DOMESTICATION OF GUINEA PIGS FROM A SOUTHERN PERU-NORTHERN CHILE WILD SPECIES AND THEIR MIDDLE PRE-COLUMBIAN MUMMIES

DOMESTICACIÓN DEL CUY A PARTIR DE POBLACIONES ORIGINARIAS DEL SUR DEL PERÚ Y NORTE DE CHILE, CON LA DESCRIPCIÓN DE SUS MOMIAS PRECOLOMBINAS

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ABSTRACT

To investigate the origins and domestication of guinea pigs, or cuyes (*Cavia porcellus*), we re-analyzed 12S rRNA (759 bp) and cytochrome *b* gene (1140 bp) sequence data from relevant species and breeds. Seventeen pre-Columbian mummified cuyes from southern Peru and northern Chile sites are described and compared with both domesticated (living Andean creole and European breeds) and wild species. All molecular analyses point to the western *C. tschudii* rather than to the eastern *C. aperea* as the ancestral wild species. Domesticated Andean and European cuyes were different both in biochemical and morphological analysis ; both breeds exhibited a lower neurocranium than that of *C. tschudii*. Principal component analysis of skeletal measurements showed that most of the mummies anayzed were juveniles, but at least 2 appeared to be adults when compared with wild and Andean cuyes. The degree of domestication in these mummies was evaluated under the criteria of the "domestication syndrome": their size, hair color and design polymorphisms, and lower skulls demonstrated that they were fully domesticated in southern Perú-northern Chile more than 500 years before the arrival of Spaniards to the Americas; this was the first or major step in the process of cuy domestication. The second stage was the European one, under a different selection regime acting for another 500 years. The third stage is ongoing, with heavy selection for size and meat volume.

Key words: Andes, Caviidae, Chile, Perú, 12S, cytochrome *b*, skull, domestication syndrome, guinea pig

RESUMEN

Para investigar los orígenes y la domesticación de los cobayos o cuyes (*Cavia porcellus*), hemos re-analizado los datos de secuencias para 12S rRNA (759 pares de bases) y del

gen para citocromo *b* (1140 pares de bases) en especies y cepas relevantes. Se describen 17 cuyes precolombinos momificados del sur del Perú y norte de Chile, los que son comparados con domesticados (cepas criollas andinas y europea) así como con especies silvestres. Todos los análisis moleculares indican que la especie ancestral es *C. tschudii* de los Andes Occidentales más que la oriental *C. aperea*. Los cuyes domésticos de los Andes y de Europa resultaron diferentes tanto en los análisis bioquímicos como morfológicos; ambas cepas mostraron neurocráneos más bajos que aquéllos de *C. tschudii*. El análisis de componentes principales de medidas esqueléticas mostró que la mayoría de las momias analizadas eran juveniles, pero al menos 2 aparecieron como adultos cuando se los comparó con los cuyes silvestres y andinos. El grado de domesticación de estas momias fue evaluado según los criterios del "síndrome de domesticación": sus tamaños, color de pelaje y polimorfismos de diseño mostraron que ellos ya estaban completamente domesticados en el sur del Perú y norte de Chile más de 500 años antes de la llegada de los españoles a las Américas; ésta fue la primera o principal etapa en el proceso de domesticación del cuy. La segunda etapa fue la europea, bajo un régimen diferente de selección actuando durante otros 500 años. La tercera etapa es la actual, con fuerte selección para tamaño y volumen de carne.

Palabras claves: los Andes, Caviidae, Chile, Perú, 12S, citocromo *b*, craneo, sindrome de domesticación, cuy

INTRODUCTION

Cuyes, cavies, or "guinea pigs" (*Cavia porcellus* (Linnaeus 1758)) are small mammals of South American origin (Wagner and Manning, 1976), still kept today as "criollos" (Chauca, 1997) by the native peoples of the Andes for food and cultural practices (Morales, 1994). They are also well known as domestic pets and laboratory models utilized worldwide since their introduction to Europe in the XVI Century from undocumented sources (Woods, 1993). Along with llama and alpaca, the cuy is one of only 3 mammal species to have been domesticated in the Americas, probably within the single domestication center of the New World: the Central Andes (Wing, 1986). By the time the Spaniards arrived in the Americas, cuyes were fully domesticated (Clutton-Brock, 1999), but very few details of the early process of domestication are known.

