deschamps et al., 2012; Olivares et al., 2012). On the basis of the information yielded up to date by capybaras, the Chapadmalalan is not represented in this formation. But, on the other hand, on the basis of octodontid rodents, some levels of the Irene Formation are known to be older and were assigned to the Huayquerian (Verzi et al., 2008 and references therein).

"*Ch. perturbidum*" is also reported for the "Mesopotamiense" (Bondesio, 1975) through two unpublished, isolated and fragmented upper molars (MLP 74-IV-10-1 and MLP 74-IV-10-2). These remains have no precise stratigraphic provenance; consequently, they may come from the younger overlying levels of the Ituzaingó Formation, referred to the Pliocene (Herbst, 2000 and references therein), as already stated by Bondesio (1975). Thus, the Paraná cliffs would be the only section in which different species are recorded in different stratigraphic levels, because in addition to "*Ch. perturbidum*", two other species have been recorded, *C. paranense* from the base of the Ituzaingó Formation ("conglomerado osífero"), and an indeterminate species of *Cardiatherium* probably related to *C. chasicoense* from the underlying Paraná Formation (see above).

4.1.4. Chapadmalalan

"*Chapalmatherium*" *novum* (Fig. 4H) was described on the basis of several remains, both subadults (e.g. MMP 177-S; MMP 213-S) and adults, found in the Chapadmalal Formation at the area of Chapadmalal (Ameghino, 1908; Reig, 1952, Fig. 1.21). This unit is formed by sandy and clayey silts with paleosol levels with fluvial flow structures to the top of the sequence (Zárate, 1989). The materials were found in a wide geographical area, and hence they are not considered as part of a single population or successive populations that inhabited the area. This species is more derived in some features than "*Ch. perturbidum*"; e.g. both rami of pr.II (second prism) of m2 are separated already in small (young) individuals (see arrows in Fig. 4H,J). It was also found in Calera Avellaneda (Prado et al., 1998, Fig. 4I,J) at levels of the El Polvorín Formation (Zurita et al., 2012, Fig. 1.20) which would be Chapadmalalan in age (Deschamps et al., 2012), not Montehermosan as previously proposed (Prado et al., 1998). A date of 3.3 Ma (Schultz et al., 1998, Fig. 5) was obtained from a layer located 3–5 m below the upper contact of the Chapadmalal Formation.

Reig (1952) said that this was not the only Chapadmalalan "protohydrochoerine", since already Kraglievich (1940: 547) referred to "…*la presencia de Protohydrochoerus en los estratos de esa edad, existiendo también en la Colección Scaglia un interesante material de esa misma procedencia geológica referible al género citado…*" (…the presence of *Protohydrochoerus* in strata of this age, existing as well in the Scaglia Collection an interesting material

with this geologic provenance referable to the mentioned genus…). However, what Kraglievich (1940) assigned to *Phugatherium perturbidus chapadmalalensis* n. var. is only a distal portion of humerus (MACN 6398). No studies of postcranial elements have been accomplished yet as to determine whether this material belongs to "*Ch. perturbidum*"; hence, this cannot be taken as a proof of this species in the Chapadmalal Formation.

"*Cardiatherium* sp." (Fig. 4K) was reported by Bondesio and Pascual (1981) from a travertine deposit of the La Playa Formation in the Tuclame Quarry, Córdoba, Minas Department (Fig. 1.12), formed by hydrothermal processes related to the andesitic effusions of the late Tertiary volcanism (Gordillo and Lencinas, 1979). It is represented by a mandible fragment with p4-m1 (MMP 774) that in occlusal morphology is quite similar to an adult *Cardiatherium*, but it is very small. Taking into account the ontogenetic change (Vucetich et al., 2005), it could be assumed that when adult, the fissures would completely cross the cheek teeth, separating the prisms as in "*Chapalmatherium*", in which case it would be "*Chapalmatherium novum*" because of the p4 morphology. In this case, the La Playa Formation would be Chapadmalalan (late Pliocene, Piacenzian) in age. But, on the basis of comparison with young individuals (of the same size) of the living species *Hydrochoerus hydrochaeris* (Fig. 4R,S) it can be assumed that it could even be a juvenile of the *Neochoerus-Hydrochoerus* group, which is represented only since the Pleistocene. These observations suggest that the La Playa Formation would be younger than it was previously proposed because of the accompanying fauna, so far "Pliocene", both Huayquerian or Montehermosan, according to Kraglievich and Reig (1954), or Huayquerian, according to Bondesio and Pascual (1981)—when the Huayquerian was considered Pliocene—. In fact, the accompanying fauna is not useful in determining the age, *Cyonasua groeberi* is not represented in other localities. According to Lucero Michaut and Olsacher (in Gómez and Lira, 1998; see also Olsacher, 1942) these travertines could be late Pliocene to Pleistocene. Our interpretation of the capybara remains supports this statement.

