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RESEARCH ARTICLE

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Identification of guinea pig remains in the Pucará de Tilcara (Jujuy, Argentina): Evidence in favour of the presence of the Andean breed in the Quebrada de Humahuaca

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Abstract

In this article, we identified rodent remains found in the Pucará de Tilcara, an archaeological site from the Argentine Northwest that was occupied by humans from 1,100 AD until the Spanish conquest. The zooarchaeological analyses were carried out using anatomical descriptions and geometric morphometric analyses of the dorsal and ventral views of mandibular remains. The results and the archaeological context discussed showed that all the rodent remains could correspond to the Andean breed of domestic guinea pigs. The combination of the methods used here gave us a strong support to the taxonomical assignment. The presence of domestic guinea pigs in archaeological sites of the northwestern Argentina was never proposed. This approach allowed us to increase knowledge about the distribution of caviines in the region, and their relationship to anthropic processes.

KEYWORDS

Caviinae, geometric morphometrics, Hispanic-Indian period, northwestern Argentina, zooarchaeology

1 | INTRODUCTION

The domestic guinea pig is an animal with a great participation in the social life of the current Andean human groups. Some ethnographic works link the use of this animal to different social practices that includes its consumption as food, as well as its participation in the ceremonial sphere or for medicinal purposes (e.g., Archetti, 1997; Gade, 1967; Guaman Poma de Ayala, 1956; Morales, 1995; Rofes & Wheeler, 2003). The archaeological records of the domestic guinea pig allow us to infer that this would have also happened in the past. The domestication of wild guineas pigs would have occurred at some moment between 5,500 BC and 2,500 BC in the highlands of Peru, in the area of Ayacucho (Spotorno et al., 2006, 2007, 2004; Walker, Soto, & Spotorno, 2014; Wing, 1986). According to recent phylogenetic studies, the most supported hypothesis establishes that the domestic guinea pig, *Cavia porcellus* (Caviinae, Caviidae, Hystricomorpha; Patton, Pardiñas, & D'Elía, 2015), originated from the montane guinea pig, *Cavia tschudii* (Dunnum & Salazar-Bravo, 2010; Kimura et al., 2015; LeFebvre & deFrance, 2014; Spotorno et al., 2007).

Cavia tschudii is distributed from Peru to the Northwest region of Argentina in humid grassland environments, in some cases near rivers, from sea level to 4,500 m asl (Patton et al., 2015; Redford & Eisenberg, 1992). Specifically in Argentina, *C. tschudii* records are scarce and are distributed across the provinces of Catamarca, Tucumán, Salta and Jujuy (Ortiz & Jayat, 2012). In Jujuy, its presence only has been registered in the eastern part of the province, near the towns of El Palmar, Duraznillar, Yala and El Duraznillo (Díaz &

Barquez, 2007; Ortiz & Jayat, 2012). These records, as well as others in Argentina, are associated to high-altitude grasslands and humid forests of the Yungas (mountain jungles of Argentine Northwest; NWA), where *C. tschudii* frequently inhabits burrows (Ortiz, 2003; Ortiz & Jayat, 2012; Redford & Eisenberg, 1992). The other wild caviine species present in Jujuy are *Cavia aperea*, *Galea musteloides*, *Microcavia australis* and *M. shiptoni*.

On the other hand, by the time the Spaniards arrived to American continent, the geographic distribution of the domestic species ranged from the Venezuelan Northwest to the central sector of Chile, which is broader than the species distribution today (Gade, 1967). Latcham (1922) suggested that the distribution of *C. porcellus* in the central sector of Chile could probably be due to a diffusion by the Inca Empire to the Araucanians. In a recent work, it was proposed that this species would be comprised of two domesticated lineages, one European and the other Andean (Spotorno et al., 2007). It is important to emphasize that the current European domestic lineage differs greatly from the Prehispanic *C. porcellus* lineage and even from the current South American one, the latter being more similar morphologically and perhaps in their genetics with respect to their wild ancestor *C. tschudii* (Spotorno et al., 2007). These authors suggested that the archaeological mummies of guinea pigs could be considered as an intermediate between the current domestic species and the wild one, taking into account the "domestication syndrome," which is characterized by an increase in body weight, changes in the colour and size of the animal's eyes, ears and face and reduction of the size of the brain and dentition (Thorpe & Smartt, 1995; Rofes & Wheeler, 2003; Spotorno et al., 2007).

Most of the records of guinea pigs in archaeological sites in the central sector of the Andes belong to the late pre-ceramic period (2,500–1,800 BC; e.g., Izumi & Terada, 1972; Sandweiss, 1992). Some of the oldest remains found in pre-Inca contexts of the central sector of the Andes correspond to the locations of Ayamachay and Puente in Ayacucho. In these sites, a high-osteometric variability has been detected in mandibles, possibly a product of anthropic manipulation by 5,500 BC (Rofes & Wheeler, 2003). In Kotosh, the presence of *C. porcellus* was confirmed around 2,500 BC, also from osteometric analysis (Wing, 1972, 1975, 1977, 1986). On the other hand, buried domestic guinea pigs discovered at the Chavín de Huantar site were placed in the late Janabarriu phase 400–200 BC (Burger, 1992). Lumbreras (1989) found remains of this species assigned to the Urabarriu phase (1,000–500 BC) in the Old Temple of Chavín. In the archaeological site of El Yaral, South of Peru in the middle valley of the Osmore River basin ascribed to the late period, 112 mummified domestic guinea pigs were found buried under houses; it was proposed that they represented offerings intended to appease the wrath of the gods, ask favours or ensure the welfare of the house owner (Rofes & Wheeler, 2003).

The consumption of *C. porcellus* in the Inca Empire (1,438–1,542 AD) seems to be related more to ritual practices than to be part of the daily diet of people. One of the documented practices for seeing the future in the Inca Empire consisted of opening the animal with the nails to see their viscera and predict future events (Gade, 1967). Even some of these practices are mentioned in the early colonial chronicles. Guaman Poma de Ayala (1956) mentions the sacrifice of 1,000 white domestic guinea pigs and 100 black llamas in a central plaza in Cuzco. At present, in Peru, these animals are eaten on special occasions as the day of all souls, forming part of the practices of deep prehispanic roots (Gade, 1967).

Despite the description of the finding of caviines in archaeological sites of the Argentine Northwest (Salta, Jujuy, Tucumán, Santiago del Estero and Catamarca provinces), there are few mentions that specifically refer to *C. tschudii* or its domestic relative *C. porcellus* (e.g., Fernández Distel, 1974; Ortiz, 2003; Rodríguez Loredo, 1997). So far, most of the evidence is found in the Inca period (1,480–1,536 AD in NWA), such as the record of a mandible in Huachichocana cave III, Jujuy (Fernández Distel, 1974). Also in the Puerta de la Paya deposit, Salta, remains of *C. tschudii* were identified to be about 500 years old (Ortiz, 2003; Tonni, 1984). In the Potrero-Chaquiago site, Catamarca, five individuals of domestic guinea pigs that would have been consumed as food were identified (Rodríguez Loredo, 1997). Finally, Ortiz and Jayat (2012) mention the presence of *Cavia* cf. *tschudii* in additional places like Inca Cueva 5 and La Cueva, Jujuy.

