A NEW GUINEA PIG (RODENTIA, CAVIOMORPHA) FROM NORTHWESTERN ARGENTINA: IMPLICATIONS FOR THE ORIGIN OF THE GENUS CAVIA

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ABSTRACT—We describe a new caviomorph rodent, Cavia cabrerai, sp. nov. (Caviidae, Caviinae), from the upper levels of Andalhuala Formation (San Fernando Norte locality, Catamarca Province, northwestern Argentina), which represents the oldest fossil record of the genus. The new species differs from extant and extinct species of Cavia by a unique combination of characters: large size, proportionally anteroposteriorly elongated molars, slightly anteroposteriorly compressed prisms, relatively shallow primary lingual flexids, abundant cement in the lingual flexids, and anterolinguinal widening of the second crests of check teeth. A phylogenetic analysis indicates that Cavia cabrerai, sp. nov., is the sister taxon of extant Cavia species and displays dental characters more plesiomorphic than the latter. Some characters of C. cabrerai, sp. nov., namely, compression of prisms and depth of flexids, are morphologically intermediate between the related extinct Caviinae Palaeocavia and the extant species of Cavia. An ash bed dated at 4.72 ± 0.08 Ma that overlies the fossiliferous level of the new material supports the presence of Cavia close to the Miocene–Pliocene boundary. The origin of Cavia may have been triggered by the expansion of relatively open and arid environments that arose near the Miocene–Pliocene boundary.

http://zoobank.org/urn:lsid:zoobank.org:pub:3A6E6666-1FBE-4C6E-95CA-4B33927A414D

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The extant species of genus Cavia, usually known as guinea pigs but also called ‘cuyes,’ ‘apereás,’ ‘cuises,’ ‘cavies,’ or ‘préas,’ depending on geographical location, are caviomorph rodents that are relatively common in Neotropical mammalian communities. The wild species are essentially terrestrial and medium-sized caviids (subfamily Caviinae sensu Madoz-Jañé, 1953; Pascual and Ortega Hinojosa, 1966; Quintana, 1996, 1997). This dental morphology is more complex than that of any other non-Cavia Caviinae (e.g., Microcavia and Galea) or Dolichotinae (e.g., Dolichotis).

Three extinct species of Cavia have been described: C. galileoi Verzi and Quintana, 2005, from the late Pleistocene of Buenos Aires Province, and C. vates Winge, 1887, and C. lamigae Lock and Montenegro, 1985, both from late Pleistocene–Holocene deposits of the Lagoa Santa caves, in the Brazilian state of Minas Gerais. Fossil records of Cavia are also known from the middle Pleistocene of Uruguay (Ubilla and Alberdi, 1990) and the Holocene of diverse archeological sites throughout South America (Dunnum and Salazar-Bravo, 2010, and references therein). Fossil specimens of C. porcellus have been reported from the Quaternary of Minas Gerais (Winge, 1887) and of Cavia aperea and C. magna from the Holocene of Rio Grande do Sul, Brazil (Hadler et al., 2008). In contrast to these relatively modern fossil records, divergence estimates from molecular data indicate that the genus (crown clade) originated in the early Pliocene (4.1 ± 1.6 Ma; Opazo, 2005) or earlier, well into the late Miocene (Dunnum and Salazar-Bravo, 2010; see also Madoz-Jañé and Pérez, 2016).

In this contribution, we describe new specimens of Cavia from early Pliocene sediments corresponding to the Formation,
cropping out in San Fernando Norte locality (Belén Department, Catamarca Province, northwestern Argentina; Fig. 1A, B), which represent the oldest fossil record of the genus in South America. We discuss their taxonomic assignment to a new species and analyze their phylogenetic relationships. Based on a $^{40}$Ar/$^{39}$Ar age of $4.72 \pm 0.08$ Ma for the upper levels of Andalhuala Formation (Bonini et al., in press; Fig. 1C), which constrains the age of the fossiliferous level, we assess the early origin of the genus and the paleoenvironmental implications of the new finding.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MCH-P, Museo Arqueológico Provincial ‘Condor Huasi,’ Sección Paleontología, Belén, Catamarca, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MNHN, Museo Nacional de Historia Natural de Montevideo, Montevideo, Uruguay; MPS-Z, Museo de Ciencias Naturales ‘P. Antonio Scasso San Nicolás’, Buenos Aires, Argentina; MZUSP, Museum of Zoology of the University of São Paulo, São Paulo, Brazil; UFSC, Universidade Federal do Rio Grande do Sul, Brazil; ZMUC, Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark.