Despite the extensive knowledge accumulated on the biology (Cooper and Schiller, 1975; Wagner and Manning, 1976) of the European breed, *C. porcellus*, there are many controversies about its precise geographic origins (Clutton-Brock, 1999), phylogenetic relationships (Weir, 1974), and even its conspecificity with 1 of the 5 presently recognized wild species of the genus *Cavia* living in South America (Woods, 1993). For instance, *C. porcellus* was included within *C. aperea* (Eisenberg and Redford, 1999), and some recent authors still name cuyes as *Cavia aperea* f. *porcellus* (Sachser, 1998; Kunzl and Sachser, 2000; Trillmich et al., 2003); such taxonomic ascription was based on morphological studies (Huckinghaus, 1961, but see Cabrera (1953) for an alternative view) and the important fact that fertile hybrids were produced from *C. aperea* x *C. porcellus* crosses (Pictet and Ferrero, 1951; Rood, 1972). However, fertile hybrids also were produced by crossing *C. porcellus* with *C. tschudii* collected in Cusco, Peru (Castle, 1916). By contrast, crosses of domestic cuyes with a third living species,

C. fulgida from Brazil, gave infertile males (Detlefsen, 1914). Therefore, and considering that most agree that species are closed genetic systems in nature (Harrison, 2002), the 2 most probable living candidates for the ancestral species of domestic cuyes are the eastern *C. aperea*, now ranging from Colombia through Argentina (Eisenberg and Redford, 1999), and the western *C. tschudii,* from southern Peru and northern Chile (Eisenberg and Redford, 1999). Given the disjunct geographic distribution of these 2 species, the determination of the ancestral species would be a clue of the whereabouts of the original area of domestication (Weir, 1974).

The most promising solution to the question of guinea pig origins involves the application of modern molecular techniques (Hillis et al., 1996). Although Rowe & Honeycutt (2002) have recently reassessed the work of Nedbal (1994), adding 2 nuclear sequences to the original work with 12S plus morphological and ecological correlates, neither study examined the *C. aperea* and *C. tschudii* sequences simultaneously. In the present study we reexamine 12S sequence data to compare results with those based on the complete cytochrome *b* gene sequences of *Cavia* species (Spotorno et al., 2004) and address the question of cuy origins.

Direct evidence about the domestication process is preserved in numerous naturally mummified cuyes of different periods recovered from many Andean archeological sites (Fig. 1). Sacrificial cuyes were included as religious offerings in human tombs or house settlements (Gade, 1967; Sandweiss and Wing, 1997); many anatomical features are preserved in these burials due to the extreme aridity in these areas. In general, these cuyes have been studied more as cultural objects than as complex biological entities (Archetti, 1997). Herein, we describe and analyze 16 cavy mummies recently excavated from southern Peru at the El Yaral site (Rofes, 1998; Rofes and Wheeler, 2003), as well as a single cuy mummy found in a northern Chile site, Punta Pichalo, Pisagua, excavated early in the 20th century by the German archeologist M. Uhle (Uhle, 1917). These 2 sites are located within the present geographic distribution of the extant *C. tschudii* (Eisenberg and Redford, 1999).

The purposes of the present paper are: (1) to re-analyze 12S molecular data relevant to the origin and divergence of the domestic guinea pigs, (2) to document and analyze 17 pre-Columbian mummified cuyes from southern Peru and northern Chile sites, (3) to evaluate whether such pre-Hispanic cuyes were fully domesticated, by comparing them with actual Andean breeds and wild species, and (4) to suggest a plausible scheme describing the processes which occurred during the domestication of cuyes.

MATERIAL AND METHODS

*Specimens***.** Wild and domestic animals or archeological samples were obtained in the field from rural houses or from museum collections. Skulls and skins, whenever available, were prepared as voucher specimens; most were deposited in the collection of the Laboratorio de Genómica Evolutiva, Instituto de Ciencias Biomédicas, Facultad de Medicina, Universidad de Chile, Santiago, Chile (acronym LCM). Taxonomy follows Woods (1993). Original localities of examined specimens, and sources (collection numbers) are in Appendix 1. GenBank accession numbers of sequences are listed below.