1.1 | Pucará de Tilcara

Pucará de Tilcara is one of the most important archaeological sites in Argentina for its historical and patrimonial value. It was occupied between 1,100 AD and the Spanish conquest (Greco & Otero, 2016). It is located in the Quebrada de Humahuaca, which is a narrow valley that stretches along 120 km in north–south direction in the centre of Jujuy province connecting the Puna and the regions of low valleys and Yungas. The archaeological collections recovered in different contexts of the Pucará de Tilcara have allowed reconstructing part of the prehispanic history of the Quebrada de Humahuaca, particularly during the Inca occupation of NWA (Figure 1). It is located on an 80-m-high hill on the left bank of the Rio Grande in the central region of the Quebrada de Humahuaca site, covering 17.5 ha, almost the entire surface of the hill. During the Inca domination, it functioned as the political and productive regional centre (Otero, 2015). It is estimated that it could have been inhabited by 2,500 people, mostly dedicated to the production of handicrafts within the state economic structure.

The concentration of workers to manufacture sumptuary objects made of metal and rocks, involved the organization of the population and craft activities in houses-workshops (Otero & Tarragó, 2017). So far, more than 60 workshops distributed across different sectors of the Pucará de Tilcara were identified. After their abandonment, these spaces of work and habitation were used as burial spaces during both the Inca period and the Hispanic-Indian period (1,400–1,600 AD).

The discovery of bony remains of caviines in the Pucará motivated the development of this project. Our main goals were the studies of these remains to make their taxonomic assignments and analyse the significance of the presence and probable uses of guinea pigs in archaeological sites of Northwestern Argentina.

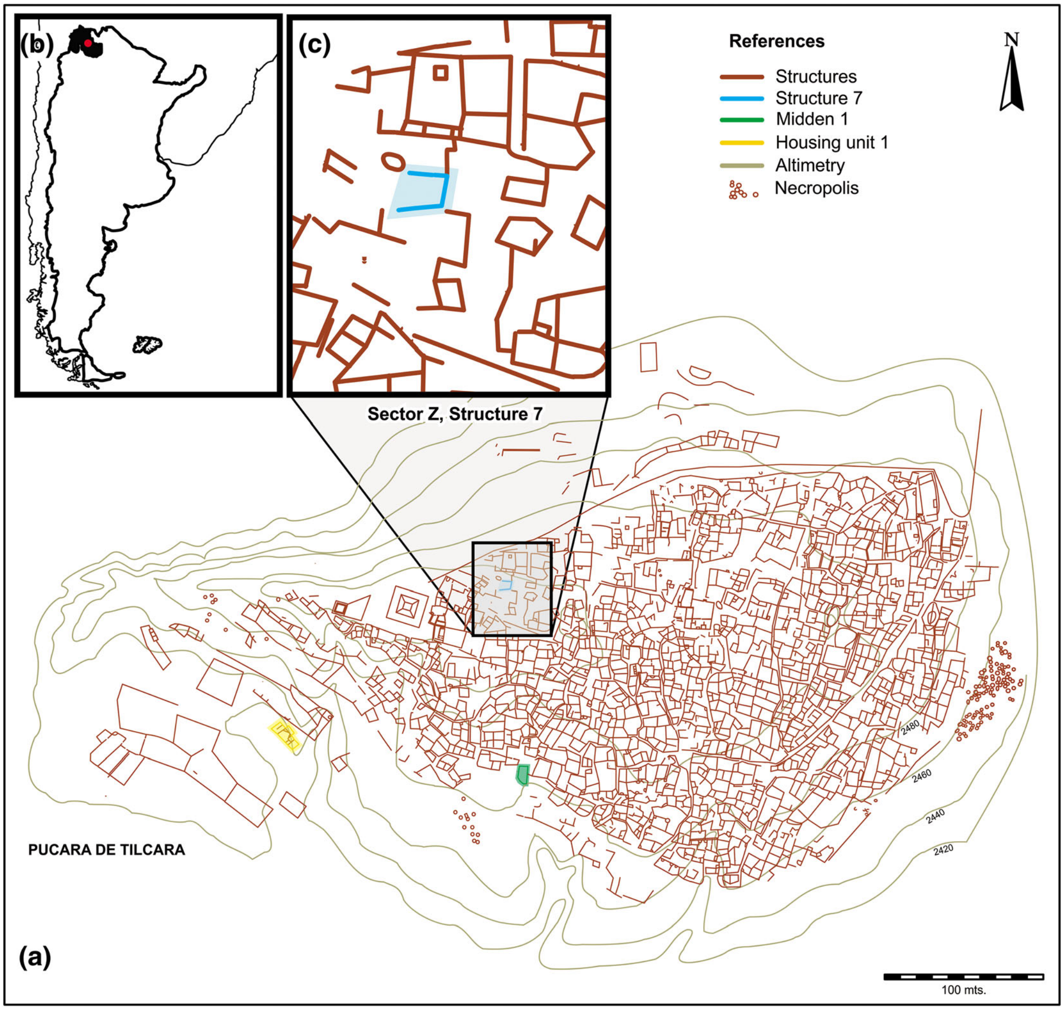

FIGURE 1 Map of Pucará de Tilcara, (a) showing structures, (b) map of Argentina and geographic location of modern Jujuy province and (c) detail of the studied structure [Colour figure can be viewed at wileyonlinelibrary.com]

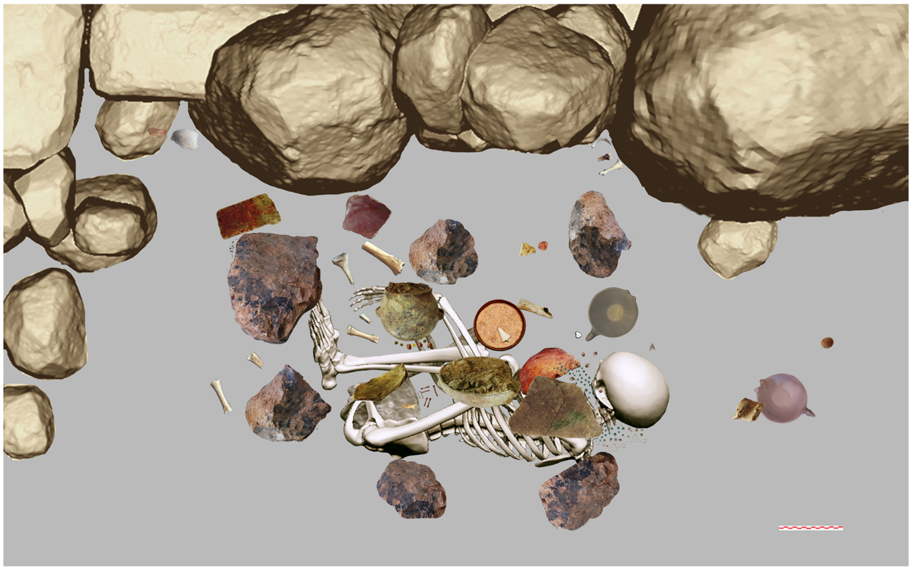

FIGURE 2 Reconstruction of Structure 7, Sector Z. Scale bar = 140 mm [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

Field work was carried out in the Pucará de Tilcara during the last decades, involving the excavation of two artisan workshops occupied during the Inca domination. In these workshop houses, remains of rodents that could refer to mortuary offerings and probably to their consumption as food were recovered. On the one hand, the Housing Unit 1, characterized as one of the large workshop-houses that are located in the Southwest Facade of the Pucará de Tilcara. On the other hand, in Structure 7 of Sector Z, we found the remains of an adult woman, whose trousseau reflects her distinctive high social status (Figures 1 and 2). This enclosure corresponded to a lapidary workshop occupied from Inca times. Among the objects and materials included as an offering, four complete ceramic vessels and numerous fragmented pieces were recovered, instruments to grind minerals, pigments, pieces of flints, malachite necklace beads and lapizlazuli, a gold and silver plate and archaeofaunistic remains (Figure 2). In order to date this woman remains, radiocarbon accelerator mass spectrometer (AMS) dating of human and camelid bone remains of the Structure 7 was performed.