MATERIALS AND METHODS

Comparative Specimens

The new material here described is housed in the MCH-P. It was compared with specimens of extant species of *Cavia* housed in the MACN, MLP, and MPS-Z (Supplementary Data 1). Additional information on extant species of *Cavia* was obtained from the literature (Cabrera, 1953; Ximénez, 1980; Quintana, 1998; Candela and Bonini—A new guinea pig from Argentina (e1352591-2)
Cherem et al., 1999; Bonvicino et al., 2008; Cherem and Ferigolo, 2012; Dunnum, 2015; Brito and Fernández de Córdova, 2016). Data on the extinct Cavia galileoi (late Pliocene, Argentina), C. vates, and C. laminiae (Pleistocene–Holocene of Brazil) were taken from Winge (1887), Locks and Montenegro (1985), and Verzi and Quintana (2005). The type of C. vates was studied through photos provided by the curator of the Lund Collection of ZMUC. The new specimens were also compared with materials corresponding to the extant caviines (sensu Madozzo-Jaén and Pérez, 2016) Microcavia, Cavia, and Galea, and the extinct Dolicavia minuscula (Ameghino, 1908), Palaeocavia impar (Ameghino, 1888) and Palaeocavia chapalmalense (Ameghino, 1908). The comparative study of caviines was also based on information published in several contributions (Ameghino, 1888, 1889, 1908; Kraglievich, 1930, 1940; Cabrera, 1953; Pascual and Ortega Hinojosa, 1966; Quintana, 1996, 1997, 1998; Verzi and Quintana, 2005; Madozzo-Jaén and Pérez, 2016). Dental nomenclature follows Quintana (1996), Madozzo-Jaén and Pérez (2016), and Verzi and Quintana (2005). Measurements were taken in mm.

Other Abbreviations—AWPP, anterolingual widening in anterior crest of posterior prism of teeth; HPI, primary internal flexid (= lingual flexid).

Body Mass

Body mass (BM) of C. cabrerai, sp. nov. was estimated using the equations obtained by Legendre (1986), based on the occlusal area of m1. We compared the body mass estimated for C. cabrerai, sp. nov., with the values obtained by applying this equation to molars of two specimens of C. aperea and C. porcellus (Table 1) with known body masses (Table 2).

Phylogenetic Analysis

In order to assess the phylogenetic relationships of the new species within Caviidae, a cladistic analysis was performed using a modified version of the combined data set of Madozzo-Jaén and Pérez (2016:supplementary data 2), which originally included 54 taxa (53 cavioid taxa and one octodontoid for root-portion). 117 morphological characters, and DNA sequences from two mitochondrial (12S and Cytb) and two nuclear (Ghr and Tdh) genes from GenBank for 11 extant taxa (Madozzo-Jaén and Pérez, 2016:supplementary data 1). We included the new species C. cabrerai sp. nov. in the data set of Madozzo and Pérez (2016) (Supplementary Data 2), which was analyzed with methodology identical to the one applied by these authors. Thus, equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff et al., 2008), treating gaps as missing data for the DNA sequences; a heuristic search of 1000 Wagner tree replicates followed by tree bisection reconnection (TBR) branch swapping was conducted to find the most parsimonious trees (MPTs), collapsing zero-length branches under the strictest criterion. Unstable taxa, identified in the set of MPTs (Madozzo-Jaén and Pérez, 2016), were pruned in order to derive an informative reduced consensus. In a first analysis, we considered as ordered the same 22 multistate characters as in the original data set (Madozzo-Jaén and Pérez, 2014:supplementary data 1). In a second analysis, we also considered character 96, originally defined as 'Depth of HIP in m1–m2' with four character states: “shallow (0); up to 25% (1); up to 50% (2); reaching the labial end (3); dividing the prism (4)” (Madozzo-Jaén and Pérez, 2016:supplementary data 1), as ordered, on the basis of the increasing degrees of similarity between the character states identified for this character. The new species was scored as 2 for this character, whereas the extant Cavia species were scored as 3. In the second analysis, the character states for character 86 (i.e., ‘Shape of the anterior lobe of m1–m2’; Madozzo-Jaén and Pérez, 2016:supplementary data 1) were also modified. Based on new information provided by the study of the new species (see below), we identified five states for character 86: triangular (0); heart-shaped (1); lanceolate (leaf-shaped) (2); laminar, being less anteroposteriorly compressed than the anteroposterior diameter of the hypoflexid (3); and strongly laminar, being equally or more anteroposteriorly compressed than the hypoflexid (4). Cavia cabrerai, sp. nov., was scored as 3 for this character (as in the first analysis), whereas the extant species were scored as 4 (Supplementary Data 2).