Tauber (2000) assigned to *Cardiatherium* aff. *talicei* one specimen (CORD-PZ 4090; Fig. 4L) found in the filling of the narrow hollows produced by dissolution of marble of the metamorphic Precambrian basement, in an incipient karstic landscape (Tauber, 2000) at Cantera Maero, Las Caleras, Córdoba (Fig. 1.13). But, again, its size is very small (the anteroposterior diameter of the p4 is 14 mm, being 17.6 mm in *C. talicei*), the p4 morphology is quite different (e. g. the h.p.i. or primary internal fissure, is transverse, and in *C. talicei* it is posterolingual-anterolabial; the anterior wall of the first prism, pr.I, is straight, being concave in *C. talicei*), and the pr.I of m1 is already separated by the deepening of the h.f.e. or fundamental external fissure (Fig. 4L). These features are typical of Pliocene capybaras, and among them, the anterior prism of p4 is more similar to "*Chapalmatherium*" *novum* than to "*Ch. perturbidum*". The record of "*Chapalmatherium*" cf. *novum* in Las Caleras matches with the rest of the taxa recorded in this deposit (e.g. *Thylophorops chapalmalensis*, *Doellotatus chapalmalensis*, *Ringueletia simpsoni*, *Tremacyllus impresus*; see Tauber, 2000) mostly Pliocene in age.

Recently, the genus *Chapalmatherium* was reported from the Castilletes Formation in northern Colombia without figures or additional data (Moreno-Bernal et al., 2013), and hence, the taxonomic assignment could not be confirmed.

4.1.5. Marplatan?

Another species that has not been revised since the original descriptions is *Hydrochoeropsis dasseni*. It was found in the Uquía Formation (Kraglievich, 1930: 515), Uquía (Fig. 1.8) without stratigraphic provenance, although according to Reguero et al. (2007) it probably comes from the middle levels correlated to the Marplatan (originally, Uquian). The occlusal design of upper teeth is similar to that of the typical Pliocene capybaras, but skull characters (among them, a wide and robust rostrum) suggest it may belong to a different lineage than "*Chapalmatherium*". This skull deserves further anatomical analyses in a phylogenetic context.(M.G. Vucetich and C.M. Deschamps, personal observation)

4.2. Uruguay

The discoveries of capybaras in the Barrancas de San Gregorio, Uruguay (Fig. 1.16) were a renowned step in the studies of fossil capybaras. The first papers of Francis and Mones (1965a,b) triggered the interest in this group that led Mones (1991 and references therein) to accomplish an important taxonomic revision of the family Hydrochoeridae.

Cardiatherium orientalis was described as *Kiyutherium orientalis* upon a mandible (SPV-FHC 27-XI-64-20; Fig. 3D) found in Barrancas de San Gregorio. It was found in the Camacho Formation (Kiyu Lithofacies) which is composed of greenish-gray friable and medium compressed pelites that represent the facies of a late Miocene transgressive event. The terrestrial mammals intermixed with estuarine and marine fauna suggest transport into a paralic environment, including coastal lagoons and floodplains in an estuarine or deltaic system. Skeletal remains frequently appear with some degree of articulation and low degree of weathering and deformation, suggesting limited transport and quick burial after deposition (Rinderknecht et al., 2010).