Our analysis of the zooarchaeological material found in Structure 7 revealed 488 specimens of different vertebrates (Table 1), including a mandible of a caviine in direct association to the mentioned woman remains (specimen Til1, E7, SZ; Figure 3). Additionally, 14 specimens of caviines from Midden 1 (M1) of the Pucará de Tilcara (Figure 1) were considered in the anatomical study presented here. All of them were included in the qualitative analysis. Among them, seven mandibles (plus the specimen Til1, E7) were sufficiently complete to be included in the quantitative analyses (see Table 2).

In order to study the morphology and to make the taxonomic allocation of these rodent remains, we analysed a comparative sample of mandibular elements of 58 adult specimens belonging to different species of *Cavia*, *Microcavia* and *Galea* (Caviinae; Table 2). Given the large variety of common names given to caviine species, we followed the names given by Patton et al. (2015) and used the terms Andean and European breeds to distinguish the lineages of *C. porcellus* (Spotorno et al., 2007). We considered representatives of different caviine genera of similar morphologies, including all the wild species that inhabit the region of NWA that could be present in the archaeological site without relationship with anthropic activities. Specifically for *C. porcellus*, our sample consisted in specimens belonging to the European breed. Additionally, for the case of the archaeological specimens assigned to the *Cavia* genus, the comparative analyses considering different *Cavia* species allowed us to determine to which species (wild or domestic) the remains belonged. The specimens analysed are housed in the following mammalogical collections: Field Museum of Natural History (FMNH; Chicago, USA), Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA; Mendoza, Argentina), Museo Argentino de Ciencias Naturales (MACN-Ma; Buenos Aires city, Argentina), Museo de La Plata (MLP; La Plata, Argentina) and Colección Miguel Lillo (CML; San Miguel de Tucumán, Argentina).

TABLE 1 Number of specimens (NSP) collected for each taxon from the Pucará de Tilcara (Jujuy, Argentina), Sector Z, Structure 7

Taxon	NSP
Rodents	
Cavia	1
Galea	1
Octodontomys	10
Caviidae cf. *Cavia*	1
Caviidae	3
Rodentia	8
Other vertebrates	350
Aves	4
Lama	1
Camelidae	74
Artiodactyla	20
Cricetidae	14
Dasypodidae	1
Total	488

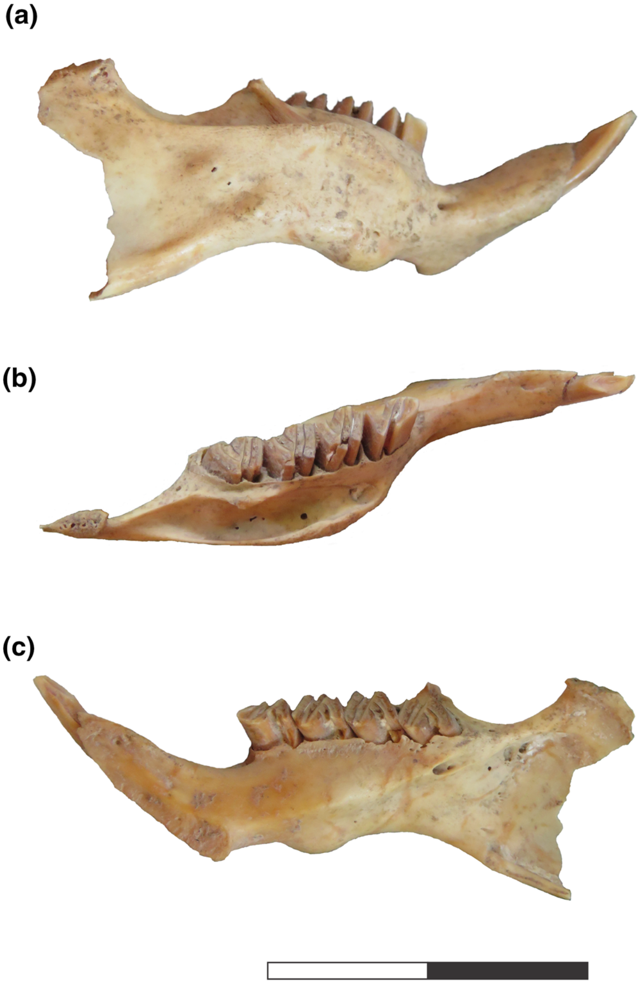

FIGURE 3 Rodent mandible found associated with the remains of an adult woman in the Structure 7, Sector Z in (a) lateral, (b) dorsal (c) and medial views. Scale bar = 20 mm [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Studied specimens of caviinae species of *Cavia*, *Microcavia* and *Galea* considered in both the descriptive and geometric morphometric analyses

Specimen	Species	Sex	Lateral view	Dorsal view	Side
CML 9797	*Cavia aperea*	-	x	x	R
FMNH 119079	*Cavia aperea*	F		x	R
FMNH 119094	*Cavia aperea*	M	x	x	R
FMNH 119096	*Cavia aperea*	F	x		R
MACN-Ma 14166	*Cavia aperea*	M	x	x	L
MACN-Ma 15361	*Cavia aperea*	M	x		R
MACN-Ma 16588	*Cavia aperea*	M	x	x	L
MACN-Ma 22587	*Cavia aperea*	M	x	x	R
MLP 11.VIII.99.54	*Cavia aperea*	-	x		R
MLP 12.II.92.1	*Cavia aperea*	M	x		R
MLP 1803	*Cavia aperea*	-	x	x	R
MLP 30.V.00.27	*Cavia aperea*	-	x	x	R
MLP 563 (M13)	*Cavia aperea*	-	x	x	R
FMNH 26634	*Cavia fulgida*	F	x	x	R
FMNH 26635	*Cavia fulgida*	F	x	x	L
FMNH 47958	*Cavia fulgida*	M	x		L
FMNH 122151	*Cavia porcellus*	F		x	R
FMNH 122239	*Cavia porcellus*	F		x	R
FMNH 54246	*Cavia porcellus*	M	x	x	R
FMNH 90948	*Cavia porcellus*	M	x	x	R
FMHN 78389	*Cavia tschudii*	M	x	x	R
FMNH 19479	*Cavia tschudii*	M	x	x	L
FMNH 23306	*Cavia tschudii*	M	x	x	R
FMNH 46107	*Cavia tschudii*	-		x	R
FMNH 49440	*Cavia tschudii*	F	x	x	L
FMNH 49442	*Cavia tschudii*	M	x		R
FMNH 49444	*Cavia tschudii*	F	x	x	R
FMNH 74863	*Cavia tschudii*	M	x	x	R
FMNH 78390	*Cavia tschudii*	F	x	x	R
MACN-Ma 36.865	*Cavia tschudii*	-	x	x	R
MACN-Ma 15324	*Galea musteloides*	M	x	x	L
MACN-Ma 34193	*Galea musteloides*	-	x	x	L
MLP 15.X.98.5	*Galea musteloides*	-	x		R
MLP 5.II.49.5	*Galea musteloides*	F	x		R
MLP 6.XII.35.2	*Galea musteloides*	-	x	x	R
MLP 676	*Galea musteloides*	-	x		L
MLP 738–4	*Galea musteloides*	-	x		R
MLP 738–6	*Galea musteloides*	-	x		L
FMNH 20282	*Galea spixii*	M	x	x	R
FMNH 20283	*Galea spixii*	F	x	x	R
FMNH 20289	*Galea spixii*	M	x	x	R
IADIZA 03825	*Microcavia australis*	-	x	x	L
IADIZA 06249	*Microcavia australis*	M	x	x	L