**GEOLOGICAL SETTING AND AGE**

The San Fernando locality is situated in Belén Department, approximately 50 km north-northeast of Belén City, in northwestern Catamarca Province (Fig. 1A, B). The locality is divided into two villages: San Fernando Sur or Capillan (27°20’S, 67°53’W) and San Fernando Norte or La Villa (27°16’S, 66°54’W). The Neogene lithostratigraphic units recognized in San Fernando Norte locality, from which the new specimens were studied, are the following (Ameghino, 1888; Kraglievich, 1940; Cabrera, 1953; Pascual and Ortega Hinojosa, 1966; Quintana, 1996; 1998; Verzi and Quintana, 2005; Madozzo-Jaén and Pérez, 2016). Dental nomenclature follows Quintana (1996), Madozzo-Jaén and Pérez (2016), and Verzi and Quintana (2005). Measurements were taken in mm.

**TABLE 1.** Mandibular and lower cheek teeth measurements (in mm).

| Dimension        | Cavia cabrerai, sp. nov. MCH-P 170 | C. cabrerai, sp. nov. MCH-P 196 | C. galileoi MACN 19721 | C. aperea MPS-Z 211 | C. porcellus MPS-Z 212 | C. magna AMNH 235998*
|------------------|-----------------------------------|---------------------------------|----------------------|----------------------|------------------------|----------------------|
| APL p4           | 4.22                              | 3.38                            | 3.20                 | 4.04                 |                        |                     |
| AW p4            | 2.75                              | 2.36                            | 2.62                 |                      |                        |                     |
| PW p4            | 3.40                              | 3.05                            | 2.88                 | 3.14                 |                        |                     |
| APL m1           | 4.44                              | 4.17                            | 4.16                 | 3.22                 | 3.70                   |                     |
| AW m1            | 3.81                              | 3.46                            | 3.27                 | 3.22                 | 3.46                   |                     |
| PW m1            | —                                 | 3.44                            | 3.62                 |                      |                        |                     |
| APL m2           | 4.36                              | 3.29                            | 3.64                 |                      |                        |                     |
| AW m2            | 3.24                              | 3.24                            | 3.53                 |                      |                        |                     |
| PW m2            | —                                 | 3.56                            |                      |                      |                        |                     |
| APL m3           | ca. 4.52                          | 3.25                            | 4.01                 |                      |                        |                     |
| AW m3            | —                                 | 3.08                            | 3.63                 |                      |                        |                     |
| PW m3            | —                                 | 3.21                            | 3.74                 |                      |                        |                     |
| P4–m3 length     | ca. 18.10                         | 13.29                           | 16.60                | 16                   |                        |                     |
| m1–m3 length     | ca. 13.89                         | 9.76                            | 11.40                |                      |                        |                     |
| Lower diastema length | ca. 14.70         | 12.27                           | 12.63                |                      |                        |                     |
| Mandibular height | 7                                | 5.94                            | 6.64                 |                      |                        |                     |

**Abbreviations:** APL, anteroposterior length; AW, anterior width; PW, posterior width.

*From Ximénez (1880).

