Paleontology, evolution and systematics of capybara

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1. INTRODUCTION

Caviomorph rodents, the New World Hystricognathi, are one of the most noteworthy groups of mammals in South America. Isolated for more than 30 million years, they have given rise to several extraordinary rodents including the pacas (*Cuniculus* spp.), cavies (*Cavia* spp.), vizcachas (*Lagostomus* spp.), agouties (*Dasyprocta* spp.), as well as two giants: *Phoberomys,* from the late Miocene (6 Ma; mega annum = million years) which probably weighed more than 400 kg (Sánchez Villagra et al. 2003), and *Josephoartigasia monesi* probably from the Pleistocene, at about 1000 kg (Rinderknecht and Blanco 2008). Capybaras (*Hydrochoerus* spp.) are particularly conspicuous because of their size - they are the largest living rodents - and their aggregation in herds (Ojasti 1973; Macdonald 1981; Macdonald et al. 2007). This chapter examines their paleontology and evolution, focusing particularly on another striking feature: their unpaired ever-growing cheek teeth whose very complicated occlusal surface design changes throughout the capybara’s life (Vucetich et al. 2005).

Capybaras are undoubtedly allied to the living cavies and Patagonian “hares” and their extinct relatives. However, the relationships between capybaras and these taxa are not clear. The fossil capybara record begins in the Chasicoan South American Land-Mammal Age (SALMA), during the early late Miocene (ca. 9-7 Ma), in Central Argentina (Fig. 1). Ameghino (1883) was the first to describe an extinct species of capybara, based on a fragmented mandible from the “conglomerado osífero” in the Ituzaingó Formation, Huayquerian SALMA, late Miocene, which outcrops in the vicinity of the city of Paraná, Entre Rios Province, Argentina (Fig. 2). A large number of new genera and species, grouped in four subfamilies, were later nominated, following findings of additional fragmentary remains of different sizes and differing occlusal cheek teeth design (Mones l991). Originally, capybaras were considered to be highly diversified, with a long, slow evolutionary history. Recent findings have, however, permitted a new interpretation of the fossil record. With this in mind, we describe the evolutionary history of capybaras and discuss their relationships with other South American hystricognath rodents based on paleontological data.

2. THE ORIGIN AND EARLY RADIATION OF SOUTH AMERICAN HYSTRICOGNATH RODENTS

Caviomorphs are immigrants to South America. It is generally believed that they are more closely related to the Old World hystricognaths than to any other group of rodents, whether they are considered monophyletic or not (Lavocat 1976; Patterson and Wood 1982; Martin 1994; Nedbal et al. 1994; Bryant and McKenna 1995; Marivaux et al. 2002; Poux et al. 2006; Blanga-Kanfi et al. 2009; Sallam et al. 2009; Vilela et al. 2009), and that they probably came from Africa by raft during the late Eocene (about 37 Ma; Vucetich et al. 2010a).

The oldest known hystricognath rodents of South America come from Tinguiririca in Chile (Figs. 1 and 2; Flynn et al. 2003 and references therein), and La Cantera site in Gran

Barranca, Patagonia, Chubut Province, Argentina (Vucetich et al. 2010a), estimated at 31.5 Ma and 31.5-28 Ma respectively (Figs. 1 and 2). The rodents found in Santa Rosa, Peru, were proposed as the oldest in South America, but estimations of the age of this site are dubious, being between late Eocene-late Oligocene (37-23 Ma; Figs. 1 and 2; Campbell 2004; Frailey and Campbell 2004; Shockey et al. 2004). The rodents from this site are abundant,brachyodont (Box 1) and relatively homogeneous in morphology when compared to those of other old fauna. In Tinguiririca and La Cantera, remains are scarcer but show great morphological diversity with a clear trend toward hypsodonty (high crown teeth; Box 1) in some taxa (Wyss et al. 1993; Flynn et al. 2003; Vucetich et al. 2010a).

The degree of diversification shown by these rodents suggests that the initial radiation occurred well before these records. Vucetich et al. (1999) suggest that caviomorphs colonized South America during the late or even early Eocene (ca. 55-34 Ma; Fig. 1). Taking the same line, Poux et al. (2006) suggest that caviomorphs radiated during the late Eocene, before the early Oligocene (33.9 Ma) cooling (Fig. 1; Zachos et al. 2001). Opazo (2005) disagrees, suggesting that radiation took place a little later in the early Oligocene. The earliest differentiation probably did occur before the early Oligocene cooling (Antarctic Glaciation; Fig. 1), but differentiation of the first high-crowned caviomorphs, that is primitive cavioids and chinchilloids appears to have occurred in association with this cooling.

Southern South America provided special conditions for the early development of hypsodonty. On the one hand, there was a general trend toward climatic deterioration after the Eocene-Oligocene transition (33,9 Ma), which would have been more intense at high latitudes. On the other hand, during the early Cenozoic (60-20 Ma), periods of intense volcanism affected Patagonia, providing large volumes of volcanic glass in the sediments (Mazzoni 1985; Bellosi 2010). These two elements, climatic deterioration and a large amount of abrasive material, deposited on plants that early rodents ate, favored the development of hypsodonty (Kay et al. 1999). These conditions could explain why rodents with a tendency to hypsodonty are recorded in Tinguiririca and La Cantera, but not further north in Santa Rosa (Fig. 2), which probably saw milder climatic conditions and no volcanic glass in the sediments.

3. DIVERGENCE OF THE HYDROCHOERIDAE

Although the oldest caviomorphs derive from the early Oligocene (Fig. 1), it is not until the late Oligocene (Deseadan SALMA – ca. 28-25 Ma; Fig. 1) that the caviomorph record becomes abundant and continuous (Vucetich et al. 1999). Eocardiids (Box 2; Figs. 1 and 3), considered the stem group for Caviidae and Hydrochoeridae (Box 2), are first recorded in Argentinean Patagonia at Cabeza Blanca, Chubut Province, and La Flecha, Santa Cruz Province (Fig. 2) during the Deseadan SALMA (Fig. 1). No eocardiids have been recorded in the Deseadan of Salla-Luribay, Bolivia (Fig. 2) or in Santa Rosa. From this, it can be inferred that the diversification of the Cavioidea s.s. (Box 2) took place in Patagonia, or at least in the southern part of the continent. The diversification and later evolution of the Cavioidea s.s. involved the development of high-crowned cheek teeth. The evolution of hypsodonty in this group can be followed from the Deseadan SALMA onwards, starting with the mesodont (slightly higher-crowned than brachyodont) *Asteromys* (Fig. 4a), then the protohypsodont species of *Luantus* from the Colhuehuapian–"Pinturan" SALMAs (Figs. 1 and 4b), up to the euhypsodont *Eocardia* (Figs. 3 and 4c) of the Santacrucian SALMA (late early Miocene – 16.5-15.5 Ma; Fig. 1). This was a rather slow process of change that took about 12 million years, during which euhypsodonty and heart-shaped teeth, characteristic of the Cavioidea s.s., arose. In fact, it is very difficult to separate the most derived species of eocardiids from the first Caviidae only based on tooth morphology (but see Pérez 2010b; Pérez and Vucetich 2011).

The last eocardiids come from the “Colloncuran” (early middle Miocene; ca 15.5 Ma) of northern Patagonia (Figs. 1 and 2). The first modern Cavioidea s.s. (Caviinae, Dolichotinae and Hydrochoeridae) come from the middle Miocene of La Venta in Colombia, Laventan SALMA, 11.8-13.5 Ma (Figs. 1 and 2; Fields 1957; Madden et al. 1997; Walton 1997) with the dolichotine *Prodolichotis*, but they were well-diversified by the Chasicoan SALMA (Fig. 1). Species with intermediate morphology between eocardiids and modern Cavioidea s.s. (Fig. 5) were found in Patagonian sediments assigned to the "Colloncuran"- Chasicoan, and in the Laventan SALMA, Colombia (Pérez 2010a,b; Pérez and Vucetich 2011).