(Continues)

TABLE 2 (Continued)

Specimen	Species	Sex	Lateral view	Dorsal view	Side
IADIZA 07099	*Microcavia australis*	-	x	x	R
IADIZA 07210	*Microcavia australis*	-	x	x	R
IADIZA 07213	*Microcavia australis*	-	x	x	L
MLP 13.IX.95.7	*Microcavia australis*	F	x	x	L
MLP 20.XII.00.7	*Microcavia australis*	M	x	x	L
MLP 20.XII.00.9	*Microcavia australis*	F	x	x	L
MLP 26.VIII.01.22	*Microcavia australis*	F	x	x	R
MLP 339	*Microcavia australis*	-	x		R
MLP 518	*Microcavia australis*	M	x		R
FMNH 53655	*Microcavia niata*	M	x	x	R
FMNH 53662	*Microcavia niata*	F	x	x	R
CML 66	*Microcavia shiptoni*	-		x	L
FMNH 35237	*Microcavia shiptoni*	M	x	x	L
MACN-Ma 30–135	*Microcavia shiptoni*	F	x	x	R
MACN-Ma 30–137	*Microcavia shiptoni*	M	x		R
Til1, E7, SZ	Tilcara remain - *Cavia tschudii*	-	x	x	L
Til1, B1, IV (5)	Tilcara remain - *Cavia tschudii*	-		x	R
Til1, B1, VI	Tilcara remain - *Cavia tschudii*	-		x	R
Til1, B1, VI (10)	Tilcara remain - *Cavia tschudii*	-			R
Til1, B1, VI (15)	Tilcara remain - *Cavia tschudii*	-			L
Til1, B1, VI (2)	Tilcara remain - *Cavia tschudii*	-		x	R
Til1, B1, VI (22)	Tilcara remain - *Cavia tschudii*	-			L
Til1, B1, VI (4)	Tilcara remain - *Cavia tschudii*	-		x	R
Til1, B1, VI (8)	Tilcara remain - *Cavia tschudii*	-	x		L
Til1, B1, VII (19)	Tilcara remain - *Cavia tschudii*	-		x	L
Til1, B1, VIII (10)	Tilcara remain - *Cavia tschudii*	-			R
Til1, B1, VIII (2)	Tilcara remain - *Cavia tschudii*	-			R
Til1, B1, V (8)	Tilcara remain - *Galea musteloides*	-			R
Til1, B1, VII (10)	Tilcara remain - *Galea musteloides*	-	x		R
Til1, B1, VII (15)	Tilcara remain - *Galea musteloides*	-			L

Note. It indicates the collection number, species assignment (inferred for the case of archaeological remains of the Pucará de Tilcara), sex (M = male, F = female, − = unknown), analysed views (lateral and dorsal) of the mandible in geometric morphometric analyses and side (R = right, L = left).

Abbreviations: CML, Colección Miguel Lillo; FMNH, Field Museum of Natural History; IADIZA, Instituto Argentino de Investigaciones de Zonas Áridas; MACN, Museo Argentino de Ciencias Naturales; MLP, Museo de La Plata.

Archaeological remains belong to the collection of the Laboratorio de Investigaciones Arqueológicas del Instituto Interdisciplinario Tilcara (Universidad de Buenos Aires).

In addition to the traditional qualitative analysis of the dental and craniomandibular anatomy (e.g., Ortiz & Jayat, 2012), we used 2D geometric morphometric methods. Geometric morphometrics include several methods that allow addressing form (shape plus size) variation based on Cartesian landmark coordinates (e.g., Mitteroecker & Gunz, 2009). They are an effective tool for analysing variation in structures such as the mandible that is difficult to address using traditional morphometric techniques. These analyses included the lateral view of the mandible (e.g., Álvarez, Perez, & Verzi, 2011) and the dorsal view of the dorsal masseteric fossa (*sensu* Verzi, 1994), both shape traits considered by Ortiz and Jayat (2012) as the more informative ones from a systematic point of view. The specimens included in each analysis are indicated in the Table 2. For most of the anatomical terms, we follow Verzi (1994) and Pérez (2010).

Photographs of mandibles oriented to the left and dorsally were taken with a digital camera attached to a tripod. When the left side was damaged or absent in a given specimen, the right side was photographed. The distance between the mandibles and the camera was set to avoid distortions in the image taken. Landmark configurations were designed to represent the mandible shape in both views (Figure 4). Semilandmarks were included to assess in a detailed

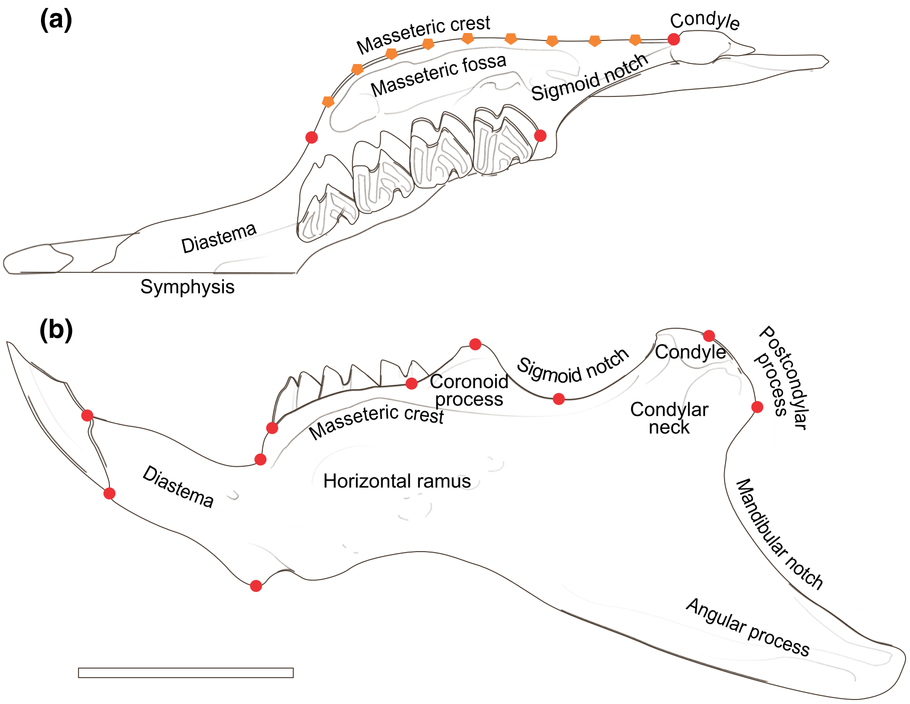

FIGURE 4 Landmark designs used for the (a) dorsal and (b) lateral views of mandible. Red circles, landmarks; orange pentagons, semilandmarks. Main osteological structures are indicated. Scale bar = 10 mm [Colour figure can be viewed at wileyonlinelibrary.com]