**Taken at diastema level in front p4.**
here described were collected, comprise, from base to top: the Las Arcas, Chiquimil, Andalhaulua, and Corral Quemado formations, and the ‘Punachotter’ unit, the Andalhaulua Formation being the most extensive unit in the area (Fig. 1C) (Muruaga, 2001a, 2001b; Bossi and Muruaga, 2009; Bonini and Georgieff, 2013). The upper levels of Andalhaulua Formation are the fossiliferous beds that have yielded the new materials studied here. These specimens were collected from facies of brown sandstone with fine to coarse grain size, with trough lenticular cross-stratified sandstones interbedded with facies of tabular reddish siltstone with massive stratification, which can be identified as channel deposits and/or sandbars (Bridge et al., 2000; Bridge and Demico, 2008; Bonini et al., in press). These sedimentary levels lie approximately 18 m below a level that has yielded an age of 4.72 ± 0.08 Ma and 45 m above another level with an age of 4.79 ± 0.15 Ma, according to Ar39/Ar40 dating (Bonini and Brandoni, 2015; Bonini et al., in press Fig. 1C). From these absolute ages, and assuming that deposition has remained constant and uninterrupted, the sedimentation rate was estimated at 0.78m/ka for these levels. On this basis, an age of approximately 0.15 Ma, according to Ar39/Ar40 dating (Bonini and Madozzo-Jaén, 2016; Fig. 2A). The mental foramen (visible in lateral view) is located above the dorsoventral midpoint of the lateral surface of the dentary and opens dorsolaterally. The anterior portion of the mandibular symphysis is higher than the level of the alveolar borders of the cheek teeth, and its posterior end is anterior to the p4 (Fig. 2B).

**Dentition**—Similar to the other species of Cavia, C. cabrerai, sp. nov., has euhyopsodont cheek teeth formed by two prisms (lobes) connected by a short and narrow lingual isthmus, which represents the bottom of the hypoflexid (Fig. 2C). The lingual isthmus is formed by a double layer of enamel filled with dentine. This isthmus is posterolabially connected with the crest posterior to the hypoflexid (= anterior crest of the posterior prism), which is more labiolingually extensive than that of Palaeocavia (Verzi and Quintana, 2005). In the new species, the hypoflexus extends across the tooth beyond the midpoint of the crown and is less penetrating than in extant species of Cavia and C. lamigae. The latter species presents a thinner lingual isthmus (Lock and Montenegro, 1985), as in extant species, in which this isthmus is formed by a single layer of enamel. In all cheek teeth, the hypoflexid is narrow and long and contains abundant cement, as in other species of the genus. Similarly to the extinct Cavia vates and C. galileoi, the cheek teeth of C. cabrerai, sp. nov., display a less laminar occlusal pattern, i.e., its anterior and posterior prisms are less anteroposteriorly compressed than those of the extant species and C. lamigae. The enamel is thicker on the labial border of the prisms and reduced on the lingual surfaces, as in other species of the genus (Madozzo-Jaén and Pérez, 2016). In all cheek teeth, the primary internal flexid (HPI) is narrower and shallower (extending to ca. 50% of

**Comparative Description**

Based on the dental measurements (Table 1) and estimated body mass (Table 2), as well as information provided by bibliographic research, Cavia cabrerai, sp. nov., may be considered as the largest known species of the genus.

**Mandible**—The set of mandibular features is similar to that of other species Cavia. The anterior-most margin of the diastema, corresponding to the alveolar border of the incisor, is missing. Its anterior end projects above the level of the alveolar border of p4. The diastema is shorter than the p4–m3 length (Fig. 2; Table 1), and a well-developed posterovenal projection of the mandibular symphysis is visible in lateral view (exposed in lateral view; Madozzo-Jaén and Pérez, 2016; Fig. 2A). The mental foramen (visible in lateral view) is located above the dorsoventral midpoint of the lateral surface of the dentary and opens dorsolaterally. The anterior portion of the mandibular symphysis is higher than the level of the alveolar borders of the cheek teeth, and its posterior end is anterior to the p4 (Fig. 2B).