We studied X-rays of 16 mummies from El Yaral site (Valley of Moquegua, southern Peru), specifically collected at the locality named M8. These animals were
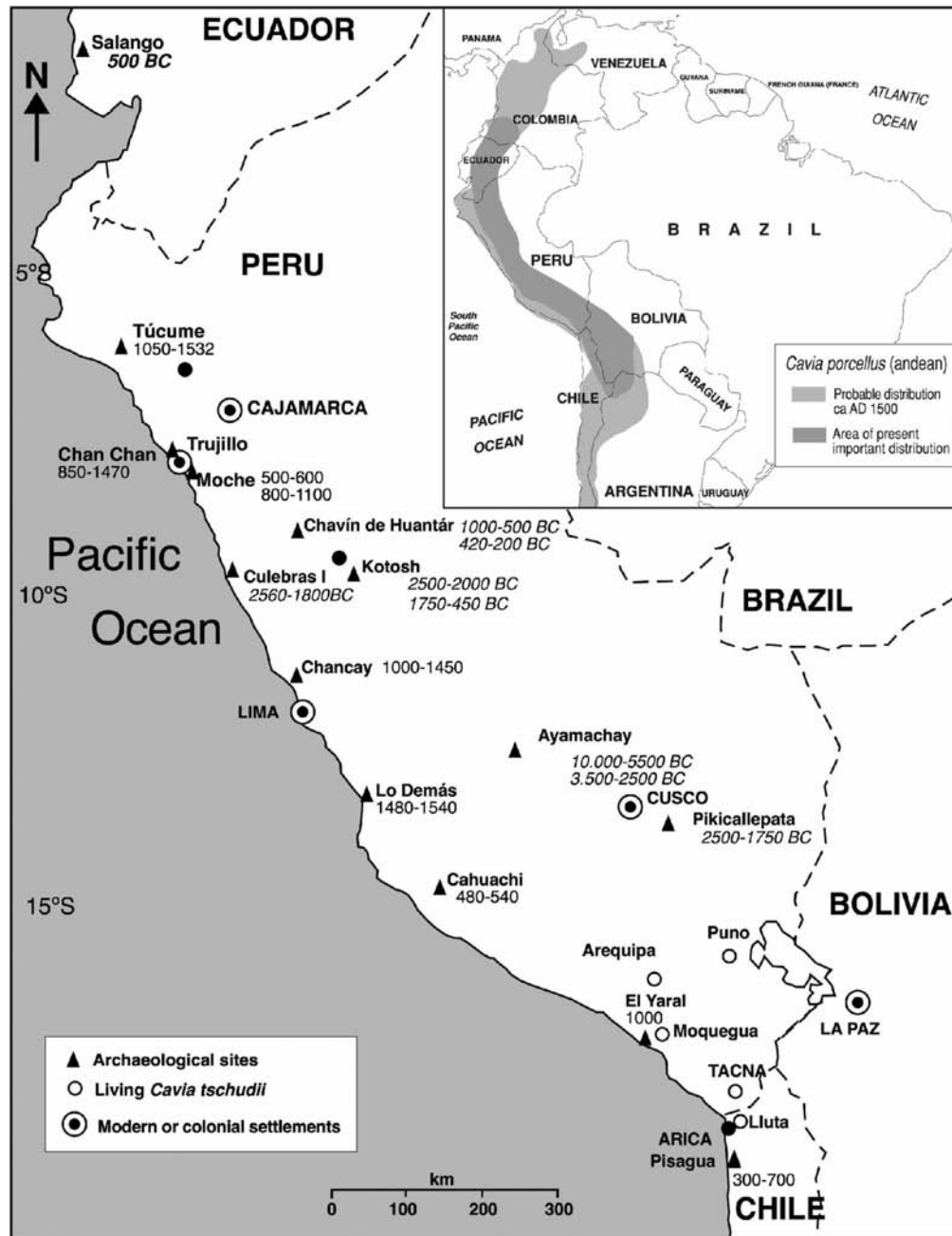
Figure 1. Map of archeological sites with guinea pig remains (modified from Sandweiss and Wing, 1997). Approximate B.P. dates are shown; B.C. dates are in italics. Modern or colonial settlements are included. Some localities of wild Cavia tschudii also shown. Inset: Historical and present distribution of domestic cuyes (Andean breed) in South America (modified from Gade 1967).

chosen from approximately 70 naturally desiccated guinea pigs, sacrificed and buried beneath 3 habitation structures of a Chiribaya occupation (Rofes, 1998). This material has been ascribed to the "Intermedio Tardío Peruano", 1000 A.D. (Rofes, 1998; Rofes and Wheeler, 2003) . Twenty-three naturally mummified llamas and alpacas were also recovered from the same site (Wheeler et al., 1998), as were their parasites (Leguia and Casas, 1998).