manner the differences in mandibular features such as its contour (see Zelditch, Swiderski, & Sheets, 2004). For landmark digitization and scaling of photographs, TPSUtil and TPSDig were used (Rohlf, 2016). The landmark configurations were superimposed by a generalized Procrustes analysis (Goodall, 1991; Rohlf, 1999) using TPSRelw (Rohlf, 2016). Semilandmarks were slid using the minimum bending energy criterion (Bookstein, 1997). Before this procedure, all right mandibles were reflected. We performed a between-groups principal component analysis (bgPCA; considering species as groups; Mitteroecker & Bookstein, 2011) to assess the main shape variations between species. Shape data (Procrustes coordinates obtained after the generalized Procrustes analysis) are projected onto eigenvectors calculated from a matrix containing the shape covariance among groups (not overall covariance as in a standard PCA). This analysis was performed using the Morpho package (Schlager, 2017; Schlager, Jefferis, & Ian, 2014) for software R 3.5.0 (R Development Core Team, 2018). As a measure of overall size of the mandible, we used the centroid size, that is, the square root of the summed squared deviations of the coordinates of each landmark from their centroid (Mitteroecker & Gunz, 2009). To evaluate size variation between species, we analysed centroid size values of the studied specimens constructing box-plots schemes in R.

3 | RESULTS

3.1 | Radiocarbon dating

The results of the radiocarbon analysis of the bone samples by AMS indicate that their death occurred during the Hispanic-Indian period (see definition González & Pérez, 1972). The human bone was dated to 1,642 ± 27 AD (D-AMS 028343), and the camelid bone was dated on 1,660 ± 24 AD (D-AMS 028344).

3.2 | Qualitative analysis

Cavia remains are easily recognized from other caviines in relation to its dental morphology, with a quadrangular outline of occlusal surface of premolars and molars that contain cement filling interlaminar folds (Figure 3b). Ortiz and Jayat (2012) established the combination of features that allow the distinction of *C. tschudii* from *C. aperea*, which are 1- general size clearly smaller, 2- anterior region of zygomatic arch more delicate, 3- posterior margin of the incisive foramen closer to the alveolus of P4, 4- shorter palate with the mesopterygoid fossa reaching the level of the first lamina of M3, 5- coronoid process poorly developed, 6- narrower expansion of the masseteric crest and shallower masseteric fossa and 7- sigmoid (lunar; Pérez, 2010) notch conformed by a plane zone delimited by two sharp ridges.

We confirmed that *C. tschudii* is usually smaller, but some specimens of this species are similar in size to the *C. aperea* ones (see “Centroid size analysis of Caviinae” section). We also agree with Ortiz and Jayat (2012) in the description of a poor development coronoid process of *C. tschudii*, but the geometric morphometric analyses did not capture the differences in the lateral expansion of the dorsal masseteric fossa and its associated crest (see “Dorsal view of the dorsal masseteric crest of *Cavia*” section). Nevertheless, some differences are highlighted regarding to the position of the crest in lateral view, being more ventrally located in the case of *C. porcellus* (see “Lateral view of the mandible of *Cavia*” section).

Regarding the sigmoid notch (Feature 7), the examination of our sample revealed the presence of two sharp ridges delimiting a plane area that are well-defined in many *C. tschudii* specimens but absent in some others (e.g., MACN-Ma 36.865, FMNH 78389, FMNH 49440; Figure 3b). This configuration is also present in some *C. fulgida* specimens. In specimens of *C. aperea*, the two ridges never occupied the entire notch margin but are present in the anterior region in some specimens (e.g., MLP 30.V.00.27), defining a plane triangular area in these cases. Finally, in the case of *C. porcellus*, this feature is variable.

The *Cavia* zooarchaeological remains included in the geometric morphometric analysis (7 mandibles; see Table 2), as well as the cranial and mandibular remains not included in the quantitative analyses, present all the features here interpreted as diagnostical for *C. tschudii*, including small to moderate size, delicate to moderate anterior zygomatic arch, posterior margin of the incisive foramen closer to the alveolous of P4, shorter palate with the mesopterygoid fossa reaching the level of the first lamina of M3 or even M2, small coronoid process and two sharp ridges variably present in the sigmoid notch.

3.3 | Geometric morphometric analysis

3.3.1 | Lateral view of the mandible of Caviinae

In the geometric morphometric analysis of the lateral view of the mandibles of cavines, the first two components explained 67.7% of the shape variation between species (bgPC1 = 52.0%; bgPC2 = 15.7%) and 63.1% of the shape variation between specimens (bgPC1 = 40.6%; bgPC2 = 22.5%; Figure 5). In this morphospace, *Cavia* representatives segregate in an exclusive region of the morphospace, on negative values of bgPC1 with a deep and short horizontal ramus, elevated anterior root of the coronoid process, deep and long diastema, deep sigmoid notch, shallow mandibular notch and short condylar neck (Figure 5). The specimens of *C. porcellus* are located in most negative values of bgPC2, whereas the remaining species overlap on central and positive values of bgPC2. The representatives of *Galea* species are located in central values of bgPC1, and, in the case of *G. spixii* individuals, there is a partial overlap with representatives of *Microcavia* species, with a moderately robust horizontal ramus and diastema, long horizontal ramus, low anterior root of the coronoid process (with respect to the alveolar line), very shallow sigmoid and mandibular notches and caudally located condyle. The representatives of *Microcavia* have positive values of bgPC1, with a short and narrow diastema, shallow and long horizontal ramus, low anterior root of the coronoid process, markedly asymmetrical sigmoid notch and deep mandibular notch. Each *Microcavia* species is located in an exclusive region of the morphospace, with *M. shiptoni* associated to extreme negative values, *M. australis* in central values and *M. niata* in extreme positive values of bgPC1 and bgPC2. One of the archeological caviine specimens, Til1 B1 VII, is located inside the *Galea* morphospace (and specifically inside the *G. musteloides* distribution). The remaining two archeological specimens, Til1 E7 SZ and Til1 B1 VI, are more similar to the *Cavia* cluster, in a region of the morphospace with high overlapping of the different *Cavia* species (Figure 5).