**TABLE 2.** Body mass (in grams) of specimens of different species of Cavia.

| Species          | Body mass | C. aperea | C. porcellus | C. magna Holotype | C. magna | C. intermedia |
|------------------|-----------|-----------|--------------|-------------------|----------|---------------|
| **Known BM**     | 1299.7    | 658.9     | 614          | 860               | 760      | 790           |
| **Estimated BM** | 1299.7    | 658.9     | 614          | 860               | 760      | 790           |

**Abbreviation:** BM, body mass.

*From Ximénez (1980).

**From Cherem et al. (1999).
the total tooth width) than in extant species, resembling C. vates. In MCH-P 196 (Fig. 2C), HPI is less anterolingually oriented and somewhat deeper than the HPI of the holotype. Unlike C. galileoi (Verzi and Quintana, 2005), and as in living species, the HPI contains abundant cement (we were not able to corroborate the existence of cement in the HPI of cheek teeth of C. vates).

The p4 is longer than wide and somewhat shorter than the m1, being proportionally larger than that of C. galileoi (Verzi and Quintana, 2005). In C. cabrerai, sp. nov., the anterior prism of p4 is slightly elongated anteriorly, being similar in shape to that of some living specimens of Cavia, but more developed than the latter, and differing from the p4 of C. vates, C. galileoi (Verzi and Quintana, 2005:fig. 4), and Palaeocavia impar (Madozzo-Jaén and Pérez, 2016). In the later species and most of the specimens of extant species examined, the anterior prism of p4 is markedly obliquely oriented and not anteriorly projected. The anterior elongation (= additional elongation) of p4 of C. cabrerai, sp. nov., is not clearly delimited by a labial flexid, unlike the condition in other cavines (Microcavia, Galea) in which this labial flexid is well developed. The degree of development of the anterior elongation of the p4 seems to be a variable feature within the genus Cavia (Verzi and Quintana, 2005:fig. 1F, H) and even within the same species (Cavia aperea), but in the latter this projection does not reach the degree of development of C. cabrerai, sp. nov. In C. cabrerai, sp. nov., the hypoflexid is narrow, long, and delimited by sinuous walls. The anterior crest of the posterior prism (posterior to the hypoflexid) has an anterolingual widening (AWPP), such as the one that characterizes the living species (Verzi and Quintana, 2005), distinguishing them from C. galileoi, C. vates, and Palaeocavia (Madozzo-Jaén and Pérez, 2016).
The m1–m3 are somewhat longer than wide and proportionally narrower than those of living species (Table 1). The anterior prisms of m1–m3 are more anteroposteriorly extended than the anteroposterior diameter of the hypoflexid of these teeth (i.e., in m1–m3 of the holotype, the anteroposterior diameter of the anterior prism is about twice the anteroposterior diameter of the hypoflexid; Fig. 2C; in MCH-P 196, the hypoflexid is somewhat more open labially than that of the holotype; Fig. 2D). On the other hand, in extant species, the anterior prism of the m1–m3 is subequal to the hypoflexid in anteroposterior diameter. Thus, in *C. cabrerai*, sp. nov., the anterior prisms are much less laminar in shape than those of extant species and resemble those of *C. vates* and *C. galileoi*. In turn, the anterior prisms of the m1–m3 are more laminar (i.e., more anteroposteriorly compressed) than the posterior prisms. The posterior borders of the anterior prisms of the m1–m3 are slightly concave posteriorly (a feature more evident in the holotype than in MCH-P 196). As in extant species, the m1–m3 of the holotype have a well-defined AWPP (Verzi and Quintana, 2005), more so than that of MCH-P 196. This feature differs from the condition in the extinct *C. galileoi* (Verzi and Quintana, 2005) and *C. vates*, which lack AWPP and present a lingually narrow second crest in all cheek teeth. The AWPP of the molars in *C. cabrerai*, sp. nov., is more developed than that of the p4. Unlike in extant species and *C. galileoi*, the posterior crest of the posterior prism in all teeth is more anteroposteriorly extended than the HPI (i.e., the posterior crest is about twice the anteroposterior diameter of the HPI). Consequently, as noted