This temporal context allows at least two interpretations. On the one hand, all modern groups could have differentiated together between 13.5 and 15.5 Ma (Fig. 1), and the lack of hydrochoerids and caviines during that period could be an artifact of the paleontological record. On the other hand, dolichotines could have differentiated before the caviines and hydrochoerids. In accordance with the second hypothesis, dolichotines have the most primitive cheek teeth morphology and enamel microstructure among modern Cavioidea s.s. (Vieytes et al. 2001; Vieytes 2003), similar to those of eocardiids. Additionally, the Caviinae and Hydrochoeridae share a more derived cheek teeth enamel microstructure (Vieytes et al. 2001; Vieytes 2003).

The cardiomyines are a group of large cavioids that are also first recorded during the Chasicoan SALMA. Like capybaras, they have an increasing number of laminae in the M3 and p4 (Figs. 4 d-e), some deep flexids (see Dental Structure, 5.1, below) and a wide palate. Cardiomyines were previously considered Caviids, but Vucetich et al. (2005) postulated them to be a sister group to capybaras (Box 2 and Appendix 1). Recent phylogenetic analyses of Cavioidea (Pérez 2010a,b) support the later hypothesis.

The differentiation of hydrochoerids would have been relatively rapid, explaining the absence of potential close ancestors from the middle Miocene strata of Patagonia (Vucetich 1984; Vucetich et al. 1993) and Colombia (Walton 1997).

4. GEOGRAPHIC DISTRIBUTION OF FOSSIL CAPYBARAS

The earliest capybaras (*Cardiatherium chasicoense*) derive almost exclusively from Arroyo Chasicó, Buenos Aires Province, Argentina (Deschamps et al. 2007); however, one specimen has recently been described in San Juan Province (Fig. 2; Deschamps et al. 2009). By the Huayquerian SALMA (late Miocene; Fig. 1), capybaras were distributed throughout most of South America, from northern Venezuela (Linares 2004; Vucetich et al. 2010b) to western Brazil (Frailey 1986), south-western Uruguay (Francis and Mones 1965) and several sites in Argentina (Fig. 2). *Cardiatherium patagonicum* represents the most southern hydrochoerid, being from Península Valdés, northern Patagonia, Argentina, and it is more derived than the remaining Huayquerian hydrochoerids.

Pliocene (5.3-2.5 Ma) representatives (*Phugatherium*) have been found in several sites in Argentina (Fig. 2). MacPhee et al. (2000) reported a new species, *Hydrochoerus gaylordi,* from the late Pliocene (dated 2.6–3.7 Ma) of the Antilles (Fig. 2), which may be the oldest record of this genus, but see below. During the Pleistocene-Holocene period (2.5 Ma to Recent), capybaras (*Neochoerus* and *Hydrochoerus*) ranged from southern North America to central Argentina (Fig. 2).

5. DENTAL STRUCTURE AND ITS BEARING ON THE SYSTEMATICS OF CAPYBARAS

5.1. DENTAL STRUCTURE

As for most extinct mammals, the taxonomy of extinct capybaras is based mainly on tooth morphology, because teeth are the most frequent remains in the mammal fossil record. The morphology of the occlusal surface is so peculiar in this group that it was necessary to develop a specific nomenclature (Box 3). Capybara teeth are easily characterized by: increasing number of laminae, especially in the last upper (M3) and lower (m3) molars; increasing depth of the re-entrant folds (flexi/flexids; see Box 3) already present in more primitive cavioids (especially h.p.i.; see Box 3); and the development of a new flexid, the h.t.i. (Box 3), which is a novelty for the superfamily Cavioidea (Vucetich et al. 2005), and the one that grows most in ontogeny. Several of these flexi/flexids cross to the opposite side in adult *Hydrochoerus*. Systematics at genus and species level is based largely on the number and depth of flexi/flexids (e.g. Pascual and Bondesio 1982; Mones 1991).

The complicated dental morphology of capybaras developed from a simpler, bi-lobed one, seen in the early Miocene (20 Ma) *Eocardia* and the living *Dolichotis* (Fig. 4c, f). The number of laminae and depth of flexids increased from the oldest *C. chasicoense* (Fig. 6a), through the Huayquerian species of *Cardiatherium* (Fig. 6b) and the Pliocene *Phugatherium* (Fig. 6c-g), to the Pleistocene–Holocene *Neochoerus* and *Hydrochoerus* (Fig. 6h).

5.2. MORPHOLOGICAL TOOTH VARIATION AND ONTOGENETIC TRAJECTORIES.

The fossil record of capybaras shows a large diversity in size and morphology. For example, the anteroposterior diameter of m1 ranges from 5.12 mm in "*Anchimys leidyi*" (Appendix 1) to 24.82 mm in *Neochoerus aesopi*. This diversity was classically interpreted as systematic richness. In contrast, Rocha and Montalvo (1999) interpreted this morphological diversity as individual variation in the analysis of one population of late Miocene capybaras from Guatraché and Chillhué lagoons (Fig. 2), in La Pampa Province, Argentina. Recently, Vucetich et al. (2005) described how cheek teeth are modified in structure through a lifetime in a fossil population from Estancia Rincón Chico (Fig. 2), in Chubut Province, also in Argentina.

Capybaras are born with all cheek teeth already erupted, even with occlusal wear, and as in other euhypsodont mammals, teeth continue growing in all dimensions throughout life. In fossil capybaras the design of the occlusal surface becomes more complex with age (Vucetich et al. 2005), because these teeth grow allometrically deepening flexids at different rates (Fig. 7). This growth pattern is unique among rodents, and was originally misinterpreted: small specimens with more simple morphology were considered primitive taxa, whereas large specimens with more complicated morphology were considered more derived (Figs. 6c-g and 7). Descriptions of morphological variants as specific characters have suggested a highly diversified taxonomy, with about 23 genera and 56 species (Mones 1991).

The most recent discovery of morphological change in ontogenetic tooth development (Vucetich et al. 2005) has resulted in the synonymy of many taxa, because some small species have been re-classified as the juveniles of larger ones. Thus, the high specific diversity suggested by typological criteria used in classical systematics may actually derive from high intraspecific morphological diversity caused by individual variation and extensive morphological change during ontogeny. In this context, the morphological difference of the species *H. gaylordi* (MacPhee et al. 2000) from the other species of *Hydrochoerus* may be due to ontogenetic variation, since it is based on a small specimen. Misinterpretation of morphological differences in teeth had in fact been so extreme that juveniles of a species were placed in one separate subfamily and the adults of that species in another. The new interpretation of ontogenetic morphological change does not support the classical subdivision of capybaras into four subfamilies. Three particularly illustrative cases are discussed in detail below.

5.2.1. Wide rostrum vs. narrow rostrum: *Cardiatherium paranense* vs. *C. orientalis*

Peculiar skull remains of capybaras found in the “conglomerado osifero” of Ituzaingó Formation, Paraná City were assigned to the subfamily Anatochoerinae and named "*Anatochoerus"* (Fig. 8c; Mones 1991), in view of the great width of the rostrum. Although not associated with mandibles assigned to *C. paranense,* the single species to which all the mandibles from these sediments were supposed to have belonged (Vucetich et al. 2005), we attribute these peculiar skulls to this species because they have a similar dental pattern and are the only skull remains of capybaras in this site (Deschamps et al. 2010). However, *C. paranense* was considered a Cardiatherinae, and therefore presents a beautiful example of materials that belong to the same species having been wrongly attributed to different subfamilies. *C. paranense* is very close to *C. orientalis* (Fig. 8d), which is known through associated mandibles and skulls found in the late Miocene of La Pampa Province (Fig. 2), but the rostrum of these skulls is much narrower than that of *C. paranense* (compare Figs 8c and 8d). In addition, the palate of *C. paranense* extends up to the end of the M3, whereas that of *C. orientalis* is shorter, reaching to about the middle of the M3 (Fig. 8c-d). Consequently, both species are considered valid despite the fact that the mandibles and occlusal morphology of teeth are quite similar (Deschamps et al. 2010).