3.3.2 | Centroid size analysis of Caviinae

The analysis of the centroid sizes of the lateral view of the mandibles of caviines reveals remarkable differences between different genera and species (Figure 6). *Microcavia* and *Galea* representatives are typically smaller than *Cavia* species, but *C. fulgida* and the smallest representatives of *C. tschudii* highly overlap with the centroid size values of the two largest species of the former genera (i.e., *Microcavia australis* and *Galea spixii*). *Cavia tschudii* shows a wide range of centroid sizes, between moderate to higher values of the sample. *Cavia aperea* and *C. porcellus* present the higher values of the sample, only overlapping with the high values of *C. tschudii*. The archeological

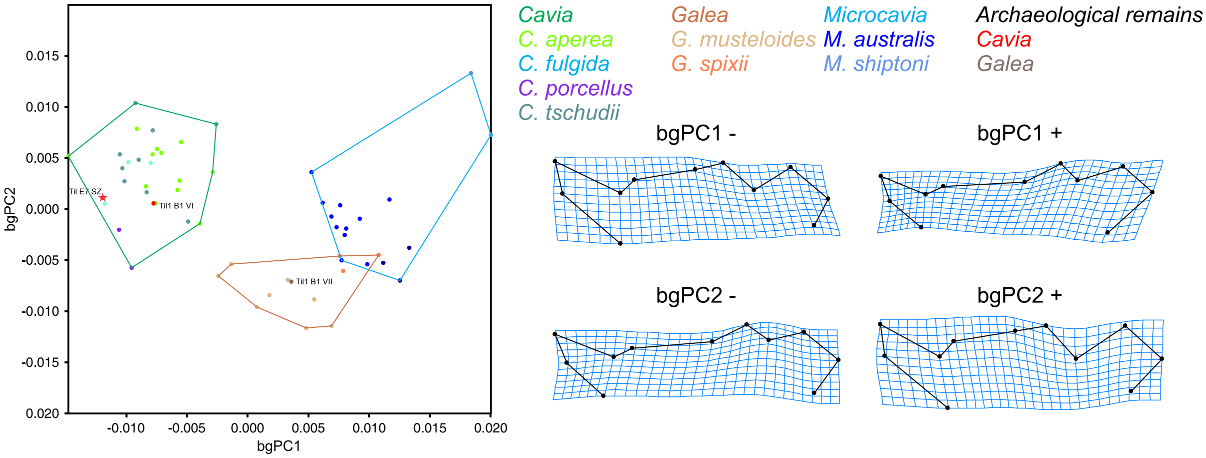

FIGURE 5 Between-groups principal component analysis (bgPCA) of the lateral view of caviine mandibles. Deformation grids of the extremes of the axes are indicated. Light green, *Cavia aperea*; dark green, *Cavia tschudii*; turquoise, *Cavia fulgida*; violet, *Cavia porcellus* (modern European breed); light orange, *Galea musteloides*; dark orange, *Galea spixii*; light blue, *Microcavia australis*; blue, *Microcavia niata*; dark blue, *Microcavia shiptoni*; red and brown, *Cavia* and *Galea* archeological specimens, respectively (star = specimen from Structure 7, Sector Z; circle = other specimens; see Table 2 for specimen codes) [Colour figure can be viewed at wileyonlinelibrary.com]

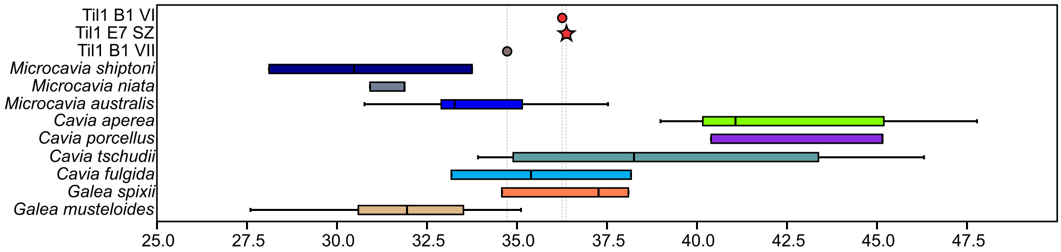

FIGURE 6 Centroid size variations (means and ranges) for lateral view of caviine mandibles. See Figure 5 for colours and symbol codes [Colour figure can be viewed at wileyonlinelibrary.com]

remain Til1 B1 VII, identified as a *Galea* representative in the previous analysis, presents a centroid size value that fit with those observed in the largest representatives of *G. musteloides* and the smallest ones of *G. spixii*.

Finally, the archeological remains Til1 E7 SZ and Til1 B1 VI, identified as *Cavia* representatives, present a centroid size values that fit with those observed in the largest representatives of *C. fulgida* and moderate to smallest ones of *C. tschudii* (Figure 6).

3.3.3 | Lateral view of the mandible of *Cavia*

In the geometric morphometric analysis of the lateral view of the mandibles of *Cavia* specimens, the first two components explained 95.2% of the shape variation between species (bgPC1 = 77.4%; bgPC2 = 17.8%) and 41.4% of the shape variation between specimens (bgPC1 = 28.1%; bgPC2 = 13.3%; Figure 7). In this morphospace, the representatives of *Cavia porcellus* segregate in an exclusive region,