The bearing levels have been considered Huayquerian, late Miocene in age on the basis of their vertebrate and invertebrate faunas (Perea and Martínez, 2005). The molariforms of *C. orientalis* are very difficult to distinguish from those of *C. paranense* or from the materials assigned to *C.* aff. *orientalis* (Vucetich et al., 2005). New skull materials, currently in study (M. Ubilla, pers. comm.), will shed light on the status of this species.

Together with the holotype of *Cardiatherium orientalis*, another capybara was found in the Lithofacies Kiyú. It is represented by an isolated m1 or m2 which was assigned to *Eucardiodon* cf. *marshi* (Ameghino) by Mones and Castiglioni (1979), which was later synonymyzed with *Anchimys marshii* (Mones, 1991). This latter species comes from the "conglomerado osífero" and was synonymized with *Cardiatherium paranense* because their representatives were considered juvenile individuals of this species (Vucetich et al., 2005). Noteworthy, as *C. paranense* is difficult to distinguish from *C. orientalis* only on the basis of the occlusal morphology of adult teeth, it is quite likely that this would also be the case among juvenile individuals. Consequently, the material cited as "*A. marshii*" from the same levels as *C. orientalis* could represent a juvenile stage of the latter. Thus, the reference of "*A. marshii*" in Uruguay does not mean that *C. paranense* is recorded in these levels. Future studies will determine the existence of one (*C. orientalis*) or two species of capybaras in the Kiyú Lithofacies.

Francis and Mones (1965a) described *Cardiatherium talicei* (Fig. 3M) on the basis of a fragmentary mandible and skull (SPV-FHC 10-VIII-63-1) from the San José Formation, Barrancas de San Gregorio (Fig. 1.16). The bearing unit, now generally known as the Raigón Formation, was deposited in a transitional deltaic estuarine to fluvial continental environment (Perea and Martínez, 2005; Perea, 2007). The temporal assignment of the bearing levels of *C. talicei* has been debated since its discovery; they have been considered Montehermosan (early Pliocene; Mones, 1991 and references therein) and even younger. Hence, if this temporal assignment is confirmed, this would be the single certain record of the genus younger than late Miocene in southern latitudes. This species differs from the holotype of the other species recorded in

Uruguay, *C. orientalis* (see above, and Francis and Mones, 1965b: 52) mainly in size—*C. orientalis* is much smaller than *C. talicei*—, and in depth of fissures of their cheek teeth—flexids of *C. orientalis* are shallower than those of *C. talicei*—. Future studies may determine whether these differences represent ontogenetic stages of a single species, as seen in *C. paranense*, rather than different evolutionary stages.

4.3. Venezuela

The Urumaco Formation, Venezuela (Fig. 1.1) was deposited in a prograding strandplain-deltaic complex (Quiroz and Jaramillo, 2010). It is divided into three members; the Middle Member is interpreted as coastal deposits with prograding meandering bars, and the Upper Member as fluvial channels and floodplain deposits with occasional marine influence (Linares, 2004). Capybaras are mentioned by Linares (2004; as *Kiyutherium*) for both the Middle and Upper members. Based on the fossil mammal content, the Middle Member was assigned to the Chasicoan, and the Upper Member, to the Huayquerian (Linares, 2004). This author stated some doubts concerning the provenance and/or the taxonomic assignment of the specimen from the Middle Member, considering that *Kiyutherium* (=*Cardiatherium*) had not been so far recorded in the Chasicoan (Linares, 2004:15). But, this paper was previous to that of Vucetich et al. (2005) in which *Kiyutherium* and *Procardiatherium* were considered junior synonyms of *Cardiatherium*. Hence, the correlation of the Middle Member with the Chasicoan, and the Upper Member with the Huayquerian SALMAs is not contradicted with the record of capybaras. Although, according to Quiroz and Jaramillo (2010:167) "…considering the difficulties of carrying out chronostratigraphic correlation of tropical land vertebrates with those of southern latitudes as known from Argentina this assignment remains tentative…". This is an interesting locality where to compare the scheme proposed for Argentina, because two successive units of the late Miocene, both with capybaras, are stratigraphically superposed.