5.2.2. The case of the Early Pliocene capybaras

The holotypes of the species *Phugatheriun cataclisticum* and “*Anchimysops villalobosi”* of the Monte Hermoso Formation (early Pliocene – 5 Ma; Fig. 2) are juvenile specimens; the former is represented by a mandible and the latter by a skull fragment. These taxa were originally assigned to the subfamily Cardiatheriinae. The only other hydrochoerid known from these levels is *Chapalmaterium perturbidum,* assigned to the subfamily Protohydrochoerinae. This species is represented by several skulls with larger mandibles and more derived cheek teeth morphology (Fig. 6f-g) than the specimens assigned to

Phugatherium (Fig. 6c-e) and "*Anchimysops*". It is quite plausible that *Phugatherium* and "*Anchimysops*" are, in fact, juveniles of the protohydrochoerine *Chapalmatherium*. If this were so, the correct name for the single Montehermosan genus would be *Phugatherium* (Appendix 1).

5.2.3. *Kerodon* as a hydrochoerid

Recently, there has been some debate on cavioid classification involving the position of the small rock-dwelling *Kerodon*, traditionally considered a Caviidae. Based on molecular analyses Rowe and Honeycutt (2002) suggested close relationships between *Hydrochoerus* and *Kerodon* (see also Pérez 2010a,b), and on this basis, *Kerodon* was transferred to Hydrochoeridae (Wilson and Reeder 2005). Some morphological characters of *Kerodon*, such as a palate with a deep mesopterygoid fossa and very simple tooth morphology (Fig. 4 g), appear quite different from those of the other hydrochoerids, both hydrochoerines and cardiomyines. Da Silva Neto (2000) also considered *Kerodon* as a caviid on the basis of other skull characters. Hence, if we accept close relationships between *Hydrochoerus* and *Kerodon*, the split of *Kerodon* from Hydrochoerinae + Cardiomyinae should have occurred at least during the middle Miocene (Fig. 1; Opazo 2005; Pérez and Vucetich 2011). The short fossil record of *Kerodon* (late Pleistocene – about 40 Ky = 400 hundred years) gives little information about its evolutionary history, and it is thus not yet possible to corroborate this statement.

5.3. Macrosystematic of Hydrochoeridae

The topics discussed above outline the current lack of support for four distinct subfamilies of caviomorph rodents as originally described: the Cardiatherinae, Protohydrochoerinae and Anatochoerinae with exclusively fossil representatives, and Hydrochoerinae including the living capybara and *Neochoerus*, its closest fossil representative. We suggest that the members of all four subfamilies belong within a single subfamily, Hydrochoerinae, which in turn should be grouped together with the subfamily Cardiomyinae within the family Hydrochoeridae (Box. 2 and Appendix 1). If *Kerodon* is more closely related to this group than to the Caviinae perhaps it deserves its own subfamily.

6. PALEOBIOLOGY

What can we infer from the fossil record about the natural history of capybaras? When did they attain their modern characteristics? Three main topics are of interest: size, semi-aquatic habits, and aggregation in herds.

Gigantism in caviomorphs is more common than in other rodents and had reached its pinnacle by the end of the Miocene in the Huayquerian SALMA (6 Ma; Fig. 1). Capybaras in particular were already large in the previous Chasicoan SALMA (Fig. 1) when they were first recognized, but continued to increase in size, peaking during the Plio-Pleistocene (5,3 Ma to 10 Ky); examples are "*Chapalmatherium*" 200 kg and *Neochoerus* 110 kg (Vizcaíno et al. in press).

Modern capybaras are semi-aquatic, and in the fossil record capybaras have always been found in lithological units interpreted as water-related settings: *C. chasicoense*, in a swampy environment (Zárate et al. 2007), *C. paranense* in a fluvial deposit (Cione et al. 2000; Herbst 2000), *C. patagonicum* in levels deposited by a freshwater channel (Cione et al. 2005) and *C. orientalis* in the only two sites of the Cerro Azul Formation interpreted as deposits of lacustrine environments, Laguna Chillhué and Laguna Guatraché (Fig. 2; Verzi et al. 2008). In many other localities of La Pampa Province, in which eolian facies that are not related to water settings of the Cerro Azul Formation are exposed, vertebrate remains are abundant (Verzi et al. 2008 and references therein) but no capybara have been found. It was generally thought that Pliocene capybaras, however, were not adapted to semi-aquatic habitats. Kraglievich (1930: 509) described the genus "*Protohydrochoerus*" (=*Phugatherium*; Appendix 1) from Monte Hermoso (Fig. 2) as a large running capybara (Fig. 9), based on the limb proportions; the humerus and femur were both longer than the radius and tibia, respectively. However, in a morphofunctional study of the limbs, Candela et al. (2006, and personal communication) concluded that they were not significantly different from those of the modern capybara, especially in the articular regions.

The body size range of the capybaras found in the Ituzaingó Formation ("conglomerado osífero"), and the late Miocene of Península Valdés is very large (Vucetich et al. 2005). These deposits cover a short time span and, therefore, we believe that they reflect a community structure in which several generations were living together, as in modern capybara herds. In sum, it appears that the basic biological characteristics of capybaras were attained before the late Miocene.

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Captions for figures and tables:

Figure 1. Stratigraphic chart showing the oldest records of caviomorph and cavioid rodents, cavioid phylogenetic relationships, and the stratigraphic record of fossil capybaras, against the main global climatic events from Zachos et al. (2001). Ma = mega annum (million years); SALMA = South American Land-Mammal Age.

Figure 2. Main localities of fossil capybaras. Locations mentioned in the text are referenced as follows: 1. Arroyo Chasicó, Buenos Aires Province, Argentina; 2. Albardón, San Juan Province, Argentina; 3. "conglomerado osífero", Ituzaingó Formation, Paraná City, Entre Ríos Province, Argentina; 4. Estado Falcón, Venezuela; 5. Estancia Rincón Chico, Península Valdés, Chubut Province, Argentina; 6. Laguna Chillhué and Laguna Guatraché, La Pampa Province, Argentina; 7. Farola Monte Hermoso, Buenos Aires Province, Argentina; 8, Grenada, Lesser Antilles. Symbols labeled a-g indicate other localities mentioned in the text: a. Tinguiririca, Chile; b. La Cantera, Chubut Province, Argentina; c. Santa Rosa, Peru; d. Cabeza Blanca, Chubut Province, Argentina; e. La Flecha, Santa Cruz Province, Argentina; f. Salla-Luribay, Bolivia; g. La Venta, Colombia.

Fig. 3. Reconstruction of fossil *Eocardia*, drawing by Bruce Horsfall, for Scott 1905.

Figure 4. Dental series in occlusal view. a. *Asteromys* (right p4-m3); b. *Luantus* (right p4-m2); c. *Eocardia* (right p4-m2); d-g. right P4-M3 of d, *Caviodon*; e. *Cardiomys*; f. *Dolichotis*; g. *Kerodon*. Anterior above.

Figure 5. Evolution of selected characters in Cavioidea s.s. a-c. mandible; d-f. m1-m3 in occlusal surface (anterior to the right). a,d. *Asteromys*; b,e. *Guiomys*; c,f. *Galea*. nMpi. notch

for the insertion of the masseter medialis pars infraorbitalis. Not to scale. The nMpi changes its relation to other crests of the mandible: in *Asteromys* it is joined to the masseteric crest, in *Guiomys* it is isolated, and in *Galea* it is joined to the horizontal crest. Cheek teeth in *Asteromys* are mesodont, retain fossettids and have different sizes; in *Guiomys* they are euhypsodont without fossettids, and similar in size; and in *Galea*, to these features they add a central dentine crest (Pérez 2010a,b; Pérez and Vucetich, 2011).