The other mummy we studied was from Punta Pichalo, Pisagua, Chile; it belonged to the Max Uhle Collection, now deposited at the Museo Nacional de Historia Natural in Santiago, Chile. It carried a label with the inscription "2.532 M.N.H.N. Caja 133. Cuerpo disecado de roedor cui?. CEMENTERIO "C" arriba. PISAGUA (PTA. PICHALO) REG. TARAPACA."; at the reverse is written "Colecc. Max Uhle. 1913". It was originally found together with many cultural objects, all listed in Cocilovo (1994). The C cemetery, or Pisagua C, was originally ascribed to the Tiwanaku Period, 400-700 AD (Uhle, 1919), although it was recently extended to encompass 300-700 AD (Cocilovo, 1994). This specimen had received only cursory cataloguing (Uhle, 1919).

Molecular Analysis. We used the following mitochondrial 12S rRNA gene sequences retrieved from GenBank: *Dolichotis patagonum* AF433939, *Dolichotis salinicola* AF433918 and AF433919, *Galea musteloides* AF433910 and 433911, *Galea spixii* AF433934, *Microcavia australis* AF433914 and AF433915, *Cavia aperea* AF433908, *Cavia porcellus* AF433909 (see Rowe and Honeycutt, 2002), and *Cavia tschudii* AY012121 (see Murphy et al., 2001), and *Cavia guianae* U12449 (see Nedbal et al., 1994). Sequences were aligned using Clustal V (Higgins et al., 1992) and proofed by hand, resulting in a total of 895 characters. Following previous analysis on this particular gene (Rowe and Honeycutt, 2002), 136 ambiguous base pairs (sites 57-62, 75-85, 115-121, 161-166, 217-231, 289-293, 299-303, 314-326, 367-382, 477-481, 653-660, 739-746, 751-760, 776-781, 881-895) were removed, leaving 759 bp for phylogenetic analysis. Maximum-parsimony (MP) analyses were conducted using PAUP*4.0b8a (Swofford, 2002). The branch-and-bound option was used to identify the most parsimonious tree(s). Heuristic bootstrap analysis with 1,000 replicates were run, and Bremer decay indexes (SI) were calculated using AutoDecay 4.0 (Eriksonn, 1999) to estimate branch support.

Maximum likelihood (ML) analyses also were implemented in PAUP* 4.0b8a (Swofford, 2002), with gaps excluded. The HKY+G model generated significantly better likelihood scores using MODELTEST (Posada and Crandall 1998); therefore this model was chosen to perform heuristic searches with the tree-bisection-reconnection (TBR) branch swapping, and bootstrap analysis.

Morphological Descriptions.   We have followed the standard nomenclature and anatomical descriptions extensively treated elsewhere for *C. porcellus* (Cooper and Schiller, 1975).

Geometric Morphometrics Analysis of Skull Shape Variation. Twenty landmarks were defined along the *Cavia* skull, chosen to recover most of its morphology. The coordinates for each specimen were registered through the program TPSDIG (Rohlf, 1998). Mean configuration for individuals in a sample was obtained by the technique of generalized adjustments of minimum squares (Rohlf and Slice, 1990), minimizing the differences due to scale, translation and rotation between specimens. Such mean configurations were used to estimate the affine and non-affine (partial warps) components of shape.

Variation in their mean positions through the different samples (*C. tschudii N* = 16, *C. porcellus* Andean breed *N* = 13, and *C. porcellus* European breed *N* = 14; original localities and museum collection numbers in Appendix 1) were analyzed by means of the Thin Plate Spline technique (relative warp analysis), available through the computer programs TPSPLINE and TPSRW (Rohlf and Slice, 1990).

Skeletal Measurements and Principal Component Analysis. Whole specimens were photographed under x-ray machines at natural size, extending their legs if possible, or taking photographs from various angles. Negatives were scanned to digital form, and measurements from images were taken through the NIH Image v. 1.61 computer program (Rasband and Bright, 1995). We performed principal components analysis on a variance-covariance matrix, with the program NTSYS-pc v 2.1a (Rohlf, 1995). To estimate standard errors for the principal components, a jackknife resampling procedure was applied using the program JACKknifed Interactive Eigenanalysis v. 1.2 (Cavalcanti, 2001).