Four isolated and fragmented teeth, UNEFM-VF-50/52 (Vucetich et al., 2010), assigned to *Cardiatherium* sp. were found in the San Gregorio Formation, San Gregorio, Venezuela (Fig. 1.2). This unit represents sedimentary accumulation in alluvial fans (Quiroz and Jaramillo, 2010). The specimens were collected in an aquatic paleoenvironment in a tropical wetland with meandering channels and inundate savanna which, based on stratigraphic position and pollen information, is assigned to the late Pliocene. According to Vucetich et al. (2010) the endurance of most of the fauna represented in this unit beyond their biochron in southern South America would be an example of the tropics as museums of biodiversity.

4.4. Southwestern Amazonia (Acre Region of Peru and Brazil)

The specimens of *Cardiatherium orientalis* reported from Peru (originally as *Kiyutherium orientalis*; Frailey, 1986, Fig. 1.4) are isolated cheek teeth undoubtedly of this genus (Fig. 3E). It was found in the Member A of the Madre de Dios Formation which comprises primary fluvial, fluvio-lacustrine (including deltaic) or lacustrine continental deposits. A high-energy, seasonal, and relatively shallow water environment was required for the deposition of the basal conglomerates of Member A (Campbell et al., 2006). The material is part of the Río Acre Local Fauna, dated as Huayquerian in age based on this and other mammals (Frailey, 1986).

The material assigned to Hydrochoeridae indet. from the Juruá River in the Brazilian Acre region (Fig. 1.3) is very fragmented and was reported from the Solimões Formation (Sant'Anna, 1994). Only three isolated and fragmented teeth could be identified: an incisor fragment (DGM 540M) and a cheek tooth fragment (DGM 537M;

Fig. 3O) from the Locality 06 (Museu), and a cheek tooth fragment (AMNH 55831; Fig. 3O) from the Locality 25 (Lago Grande). AMNH 55831 is very likely the last prism of a p4 and DGM 537M is the pr.I of a left lower molar, both referable to cf. *Cardiatherium* and the latter, resembling *C. isseli*. The Solimões Formation was deposited in a continental environment within a subsiding basin. The facies analysis, fossil fauna content, and palynological record indicate that the environment of deposition was dominated by avulsive rivers associated with megafan systems, and in flood basins (swamps, lakes, internal deltas, and splays). Soils developed on the flatter, drier areas, which were dominated by grasslands and gallery forest in a tropical to subtropical climate (Latrubesse et al., 2010).

The references of *Kiyutherium orientalis*, *Kiyutherium* sp., and *Cardiatherium* sp. in Cozzuol (2006) and Latrubesse et al. (2007, 2010) have no bibliographic source, neither illustration nor collection number, and hence, they could not be evaluated. The materials studied by Frailey (1986) and Sant'Anna (1994) probably belong to a single taxon, to date identifiable at genus level, *Cardiatherium* (=*Kiyutherium*; see Vucetich et al., 2005). Further studies and discoveries are in need to determine whether all the capybaras of the Acre Region belong to different populations of a single species. Only DGM 537M displays distinctive characters that resemble those of *C. talicei* and *C. isseli*.

4.5. Bolivia

Capybaras from Bolivia are represented by "*Chapalmatherium*" *saavedrai* (Fig. 4M,N) based on skull and mandible fragments (MNHN, Paris, AYO. 226) from the Umala Formation, Bolivia (Fig. 1.5). Prado et al. (1998) synonymized this species with "*Ch.*" *novum*. However, it shows similarities with "*Ch. perturbidum*". Among them: pr.IIa and IIb of m1 united; pr.IIa of m2 not divided (Fig. 4M), and M3 with labial fissures, although not as deep as in "*Ch. perturbidum*" (Fig. 4N). As well, the M3 has 11 prisms, being 16–18 (Kraglievich, 1940) in the Montehermosan specimens. Differences in M3 may be explained by its small size (anteroposterior diameter = 38.9 mm) compared to that of "*Ch. perturbidum*" both from Monte Hermoso (MLP 15–231a = 59 mm, Fig. 4E, and MD-FM-13-01 = 55 mm), and Irene formations (MLP 57-VII-23-2 = ca. 65 mm, Pr.I is broken; Fig. 4F), probably representing a juvenile specimen. A particular feature, the union between Pr.I and Pr.II of M3 (Fig. 4N), is not common in "*Chapalmatherium*", but it was also observed in MACN 2840 of "*Ch. perturbidum*" by Kraglievich (1940) which has 16 prisms plus a rudimentary one.