Figure 6. Lower cheek teeth of hydrochoerines in occlusal view. a. right p4-m3 of *Cardiatherium chasicoense*; b. right p4, m1 or m2 and fragment of m3 of *Cardiatherium patagonicum*; c-g. *Phugatherium cataclisticum* (different ontogenetic stages). c-e. right juvenile m1 or m2; f-g. right adult m1 or m2; h. right p4-m3 of *Hydrochoerus hydrochaeris*.

Figure 7. Relationship between ($\log_{10}$) antero-posterior length (AP) and ($\log_{10}$) h.s.i. and h.t.i. lengths of *Cardiatherium patagonicum* and *Cardiatherium paranense*. Growth lines were fitted by eye. a-d. point holotypes of some species now regarded as different ontogenetic stages of *C. paranense*. a. "*Eucardiodon marshi*"; b. "*Procardiatherium simplicidens*"; c. "*Kiyutherium scillatoyanei*"; d. *C. paranense*. Ontogenetic stages of 1 or m2 of *C. paranense* and *C. patagonicum* are shown below.

Figure 8. Late Miocene capybaras. a-b. right mandible in lateral and occlusal views of *Cardiatherium chasicoense*; c. skull in occlusal view of *Cardiatherium paranense* (="*Anatochoerus inusitatus*"); d. skull in occlusal view of *Cardiatherium orientalis*. a-b are modified from Deschamps et al. (2007).

Figure 9. Reconstruction of fossil "*Protohydrochoerus perturbidus*" (=*Phugatherium cataclisticum*) drawing by Martín Barrios for the exhibitions of the Museo de La Plata, Argentina.

Appendix 1: Capybara revised taxonomy

Synonymies already published in Mones (1991), Prado et al. (1998), Vucetich et al. (2005), and Deschamps et al. (2007) are not listed.

Order Rodentia Bowdich, 1821

Suborder Hystricomorpha Brandt, 1855

Infraorder Hystricognathi Tullberg, 1899

Superfamily Cavioidea (Gray, 1821) Kraglievich, 1930

Family Hydrochoeridae (Gray, 1825) Gill, 1872

Subfamily Hydrochoerinae (Gray, 1825) Weber, 1928

Genus *Cardiatherium* Ameghino, 1883

= Contracavia Burmeister, 1885; *Anchimysops* Kraglievich, 1927, partim; *Anatochoerus* Vucetich and Mones, 1991.

Cardiatherium chasicoense (Pascual and Bondesio, 1968**)**

Cardiatherium isseli Rovereto, 1914

Cardiatherium orientalis (Francis and Mones, 1965)

Cardiatherium paranense (Ameghino, 1883)

= *Anchimysops radicei* Kraglievich, 1940; ?*Anchimysops dubius* Kraglievich, 1940; *Contracavia minuta* (Ameghino, 1885); *Anatochoerus inusitatus* Vucetich and Mones, 1991 in Mones 1991.

Cardiatherium patagonicum Vucetich, Deschamps, Olivares and Dozo, 2005

Cardiatherium rosendoi (Bondesio, 1985)

Cardiatherium talicei Francis and Mones, 1965[1]

Genus *Phugatherium* Ameghino, 1887

= *Chapalmatherium* Ameghino, 1908; *Protohydrochoerus* Rovereto, 1914; *Anchimysops* Kraglievich, 1927, partim.

Phugatherium cataclisticum Ameghino, 1887

= *Anchimysops ultra* Kraglievich, 1940; *Chapalmatherium perturbidum* (Rovereto, 1914).

Phugatherium novum (Ameghino, 1908)

Genus *Hydrochoeropsis* Kraglievich, 1930

Hydrochoeropsis dasseni Kraglievich, 1930

Genus *Neochoerus* Hay, 1926[2]

Neochoerus dichroplax Ahearn and Lance, 1980

Neochoerus fontanai (Rusconi, 1933)

Neochoerus tarijensis (Ameghino, 1902)

Neochoerus sulcidens (Lund, 1839)

Neochoerus aesopi (Leidy, 1853)

Genus *Hydrochoerus* Brisson, 1762[2]

Hydrochoerus hydrochaeris (Linnaeus, 1766)

Hydrochoerus ballesterensis (Rusconi, 1934)

Hydrochoerus isthmius Goldman, 1912

Hydrochoerus gaylordi MacPhee, Singer, and Diamond, 2000[3]

Subfamily Cardiomyinae Kraglievich, 1930[4]

Genus *Cardiomys* Ameghino, 1885

=*Neoprocavia* Ameghino, 1889; *Parodimys* Kraglievich, 1932

Cardiomys cavinus Ameghino, 1885

Genus *Procardiomys* Pascual, 1961

Procardiomys martinoi Pascual, 1961

Genus *Caviodon* Ameghino, 1885

Caviodon multiplicatus Ameghino, 1885

Genus *Xenocardia* Pascual and Bondesio, 1963

Xenocardia diversidens Pascual and Bondesio, 1963

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[1] Possibly a junior synonym of *C. isseli*.

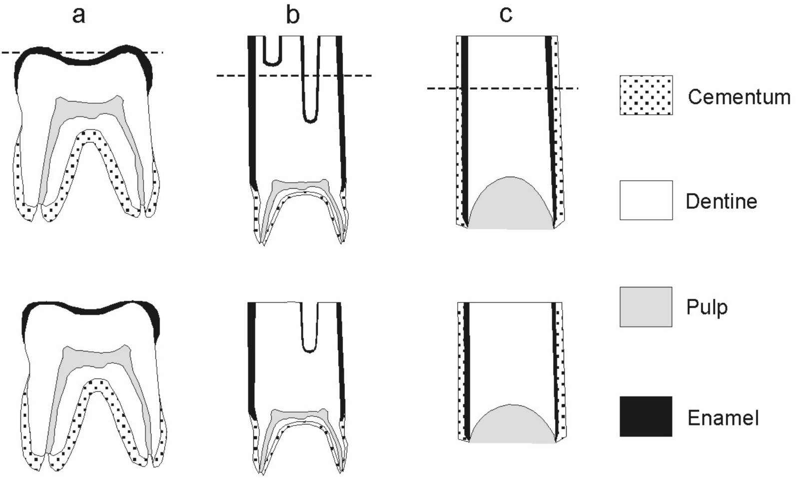
[2] Differentiation of *Neochoerus* from *Hydrochoerus* on the basis of fragmentary material, as it currently is in most cases, is dubious. Thus, the stratigraphic range of these genera has been taken from literature (e.g. Mones, 1991) without further analysis.

[3] Characters used to distinguish this species are within the range of individual or ontogenetical variation of *H. hydrochaeris*.