RESULTS

Molecular Analysis of 12S Gene Sequences from Domestic and Wild Cavies

Maximum-parsimony (MP) analysis of the 759 bp matrix detected 175 parsimony-informative characters and generated a single parsimonious tree of 320 steps. This tree (Fig. 2) had a Consistency Index (CI) of 0.75, and a Recalculated Index (RC) of 0.56. Bootstrap and Support Index values (Fig. 2) gave strong support to all branches except that of the *C. porcellus -C. tschudii* branch, which received a support of 85% bootstrap
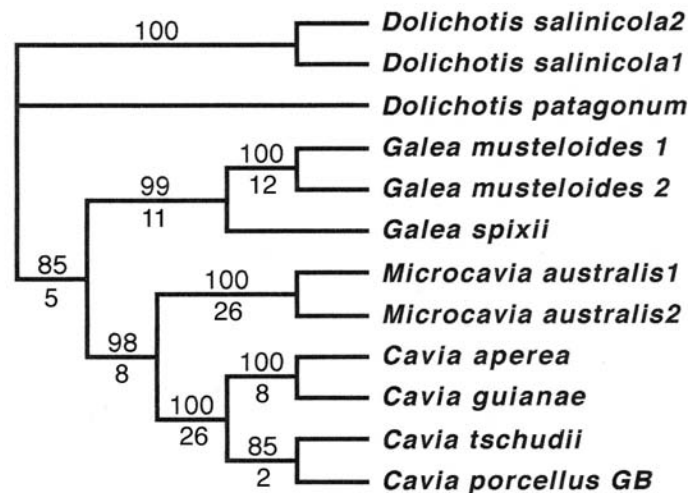

Figure 2. Maximum parsimony tree based on published 12S rRNA sequences (see Material and Methods). Bootstrap values above branches, Bremer Support Index values below them.

and a SI of 2. This branch was based on a single substitution at site 67, in contrast with the 6 substitutions shared by *C. aperea* and *C. guianae*. Given the contrasting hypothesis about the relationships of domestic cuyes, we force *C. aperea* to join *C. porcellus*; this alternative tree had 16 additional steps, a CI = 0.71, and a RC = 0.50, with no substitutions defining this hypothetical branch (Kishino-Hasegawa test as implemented in PAUP; *p* < 0.0001).

Maximum-likelihood analysis produced a tree identical to the most parsimonious one, with a –ln L of 2559.35. All bootstrap values (500 replicates) were also high except that of the *C. porcellus* -*C. tschudii* branch, which received only a 65% support. Forcing *C. aperea* to be the sister branch of *C. porcellus* produced a significantly less likely topology (-ln L = 2648.49; Kishino-Hasegawa test; *p* < 0.001).

Geometric Morphometry of Skull Modified by Domestication

The deformation in the grids recovering the shape changes in the skulls of the Andean and European breeds of *C. porcellus* compared with those of wild *C. tschudii* exhibited significant differences in the affine and non affine components (not shown). Most of the non-affine variations affected the neurocranial region (Fig. 3c), with a contraction of the braincase at the landmarks associated with the coronal, sagittal, and parietal sutures (landmarks 5 and 6 in Fig. 3), and with the most posterior point at the nuchal crest (landmark 7). When the skulls of both breeds of *C. porcellus* were compared, slight differences in the orbit, maxillary, bullae, and paracondylar process sizes and shapes were evident (left of Fig. 3), but they were not significant by the methods and landmarks used here.

Cavy Mummies from Southern Peru-northern Chile

Cavies from El Yaral, southern Peru

From this site we obtained a series of well-preserved bodies, all with their heads removed and placed above or beneath each individual (Plate I). In 7 bodies whose vertebral columns were observed under the X-rays, most if not all cervical vertebrae were twisted or bent, a clear indication of the killing method used. No visible tails were externally observed, but several internal caudal vertebrae usually were visible in the radiographs. Specimen M8-8254 showed a rounded mass 5 mm in diameter inside the mouth (Plate Ic); also, specimen 7364 showed an elongated mass 9 mm long in the same place (Plate Id). Four and 3 digits were usually seen in the manus and pes, respectively. Substantial portions of intestines and most internal organs were evident on the X rays (Plate Ib). Skin colors were variable, from uniform brown to chestnut, dark brown, and orange piebald (Table 1).