Other specimens were found in the Inchasi beds (Bolivia; Fig. 1.6) and were referred to "*Chapalmatherium*" cf. *saavedrai* (Fig. 4O). According to the illustration, the specimens MNHN-Bol-V 00338 are a part of a pr.IIa and pr.IIb of a left m1? and two posterior (antepenultimate and penultimate?) prisms of a right M3. The small size (5.6 mm of PW of the m1) suggests it is a young individual. The union of pr.IIb and pr.IIa is typical of *Cardiatherium*, but it is also seen in very young (small) individuals of "*Chapalmaterium*" (personal observation). They are smaller than any specimen of this genus from Argentina, and 50% smaller than those of Ayo Ayo (Anaya and MacFadden, 1995). These remains are too scarce to allow stating further comments.

The Umala Formation was assigned to the Pliocene, Montehermosan s.l., comprising also the Chapadmalalan. The bearing unit, a sandy-silty fluvial-lacustrine unit 600 m thick, with several cineritic levels (Hoffstetter et al., 1984), is placed above a tuff, Toba 76, dated by SCLF—single crystal laser fusion—^{40}Ar/^{39}Ar in 5.348 ± 0.003 Ma and several meters below the Toba Ayo Ayo, dated in 2.896 ± 0.006 Ma (Marshall and Sempere, 1991; Marshall et al., 1992) (Fig. 5). In this context, the levels that yielded the capybaras were correlated with the Chapadmalalan, but they are

better referred to the Montehermosan consistent with our interpretation of the capybara remains. The Inchasi beds are 120 m thick, high-energy fluvial gravels interbedded with clays and silts. According to magnetostratigraphic studies, MacFadden et al. (1993) referred these levels to the upper Gilbert-lower Gauss chrons, between 5.7–2.5 Ma, and constrain them between 4.0 and 3.3 Ma as a preferred age. They correlate these levels with the Montehermosan s.l. (=Monterhermosan + Chapadmalalan) or the Chapadmalalan in view of the fossil content, in agreement with Cione and Tonni (1994, 1996). The specimens of capybara recorded in these beds are probably a juvenile of "Chapalmatherium" cf. saavedrai as suggested by Anaya and MacFadden (1995). In this case, the Inchasi beds would be close in age to the fauna from the Umala Formation, and hence, to the Montehermosan rather than to the Chapadmalalan.

4.6. Chile

A single specimen assigned to cf. Cardiatherium (MPC-3000) from Bahía Inglesa, Chile (Fig. 1.7), was determined by Gutstein et al. (2007) as a fragment of left M3, being the first record of Hydrochoeridae of Chile. It was found in the Bahía Inglesa Formation which consists of over 42 m of siltstones, fine sands, shelly coquinas, pebble beds, and a phosphorite bonebed, unconformably overlying on a faulted Paleozoic gabbroic basement. The bonebed is composed of up to four layers, the basal one is the most fossiliferous and was assigned to the late Miocene–Pliocene (Walsh and Hume, 2001). This record poses an interesting question about the distribution of the family. Further studies are in need to shed light on its biogeographic meaning.

5. Discussion and conclusions

In a context of the morphological diversity, ontogeny, semi-aquatic habits, social structure and use of the space of modern capybaras, fossil assemblages of each species found in each of the four most important mentioned localities are interpreted as representing successive populations that inhabited areas near water bodies. The record of each locality would be a mix of individuals that shared in time the same physical space in which the remains were incorporated by attritional accumulation (Behrensmeyer, 1982). Explained in these terms, the records of capybaras for each locality would represent a short interval within the bearing lithostratigraphic units, and also short intervals within the temporal extension proposed for each SALMA.

This group of rodents was long regarded as composed of numerous taxa, each one endemic to a particular area, a scenario completely different from the one shown by the living species. This situation made them rather useless for any biocorrelation. The improvement of their knowledge has demonstrated that their members had short biochrons with wide geographic distribution, and hence, they may be considered good biostratigraphic tools. Most of the puzzle formed by isolated remains could be put together and the result is in complete accordance with other geological evidence.