![FIGURE 3. Schematic comparative drawings of m1–m3 of *Palaeocavia* and *Cavia* in occlusal view. A, *Palaeocavia chapalmalense*, MACN 15307, left m1–m3 reflected. B, *Cavia cabrerai*, sp. nov., MCH-P 170, holotype, right m1–m3. C, *Cavia cabrerai*, sp. nov., MCH-P 196, right m1? D, *Cavia aperea*, MPS-Z 209, left m1–m3 reflected. Black: enamel; gray: cement; white: dentine. Abbreviations: An, anterior; Li, lingual. Scale bar equals 10 mm.](image)

![FIGURE 4. Reduced consensus from the second cladistic analysis (ignoring the fossil taxon *Microcardiodon huemulensis*), showing the node Cavii-dae. A, node Cavii; B, node of extant *Cavia* species. The phylogenetic tree was calibrated against the first appearance of taxa in the fossil record (modified from Pérez and Pol, 2012). Abbreviations: Bon, Bonacrian; Calab, Calabrian; Chap, Chapadmalalan; ‘Coll’, Colloncuran; Ens, Ensenadan; Gel, Gelasian; H, Holocene; Hu, Huayquerian; Luj, Lujanian; ‘M’, ‘Mayoan’; M, Middle; Ma, megaannum; Marp, Marplatana; Mo, Montehermosan; Place, Piacenzian; Sa, Santacrucian; SALMAs, South American Land Mammal ages; SASA, South American Stage ages.)](image)
above, the cheek teeth of *C. cabrerai*, sp. nov., are less laminar than those of extant species, a condition that the new species shares with *C. vates*.

**Body Mass**

*Cavia magna* is the largest living wild species of *Cavia*, with an average body mass of 635 g for adult males, and reaching up to 840 g (Ximénez, 1980:table 1; Table 2). The maximum p4–m3 length (adult males) of *C. magna* reaches 16.8 mm (Ximénez, 1980:table 1). Although the posterior margin of the m3 is not completely preserved in the holotype of *C. cabrerai*, sp. nov., the remaining posterior face of this tooth indicates that p4–m3 length was at least 17.5 mm (Table 1). In addition, the lower diastema length and mandibular height (taken at diastema level) are greater than those of *C. magna* (Table 1; see also Ximénez, 1980:table 1). In all comparable dimensions, *C. cabrerai*, sp. nov., is larger than specimens of *C. aperea*, *C. porcellus*, or *C. magna* (see Table 1). In agreement with its relatively large dimensions, the BM estimated for *C. cabrerai*, sp. nov., is above 1200 g, larger than the extant wild species of *Cavia* (Table 2). The body masses estimated for two specimens of *C. porcellus* and *C. aperea* (calculated using the equation of Legendre, 1986) were consistent with their known BM (Table 2). These results support the estimated BM for *C. cabrerai*, sp. nov. On this basis, *C. cabrerai*, sp. nov., is characterized as larger than all extant wild species of *Cavia* as well as the extinct *C. galileoi*, *C. lamin-gue*, and *C. vates* (Lock and Montenegro, 1985:table 2; Table 2).

**DISCUSSION**

**Systematics of Cavia cabrerai, sp. nov., and Significance of Dental Features**

Using the character-based concept to define *Cavia*, the following traits described for *C. cabrerai*, sp. nov., support its inclusion in this genus (Kraglievich, 1930; Pascual and Ortega Hinojosa, 1966; Quintana, 1997, 1998; Verzi and Quintana, 2005; Madozzo-Jaén and Pérez, 2016): (a) second crest of molars (i.e., first crest of second prism) wider than that of the Caviinae *Palaecocavia*, *Doli-cavia minuscula*, *Galea*, and *Microcavia*; (b) tendency toward lamination of the prisms; (c) primary lingual flexid deeper than in other genera of Caviinae; (d) anterolingual widening in the anterior crest of the posterior prism of the teeth (= AWPP); and (e) hypoflexid deeper and narrower than other genera of Caviinae. Note that some of these characters are recovered as synapomorphies (characters 86 state 3 and 101 state 2) at the node that contains new fossil and extant species of *Cavia* (see below).

The prisms in the new species are more anteroposteriorly compressed, and the flexids are deeper (revealing a clear tendency toward tooth lamination) than any other non-*Cavia* Caviinae (such as *Microcavia*, *Galea*, or *D. minuscula*). In contrast to *Microcavia*, *Galea*, *D. minuscula*, *Palaecocavia*, the extinct *Cavia galileoi* (Verzi and Quintana, 2005), and *C. vates* (Winge 1887), *C. cabrerai*, sp. nov., presents a well-differentiated AWPP.