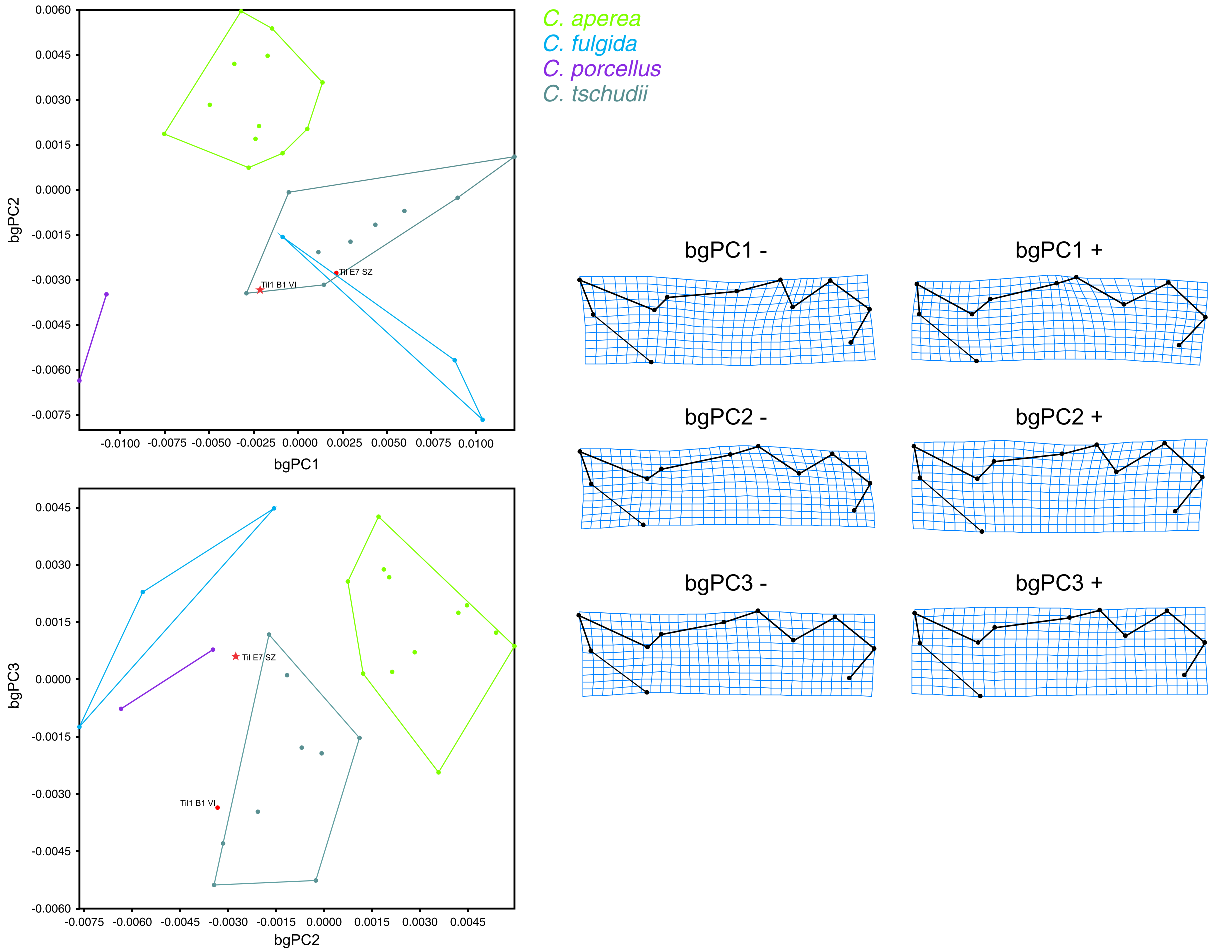

FIGURE 7 Between-groups principal component analysis (bgPCA) of the lateral view of *Cavia* mandibles. Deformation grids of the extremes of the axes are indicated. Light green, *Cavia aperea*; dark green, *Cavia tschudii*; turquoise, *Cavia fulgida*; violet, *Cavia porcellus* (modern European breed); red, caviine archeological specimens (star = specimen from Structure 7, Sector Z; circle = other specimens; see Table 2 for specimen codes) [Colour figure can be viewed at wileyonlinelibrary.com]

on negative values of bgPC1 with a long and robust diastema and a dorsal root closely located to the alveolus of the p4, ample and posteriorly located coronoid process (and near to the anterior margin of the condyle), very deep sigmoid notch and shallow mandibular notch (in comparison with other *Cavia* species; Figures 7 and 9a). The representatives of *C. fulgida* are located in central to positive values of bgPC1 and negative of bgPC2, one specimen overlapping with the *C. tschudii* area over central values of the bgPC1 and bgPC2 morphospace, with a short diastema, a dorsal root distantly located regarding to the alveolus of the p4, anteriorly located coronoid process tip, shallow and ample sigmoid notch and shallow mandibular notch. Nevertheless, both species fully segregate considering the morphospace conformed by bgPC2 and bgPC3 (bgPC3 = 9.76% of shape variation between specimens; see also dorsal analysis of *Cavia*). The representatives of *C. tschudii* are located on central values of the morphospaces of bgPC1 and bgPC2 and over positive values of bgPC1, with a shape similar to that described for *C. fulgida* but with a coronoid tip more caudally located (in an intermediate position between *C. fulgida* and *C. aperea*) and deeper mandibular notch. Finally, the specimens of *C. aperea* are located in an exclusive region of the morphospace on positive values of bgPC2 with a moderately robust and long diastema, caudally located coronoid tip (in an intermediate condition between *C. porcellus* and other species), shallow sigmoid notch and deep mandibular notch. The two *Cavia* archeological specimens, Til1 E7 SZ and Til1 B1 VI, are located along the region (or contiguous region to, in the case of the bgPC2 and bgPC3 analysis) of *C. tschudii* (Figure 7).

3.3.4 | Dorsal view of the dorsal masseteric crest of *Cavia*

In the geometric morphometric analysis of the dorsal view of the dorsal masseteric crest of *Cavia* specimens, the first two components explained 96.8% of the shape variation between species (bgPC1 = 85.7%;bgPC2 = 11.1%) and 59.2% of the shape variation between specimens (bgPC1 = 35.9%; bgPC2 = 23.3%; Figure 8). The representatives of *Cavia porcellus* segregate in an exclusive region of the morphospace, on negative values of bgPC1 and central to positive values of bgPC2, with a very wide dorsal masseteric crest and being its posterior margin flat and poorly posteriorly projected. The representatives of *C. fulgida* are also located in an exclusive region, on negative values of bgPC1 (intermediate between the values of *C. porcellus* and those of other species) and central to negative values of bgPC2, with a dorsal masseter crest wide in its middle region and with concave margin of its posterior region. The distribution area of the representatives of *C. tschudii* and *C. aperea* highly overlapped each other along the central and positive values of bgPC1 and a wide range of bgPC2 values, with a narrow dorsal masseteric crest and with a slightly concave (in *C. tschudii*) to flat margin (*C. aperea*) of its posterior region (Figures 8 and 9b). The seven archeological specimens (Til1 B1 VI [2], Til1 B1 VI, Til1 E7 SZ, Til1 B1 IV, Til1 B1VIII [2], Til1 B1 VII and Til1 B1 VI [4]) are located on positive values of bgPC1 and a wide range of bgPC2 values, far away from *C. porcellus* and secondarily from *C. fulgida* but highly overlapping with the morphospace of *C. aperea* and *C. tschudii* (Figure 8).

4 | DISCUSSION

The descriptive analysis combined with the implementation of geometric morphometric techniques resulted in a robust tool that allowed us to identify the *Cavia* specimens from Pucará de Tilcara as morphologically indistinguishable from *C. tschudii*, yet distinct from *C. porcellus* European breed or any other wild *Cavia* species analysed. What is interesting about this result is that *C. tschudii* does not currently inhabit the area of the Quebrada de Humahuaca. On the other hand, remains of another caviomorph genus were identified corresponding to *Galea*, a genus that currently inhabits the area. It is necessary to emphasize that a lineage of pre-Hispanic domestic guinea pig (*Cavia*