All the capybaras of the late Miocene are referred to the genus Cardiatherium, characterized by having cheek teeth with undivided prisms, independently from their size (ontogenetic age). They are recorded in Argentina (Buenos Aires, Río Negro, Chubut, La Pampa, San Juan, Mendoza, Catamarca, and Entre Ríos provinces), Uruguay, Chile, Peru, Brazil, and Venezuela. In the Pliocene, a strong change occurred in this group. Adult specimens are very large, with long rostrum and some prisms of their cheek teeth are already separated since juvenile stages. They are recorded with this pattern, in Argentina (Monte Hermoso, Quequén Salado River, Chapadmalal,

Olavarría, Córdoba, and Paraná cliffs), and Bolivia. However, in Venezuela and Uruguay, the typical late Miocene genus, Cardiatherium, is recorded up to the Pliocene. If this proves to be true, the record of Venezuela would be the endurance of this genus beyond its biochron in southern latitudes (Vucetich et al., 2010). The persistence of Cardiatherium in the Raigón Formation of Uruguay is surprising, and further research is needed to be understood.

The correlation of the Umala and Inchasi levels (Bolivia) with the Monte Hermoso Formation suggested here, rather than with the Chapadmalalan (e. g. Cione and Tonni, 1994, 1996; MacFadden et al., 1993), is not rejected by other mammals found in the Inchasi levels but needs further studies..

The temporal scheme of South American Cenozoic was established in the XIX Century by Ameghino (e.g. 1889, 1898). Later Pascual et al. (1965) introduced the concept of SALMAs, but the Ameghino's proposal was not substantially modified. However, despite increasing amounts of numerical ages, and detailed faunistic analyses, boundaries between Late Cenozoic consecutive SALMAs are not well defined, particularly between Chasicoan and Huayquerian and this latter and Montehermosan. These uncertainties are reflected in very different schemes of SALMAs calibration adopted by authors (compare Alberdi et al., 1997; Cione and Tonni, 1996, 2001; Deschamps, 2005, among others). The revision of the capybara record together with geological observations and numerical ages suggests adjustments of previous schemes.

No Chasicoan faunas are proved to be younger than ca. 8 Ma (see Cione et al., 2000; Cione and Tonni, 2005; Deschamps et al., 2009; Goin et al., 2012), whereas no Huayquerian faunas are older than <8.7 Ma. Until new numerical ages are obtained from Loma de las Tapias and Río de los Pozos formations, ca. 8 Ma would be an appropriate age for this boundary (Fig. 5).

Within the Huayquerian, our results suggest diachronism among the faunas. Those bearing C. paranense (from the "conglomerado osífero" and Río de los Pozos Formation) would be between <8.7 and ∼7.2 Ma. Those faunas bearing C. rosendoi (from the Andalhuala Formation) would be younger than 7.14 Ma (Latorre et al., 1997; Bossi et al., 2001; Bossi and Muruaga, 2009). Those bearing C. aff. orientalis (from the Cerro Azul Formation) would be older than 6 Ma (Verzi et al., 2008; see also Deschamps et al., 2007). As C. aff. orientalis is very close to C. rosendoi probably the bearing levels of both capybaras would be coeval between 7.14 and 6 Ma. Numerical ages suggest that the upper limit of the Huayquerian SALMA would be younger than 5.8 Ma (Marshall et al., 1986) up to 5.28 (Schultz et al., 2006).

Thus, the Chasicoan SALMA would be correlated with part of the Tortonian Stage/Age; the Huayquerian SALMA would be correlated with the late Tortonian-Messinian Stage/Age, and it could even extend to the earliest Zanclean. The Montehermosan SALMA (including the mammals from the whole Monte Hermoso Formation) would be restricted to the Zanclean. The Chapadmalalan SALMA would be correlated with the late Zanclean-early Piacenzian (Fig. 5).

The revision of the capybaras presented in this paper, suggests the necessity of careful taxonomic revisions of other groups of mammals (see e.g. Tomassini, 2012; Tomassini et al., 2013), and obtaining more numerical ages in order to improve the calibration of the South American Mio-Pliocene time scale.

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