Additionally, at least three features of *C. cabrerai*, sp. nov., present an intermediate condition between the extinct species *Palaecocavia impar*, *P. chapalmalense*, and *Palaecocavia? mawka* and the extant species of *Cavia* (Fig. 3A–D): (1) degree of tooth lamination: prisms are more compressed anteroposteriorly than those of *Palaecocavia* but less than those of extant *Cavia* species (Quintana, 1998; Verzi and Quintana, 2005); (2) a primary lingual flexid (HPI) narrower and shallower than that of extant species of *Cavia*, and deeper than that of *Palaecocavia* (Fig. 3A–D).

The high degree of anteroposterior compression of the prisms, the great depth of the HPI and the hypoflexid, the lingual isthmus formed by a single layer of enamel, and the well-defined wapp seem to be non-independent features related to the acquisition of a laminar occlusal pattern. *Cavia cabrerai*, sp. nov., shows a lesser degree of tooth lamination than the extant species.

In summary, the analysis of the dental characters supports the inclusion of *C. cabrerai*, sp. nov., within *Cavia* and indicates that this species displays a more primitive dental morphology than the extant species of the genus.

**Cladistic Analyses**

The results of our phylogenetic analyses include the new species in the genus *Cavia* (following character-based definition of this genus; see above). In the first analysis, using the same character-state coding as in the original data set (Madozzo-Jaén and Pérez, 2016), the parsimony analysis resulted in 136 most parsimonious trees (MPTs), of 3246 steps (consistency index [CI] = 0.64; retention index [RI] = 0.55). In all MPTs, *C. cabrerai*, sp. nov., is within the clade that contains the extant *C. tschudii* and *C. aperea*. However, the relationships among *Cavia* species are not resolved, and in the strict consensus obtained by Madozzo-Jaén and Pérez (2016:supplementary data 3).

Our second phylogenetic analysis resulted in 136 most parsimonious trees (MPTs) of 3248 steps (CI = 0.643; RI = 0.55), in which *C. cabrerai*, sp. nov., was recovered as the sister taxon of the extant species of *Cavia*. In the reduced consensus (Supplementary Data 4; Fig. 4) obtained from this analysis (ignoring alternative positions taken by the unstable taxon 22, *Microcaddion huemulensis*; see Madozzo-Jaén and Perez, 2016), the position of *Cavia* species in the context of Caviinae is indicated. In all MPTs the clade formed by *C. cabrerai*, sp. nov., and extant species of *Cavia* (node A in Fig. 4) is supported by four unambiguous synapomorphies: shape of the anterior lobe of m1–m2 laminar, being less anteroposteriorly compressed than the anteroposterior diameter of the hypoflexid (character 86 state 3); depth of HPI in m1–m2 up to 50% of the teeth (character 96 state 2); hypoflexid narrow and very long (character 100 state 2); and relative size of lower molars subequal (character 103 state 3). The clade of extant *Cavia* species (node B in Fig. 4) is supported by two unambiguous synapomorphies: shape of the anterior lobe of m1–m2 strongly laminar, being more anteroposteriorly compressed than the hypoflexid (character 86 state 4); and HPI in m1–m2 reaching the labial end of the teeth (character 96 state 3). The remaining topology of the strict consensus is the same as obtained in the first analysis and that of Madozzo-Jaén and Pérez (2016). The character-state changes of the characters 86 and 96 indicate that *Cavia cabrerai*, sp. nov., has a molar morphology that is plesiomorphic with respect to that of extant species of the genus.