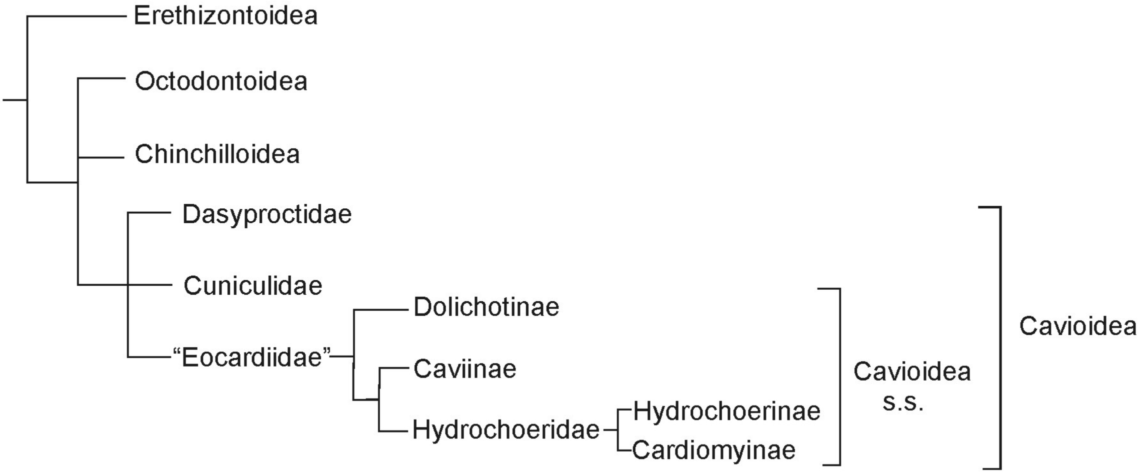
[4] Only the type species of cardiomyines are listed because a revision of the species of the whole group is still needed.

Box 1. Generalized mammals have teeth with roots and a short crown that do not change throughout life. Other mammals, like capybara, horses, and rabbits have high-crowned teeth usually named hypsodont teeth. In these teeth roots delay their development and the crown keeps on growing throughout life or at least part of it. This phenomenon is called hypsodonty. Hypsodonty is an adaptation to extend the life of teeth and, thus, the life of the animal, facing increasing rates of tooth wear resulting either from eating more abrasive plant tissues (phytoliths) or wear-inducing particles, such as wind-blown grit, that adhere to plant surfaces. Hypsodonty is also related to open environments in which animals feed closer to the ground (Janis and Fortelius, 1988; Janis et al., 2000).

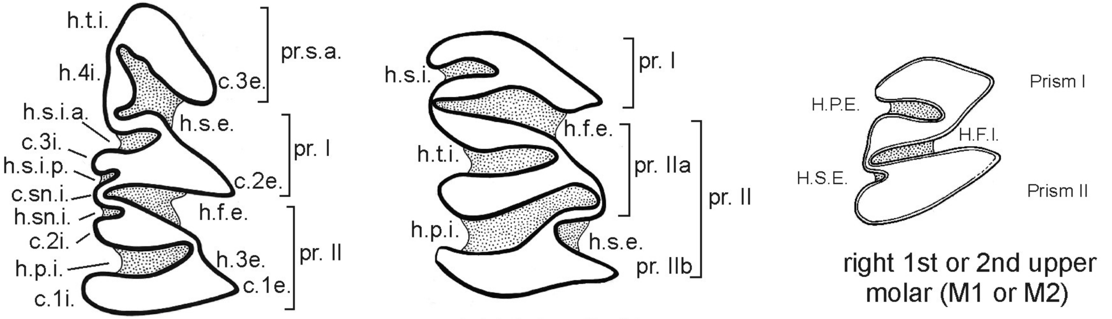
The diagrams show a. brachyodont (low-crowned), b. protohypsodont (high-crowned), and c. euhypsodont (evergrowing) teeth, and their change with wear (lower row). The occlusal morphology varies accordingly.



Box 2 Eocardiidae, Caviidae and Hydrochoeridae are a very cohesive group sharing heart-shaped cheek teeth, among other characters. All three families are grouped together in the superfamily Cavioidea, although some authors include others in this superfamily, such as Dasyproctidae, Cuniculidae and Dinomyidae. Patterson and Wood (1982) considered the three first families as the Cavioidea s.s. excluding the Dasyproctidae and other putative cavioids from this informal group. In the scheme below we illustrate proposed relationships among the Cavioidea. Relationships between Octodontoids and Chinchilloids are controversial and not discussed in this chapter.



Box 3. Mammalian cheek teeth are intensively studied because they display a number of characters with high systematic and phylogenetic value. Thus, a very detailed nomenclature has been developed, especially for the occlusal surface. In the case of capybaras the occlusal morphology of cheek teeth is so peculiar that it was necessary to develop a specific nomenclature for them (see below). Capybara teeth are euhypsodont (Box 1), formed by a prism partially (or completely) divided by re-entrant folds which are also named flexi (uppers) or flexids (lowers). It is traditional in capybara literature to maintain the abbreviated Spanish name of dental characters to avoid further complications in this already complex nomenclature. The length of re-entrant folds varies among species, but also with the age of the animal, making the interpretation of occlusal morphology a complicated but fascinating task. In primitive capybaras re-entrant folds are comparatively shallow, whereas in the most derived species, such as Hydrochoerus hydrochaeris, some of these folds cross to the opposite side, completely dividing the tooth into independent smaller prisms (Fig. 4h).

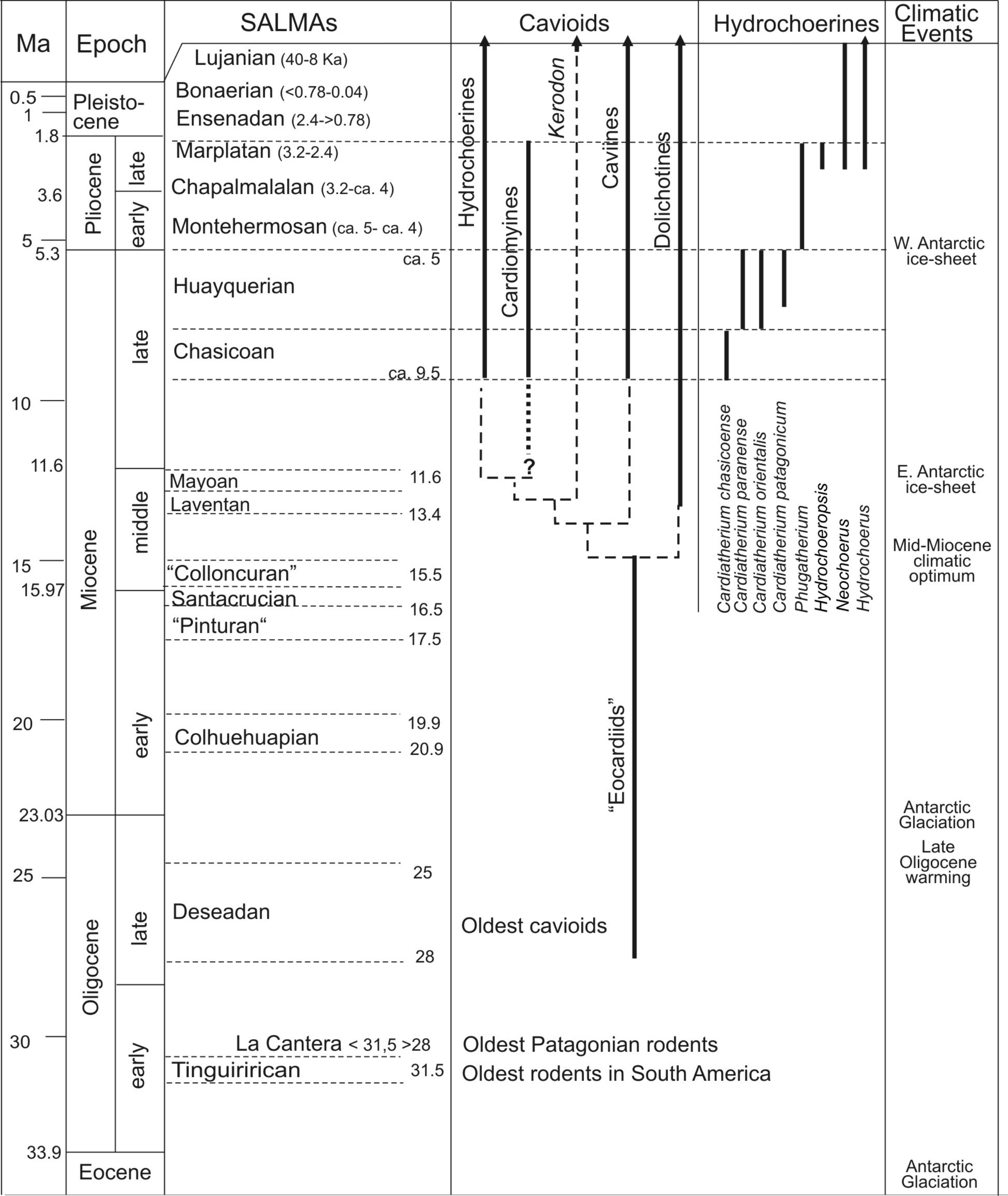


right 4th lower premolar (p4)

right 1st or 2nd lower molar (m1 or m2)

right 1st or 2nd upper molar (M1 or M2)