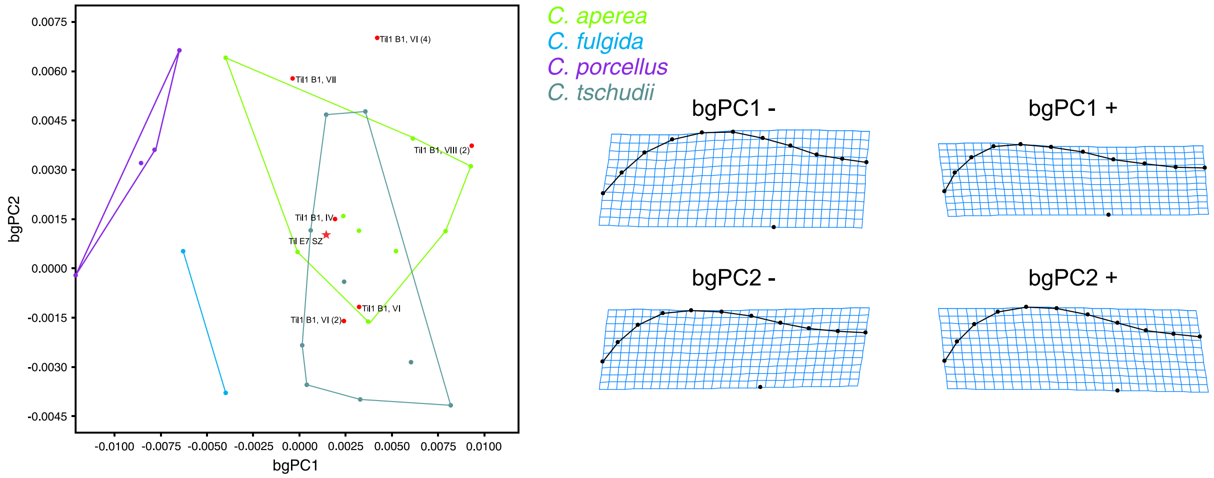

FIGURE 8 Between-groups principal component analysis (bgPCA) of the dorsal view of *Cavia* mandibles. Deformation grids of the extremes of the axes are indicated. Light green, *Cavia aperea*; dark green, *Cavia tschudii*; turquoise, *Cavia fulgida*; violet, *Cavia porcellus* (modern European breed); red, caviine archeological specimens (star = specimen from Structure 7, Sector Z; circle = other specimens; see Table 2 for specimen codes) [Colour figure can be viewed at wileyonlinelibrary.com]

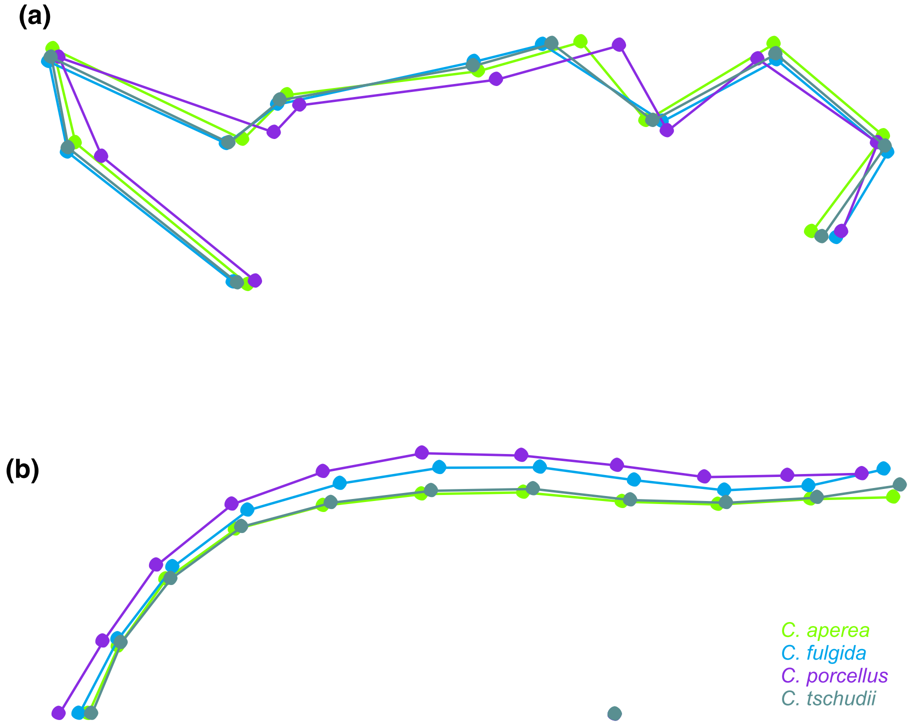

FIGURE 9 Average shape configurations of *Cavia* of the (a) lateral and (b) dorsal analyses. Light green, *Cavia aperea*; dark green, *Cavia tschudii*; turquoise, *Cavia fulgida*; violet, *Cavia porcellus* (modern European breed) [Colour figure can be viewed at wileyonlinelibrary.com]

porcellus Andean breed) is morphologically indistinguishable from its wild ancestors, that is, *Cavia tschudii* (Spotorno et al., 2007). Therefore, the similarity between the remains of Pucará de Tilcara and *Cavia tschudii* does not preclude the possibility that these remains belong to domestic guinea pigs. Moreover, the finding of coprolites of apparent caviine origin (Otero personal observation) in a small semicircular structure of Pucará de Tilcara (Otero, 2013: 153) reinforces the possibility that the remains would correspond to domestic guinea pigs. The possibility that human groups inhabiting the Pucará de Tilcara would have hunted or interchanged *C. tschudii* from other regions cannot be discarded from a morphological analysis, but it does not allow explaining the latter facts.

An alternative interpretation was the proposal of Teta and Ortiz (2002). They assigned remains of guinea pigs from archaeological sites of Northwestern Argentina (Inca Cueva 5 site and some Incaic sites) to *C. tschudii* and suggested that this was evidence of the presence of this species inhabiting the Quebrada de Humahuaca during pre-Hispanic times. To justify this, the authors suggested a different palaeoenvironment from the present in the region, considering the species' preference for grassland and wetter environments. However, the records described by Teta and Ortiz (2002) are also linked to human archaeological occupations. According to our results and taking into account that *C. tschudii* is morphologically indistinguishable from *C. porcellus* Andean breed (Spotorno et al., 2007), the probability of an anthropogenic origin should be considered in future studies, especially for sites linked to Incaic occupation. The finding of guinea pigs in the particular context of Structure 7 of Sector Z of the Pucará de Tilcara has unique characteristics to this site and to the Quebrada de Humahuaca in general and reinforces the use of guinea pigs mainly in connection with ceremonial practices instead of a predominantly domestic consumption (Gade, 1967).

As seen in other cases in the Andes, the domestic guinea pigs have been participants and continue to be part of the ceremonial life of the Andean groups (e.g., Guaman Poma de Ayala, 1956; Morales, 1995; Rofes & Wheeler, 2003). The inclusion of a specimen in a burial could be due to different causes such as fertility rites that were intended to propitiate the rains (Gil García, 2002). Likewise, their presence in a burial context assignable to the Hispanic-Indian period could demonstrate the continuation of these practices and their reaffirmation in times of drastic transformation as was the Spanish conquest. As documented for other places in the Andes, the local communities that were part of the Inca Empire reinforced their cult of ancestors (Otero, Bordach, & Mendonça, 2017; Ramírez, 2008).

Our study is one of the few studies that use geometric morphometric methods in archaeological contexts, quantifying the shape of caviine mandibles with the main purpose of making taxonomic assignments of archaeological guinea pig remains. These methods allowed us to support or modify (e.g., previous proposal of a lateral expansion of the masseteric crest in *C. tschudii*; see Ortiz & Jayat, 2012) the morphological characterization of caviine species. These techniques have been used in the study of human osteological remains and other anthropogenic remains (e.g., Cardillo, 2010; Perez, 2007), but only few previous studies have used them in the context of zooarchaelogical analyses in Argentina, specifically for camelids (e.g., L'Heureux & Hernández, 2016). However, geometric morphometrics, as far as we know, have never been employed to assess morphological variation of micromammals in Andean archaeological sites. In these contexts, micromammals are typically understudied in comparison with other archaeofaunal remains, such as camelids, which are much better known due to their abundance within the material record. This approach allowed us to increase knowledge about the distribution of caviines in the region and their relationship to anthropic processes.

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CONFLICT OF INTEREST

Authors have no conflict of interest to declare.

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