**Earliest Occurrence of Cavia: Molecular and Paleontological Data**

*Cavia cabrerai*, sp. nov., represents the oldest species attributable to this genus. So far, the oldest record of *Cavia* (*C. galileoi*) was for the late Pliocene (Verzi and Quintana, 2005). Opazo (2005) estimated 4.1 ± 1.6 Ma for the divergence of extant *Cavia* species. A later molecular systematic study of several *Cavia* species estimated the origin of the genus (crown clade) to have taken place in the late Miocene (Dunnum and Salazar-Bravo, 2010). The latter authors proposed that *Cavia magna* would have originated earlier than other species of the genus, at 6.2 (4.7–7.9) Ma, whereas the split between the lineages leading to *C. aperea* and *C. tschu-dii* was estimated at 4.7 (3.4–6.3) Ma, close to the Miocene–Pliocene boundary. The absolute age of an ash bed that overlies *C. cabrerai*, sp. nov., dated at 4.72 ± 0.08 Ma (Bonini et al., in press), and the estimated age of *C. cabrerai*, sp. nov.
Paleoenvironmental Implications

_Cavia_ specimens were not recovered at the intensively prospected sediments of the Las Arcas and Chiquimil formations, nor at the lower and middle levels of the Andalhuaila Formation, outcropping in northwestern Argentina (Riggs and Patterson, 1939; Marshall and Patterson, 1981; Bossi et al., 1987; Bonini, 2014; Esteban et al., 2014; Bonini et al., 2015). Thus, the appearance of specimens of _Cavia cabrerai_, sp. nov., at San Fernando Norte suggests that this species is close to the earliest occurrence of this genus in northwestern Argentina.

It recently was recognized that the evolutionary history of _Cavia_ species seems to have been closely linked to the rise of the Andes as well as environmental changes occurring across South America (Dunnun and Salazar-Bravo, 2010). It is possible that the earliest speciation events of _Cavia_, involving the origin of _C. cabrerai_, sp. nov., were triggered by increasing seasonality and consequent expansion of relatively more arid conditions and open areas close to the Miocene–Pliocene transition (Pascual et al., 1996; Cerling et al., 1997; Zachos et al., 2001; Ortiz-Jaureguizar and Cladera, 2006). Isotopic (Latorre et al., 1997; Kleinert and Strecke, 2001, Bossi and Muruaga, 2009; Hynek et al., 2012), paleobotanic (Anzótegui et al., 2007; Garralla et al., 2016), sedimentological (Bossi et al., 1999; Muruaga, 1999, 2001a, 2001b; Bossi and Muruaga, 2009; Bonini et al., in press), and tectonic (Bossi et al., 2001; Bossi and Muruaga, 2009) studies carried out near the study area support the idea of climatic deterioration as a consequence of the rising of mountain chains east of San Fernando Norte, near the Miocene–Pliocene boundary.

In this context, it is interesting to note that _Cavia_ has laminar and more complex cheek teeth, possessing more interlaminate cement than the living and extinct small- to middle-sized non- _Cavia_ caviines and dolichotines (Microcavia, Galea, Palaeocavia, Dolicavia, and Orthomyctera). Dental complexity (sensu Evans et al., 2007) is correlated to diet and ability to process food. Consequently, compared with _Microcavia, Dolicavia, and Palaeocavia_, the greater complexity of the cheek teeth of _Cavia cabrerai_, sp. nov., can be interpreted as a way of increasing the mechanical capacity to process relatively demanding foods. _Cavia cabrerai_, sp. nov., seems to have had specialized teeth that were better adapted to consume more abrasive food items than the other extinct caviines. The hypsodonty and crown complexity, with abundant cement, of _Cavia cabrerai_, sp. nov., could be related to abrasive particle consumption (e.g., sand, dust, or volcanic glass) adhering to the surface of food or accidentally ingested, as inferred for other extinct and extant hypsodont mammals (Janis, 1988; Damuth and Janis, 2001; Jardine et al., 2012; Candela et al., 2013; Reguero et al., 2015, and references herein). In this framework, the appearance of _Cavia_ in northwestern Argentina could have been triggered by the expansion of relatively open savanna-like environments and increasingly arid conditions developed under climatic seasonality in the Andean region near the Miocene–Pliocene boundary. Note that the first appearance of the genus during the late Pliocene in the most austral latitudes of Buenos Aires Province was also associated with the expansion of arid environments (Verzi and Quintana, 2005). Future investigation is needed to assess if the appearance of _Cavia cabrerai_, sp. nov., at the Miocene–Pliocene boundary of northwestern Argentina is coincident with other species appearances or disappearances.

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