Nomenclature of cheek teeth. Nomenclature of cheek teeth. Lower teeth: h.t.i., tertiary internal flexid; h.4i., 4th internal flexus; h.s.i.a., secondary anterior internal flexid; c.3.i., 3rd internal column; h.s.i.p., secondary posterior internal flexid; c.sn.i., supernumerary internal column; h.sn.i., supernumerary internal flexid; c.2i., 2nd internal column; h.p.i., primary internal flexid; c.1i., 1st internal column; pr.s.a., anterior secondary prism; c.3e., 3rd external column; h.s.e., secondary external flexid; c.2e., 2nd external column; h.f.e., fundamental external flexid; h.3e., 3rd external flexid; c.1e. 1st external column; h.s.i., secondary internal flexid; pr. I-II, IIa-b, prisms I-II, IIa-b. Upper teeth: H.S.E., secondary external flexus; H.P.E., primary external flexus; H.F.I., fundamental internal flexus.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Pleistocene
Pliocene
late
early
Miocene
late
middle
early
Oligocene
late
early
Eocene
Lujanian (40-8 Ka)
Bonaerian (<0.78-0.04)
Ensenadan (2.4->0.78)
Marplatan (3.2-2.4)
Chapalmalalan (3.2-ca. 4)
Montehermosan (ca. 5- ca. 4)
ca. 5
Huayquerian
Chasicoan
ca. 9.5
Mayoan
11.6
Laventan
13.4
"Colloncuran"
15.5
Santacrucian
16.5
"Pinturan"
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Deseadan
28
La Cantera < 31,5 >28
Tinguiririca n
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Hydrochoerines
Cardiomyines
Kerodon
Caviines
Dolichotines
?
"Eocardiids"
Oldest cavioids
Oldest Patagonian rodents
Oldest rodents in South America
Cardiatherium chasicoense
Cardiatherium paranense
Cardiatherium orientalis
Cardiatherium patagonicum
Phugatherium
Hydrochoeropsis
Neochoerus
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E. Antarctic ice-sheet
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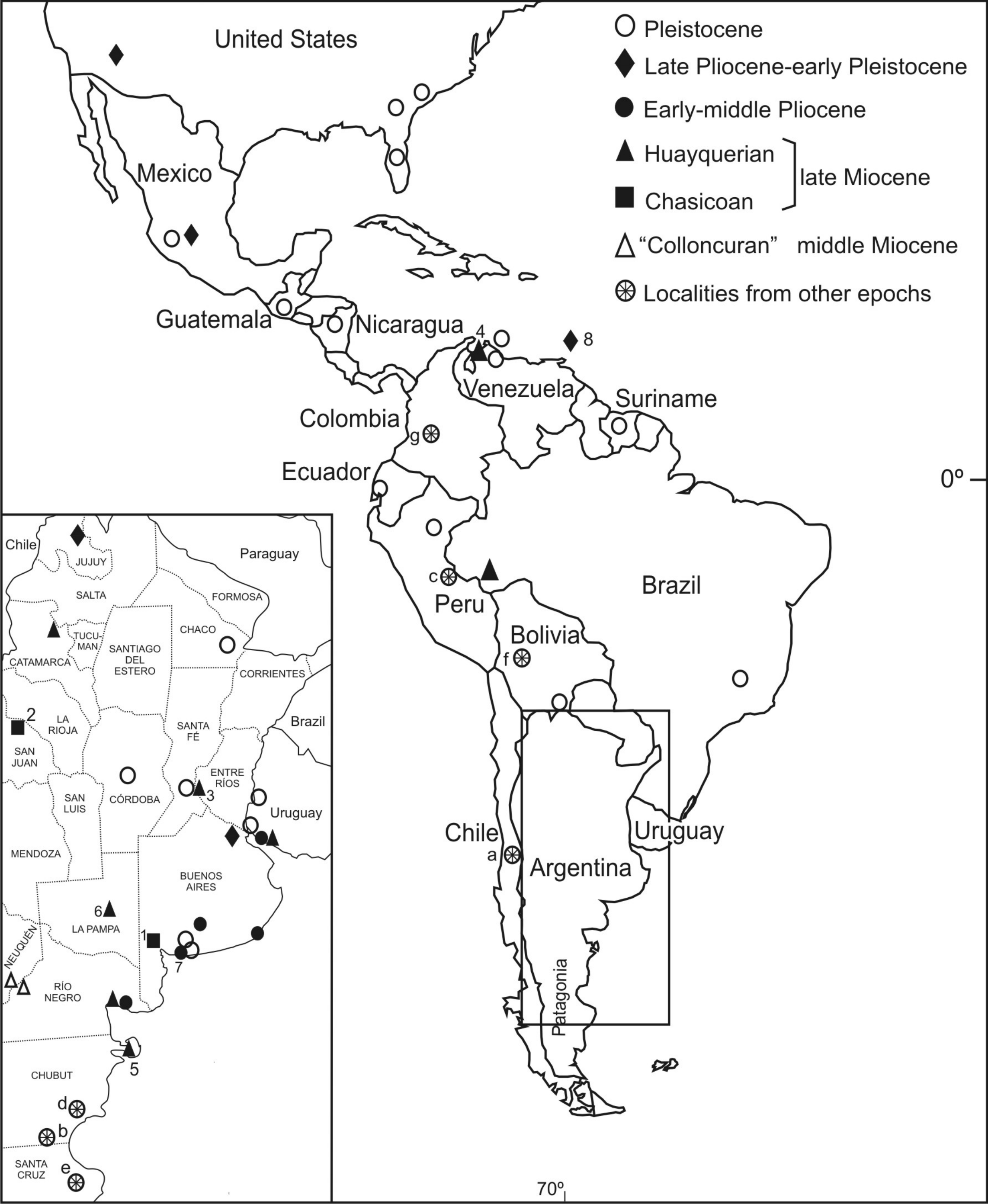
Antarctic Glaciation
Late Oligocene warming
Antarctic Glaciation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◆ Late Pliocene-early Pleistocene
● Early-middle Pliocene
▲ Huayquerian
■ Chasicoan
late Miocene
△ "Colloncuran" middle Miocene
⊛ Localities from other epochs
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Guatemala
Nicaragua
Venezuela
Suriname
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FORMOSA
TUCU-MAN
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CHACO
CATAMARCA
CORRIENTES
2
LA RIOJA
SANTA FÉ
Brazil
SAN JUAN
ENTRE RÍOS
SAN LUIS
CÓRDOBA
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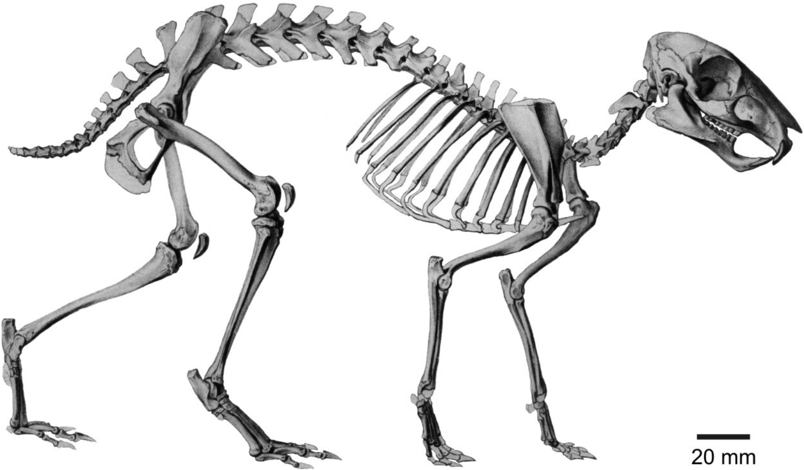
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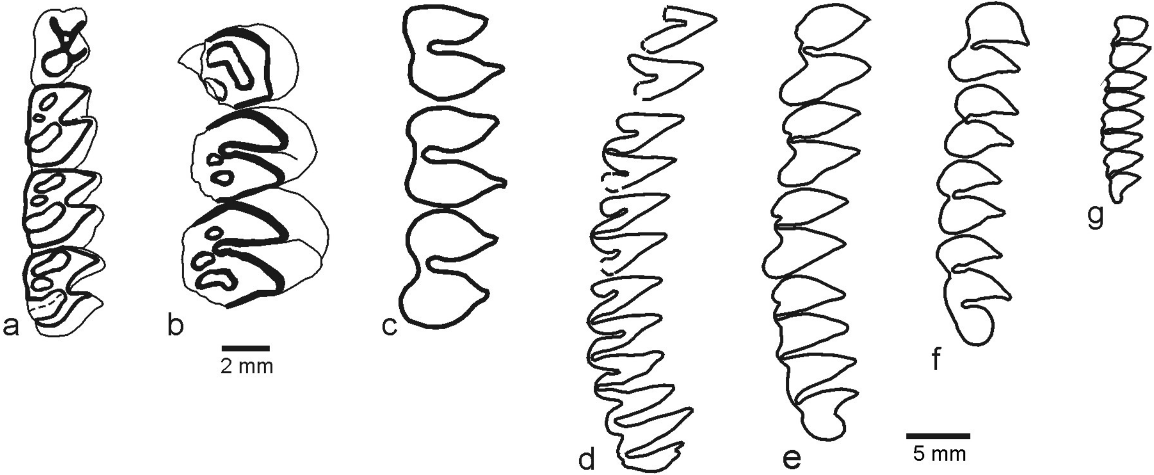
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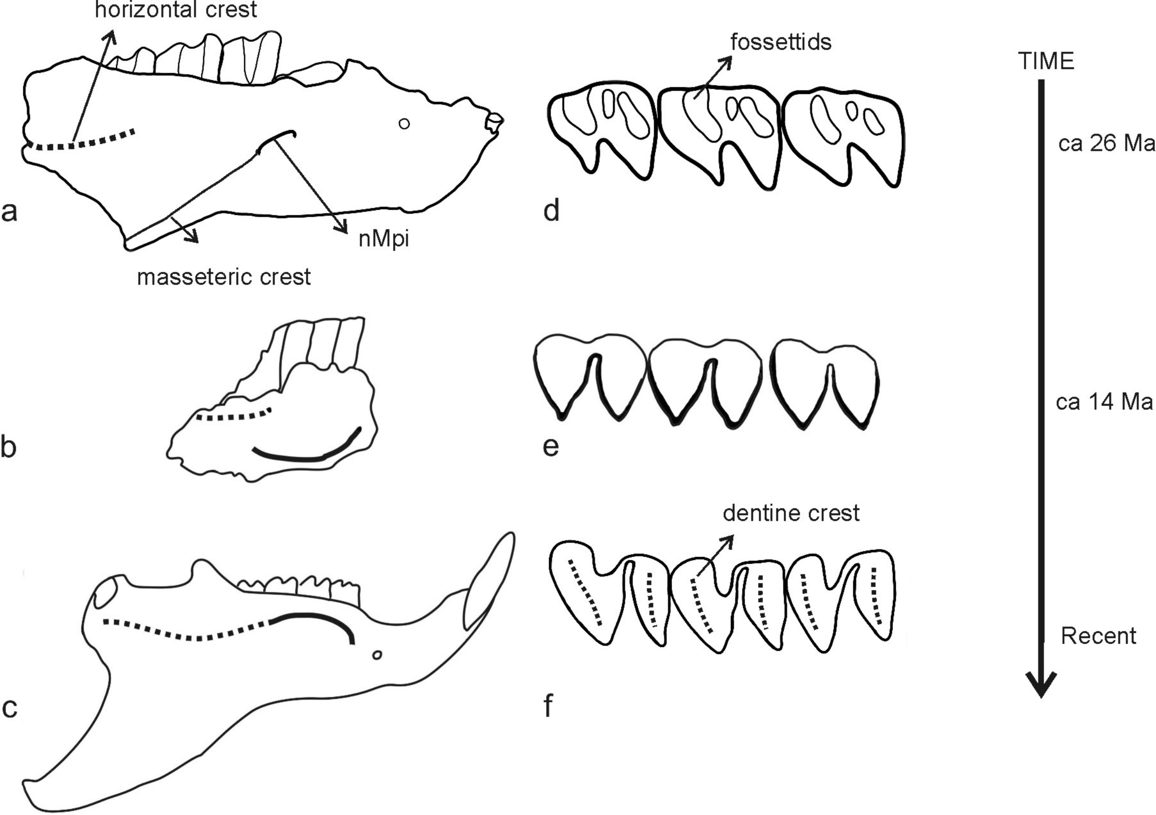
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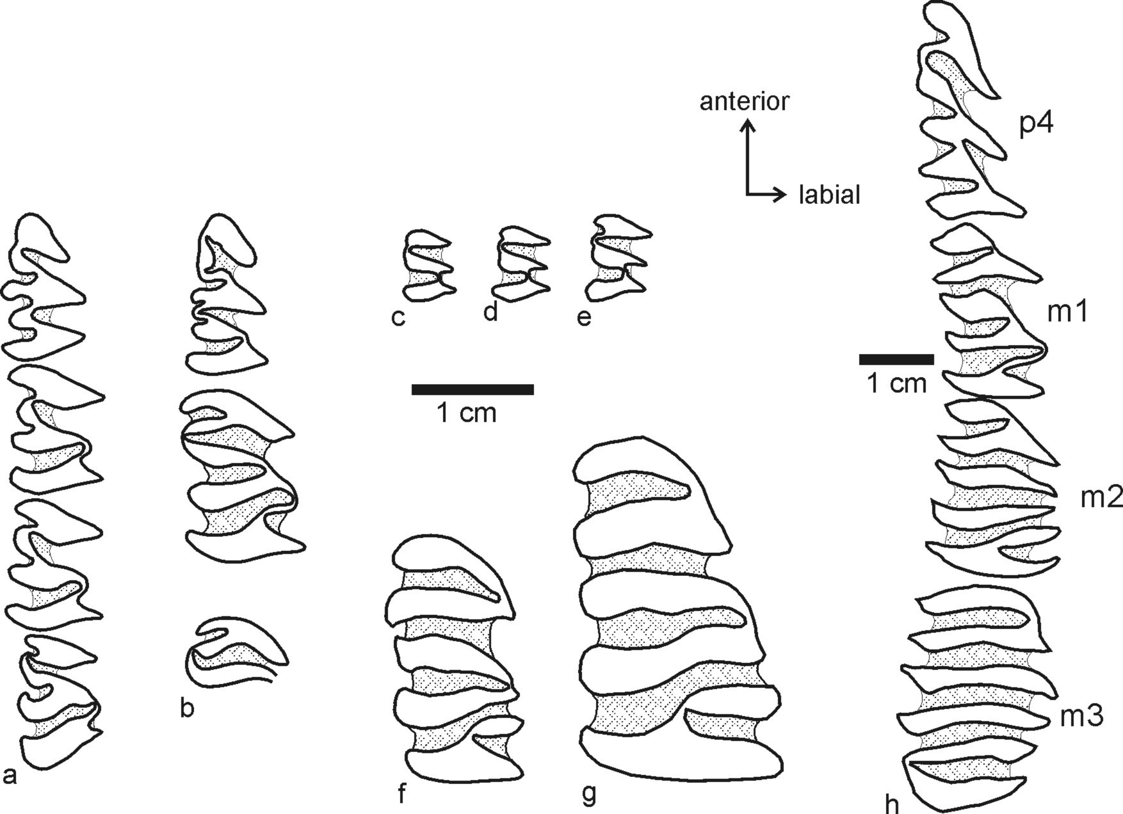
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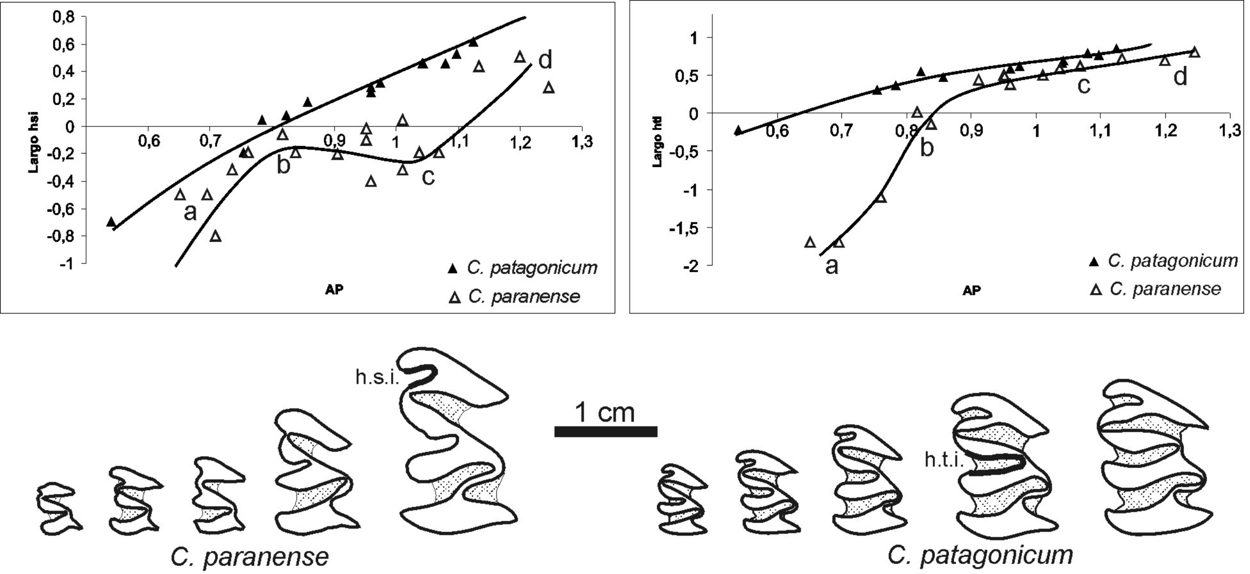
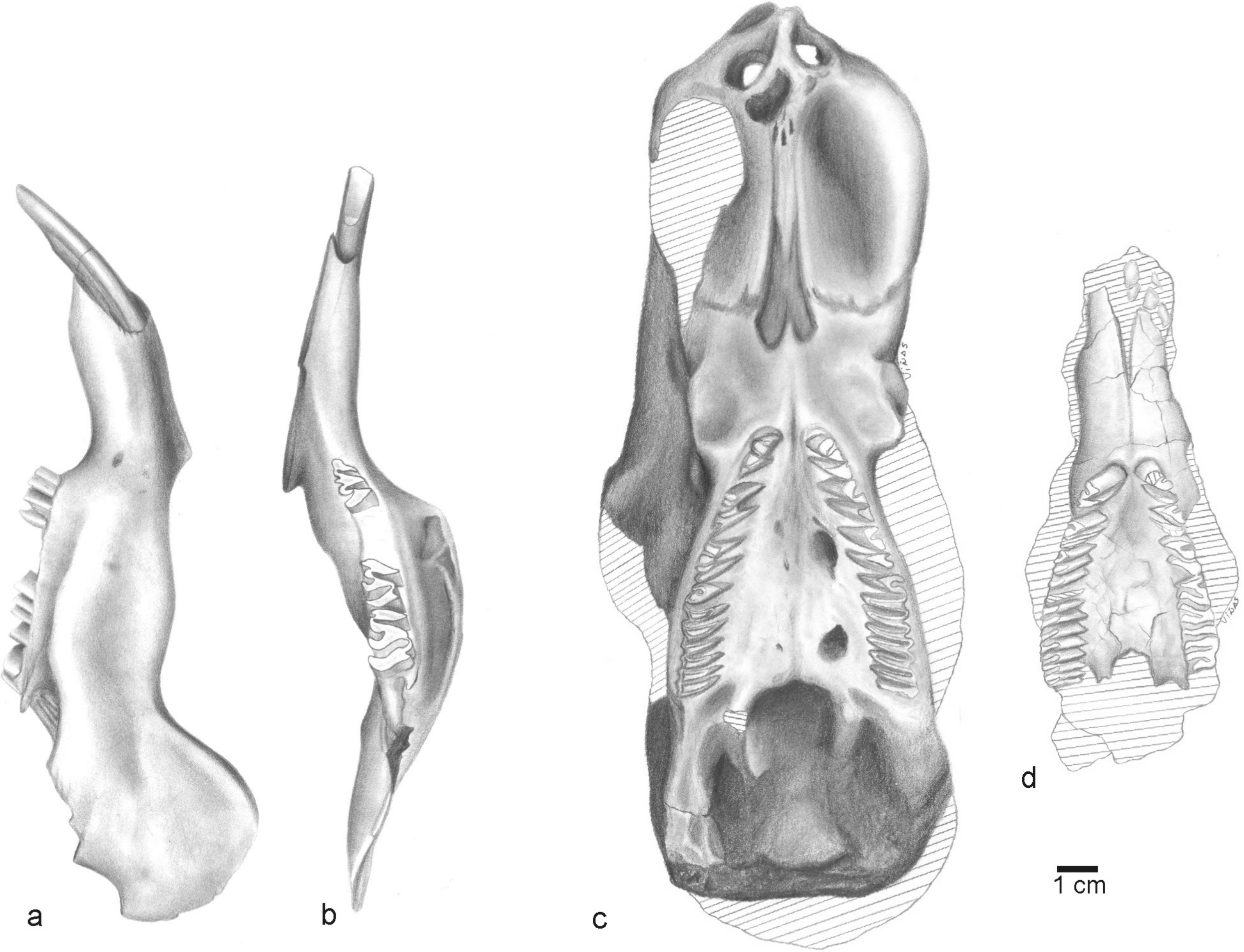
p4
m1
m2
m3
1 cm
1 cm
a
b
c
d
e
f
g
h


Largo hsi
0,8
0,6
0,4
0,2
0
-0,2
-0,4
-0,6
-0,8
-1
0,6
0,7
0,8
0,9
1
1,1
1,2
1,3
AP
a
b
c
d
▲ C. patagonicum
△ C. paranense
Largo hti
1
0,5
0
-0,5
-1
-1,5
-2
0,6
0,7
0,8
0,9
1
1,1
1,2
1,3
AP
a
b
c
d
▲ C. patagonicum
△ C. paranense
h.s.i.
1 cm
h.t.i.
C. paranense
C. patagonicum


a
b
c
d
1 cm