Most specimens appeared to be juveniles, judging from the measurements of their skulls and long bones when compared with those of wild *C. tschudii* and *C. porcellus* adults (Table 1). In fact, most mummies obtained negative values along the first axis in the principal component analysis (Fig. 4). This particular axis explained 80.4% of the total variance, and had correlations of 0.61 with the diastema length (Table 2), and then of 0.39 with humerus lengths (Table 2). Nevertheless, at least 2 of these mummies (7230 and 3026) were larger than some wild *C. tschudii* and *C. porcellus* adults included for comparison; for instance, wild specimen 3080 was a mature male with differentiated
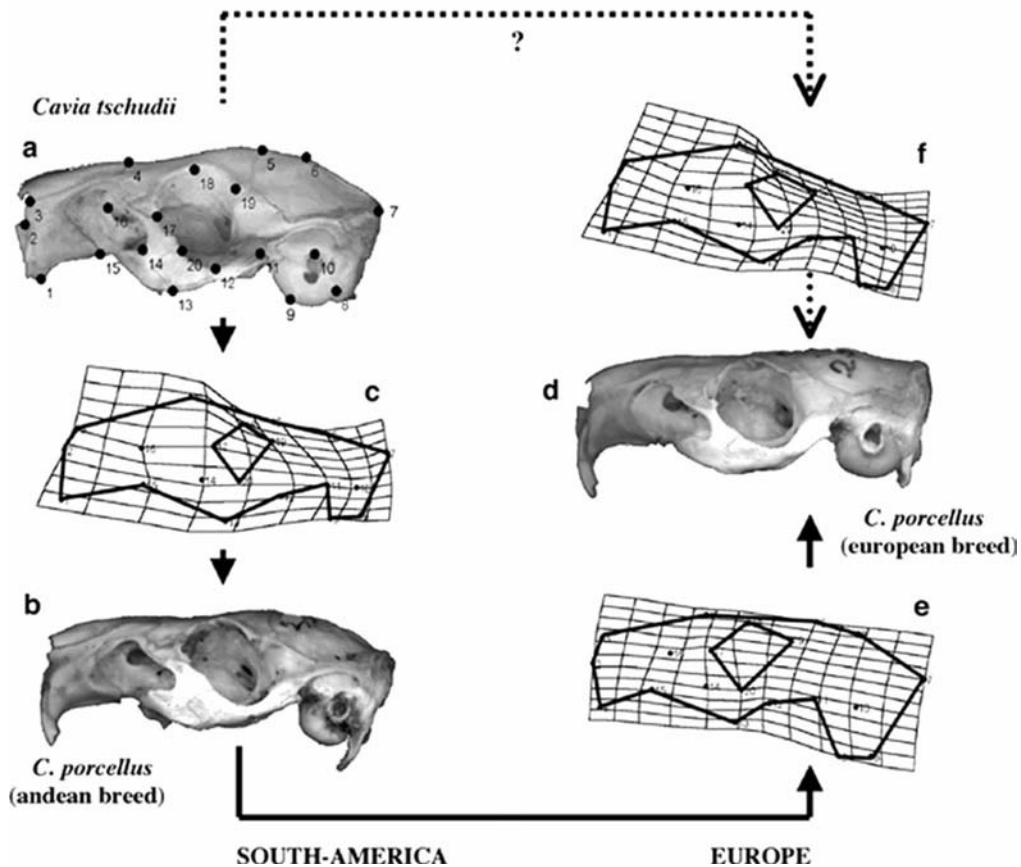
Figure 3. Geometric morphometry analysis of guinea-pig skull shape variation through domestication. A. Lateral view of a *Cavia tschudii* skull, with 20 defined landmarks chosen to describe its basic morphology. B. Lateral view of an Andean *C. porcellus* skull. C. Transformed cartesian grid obtained when the 20 landmarks of Andean *C. porcellus* were superimposed with the homologous landmarks from *C. tschudii*. D. Lateral view of an European *C. porcellus* skull. E. Transformed cartesian grid obtained when the 20 landmarks of European *C. porcellus* were superimposed with the homologous landmarks from Andean *C. porcellus*. F. Transformed cartesian grid obtained when the 20 landmarks of European *C. porcellus* were superimposed with the homologous landmarks from wild *C. tschudii*. Solid arrow shows the most plausible direction of skull shape variation associated with the *Cavia* domestication process. A less probable transition from *C. tschudii* to the European breed is also shown (dotted line).
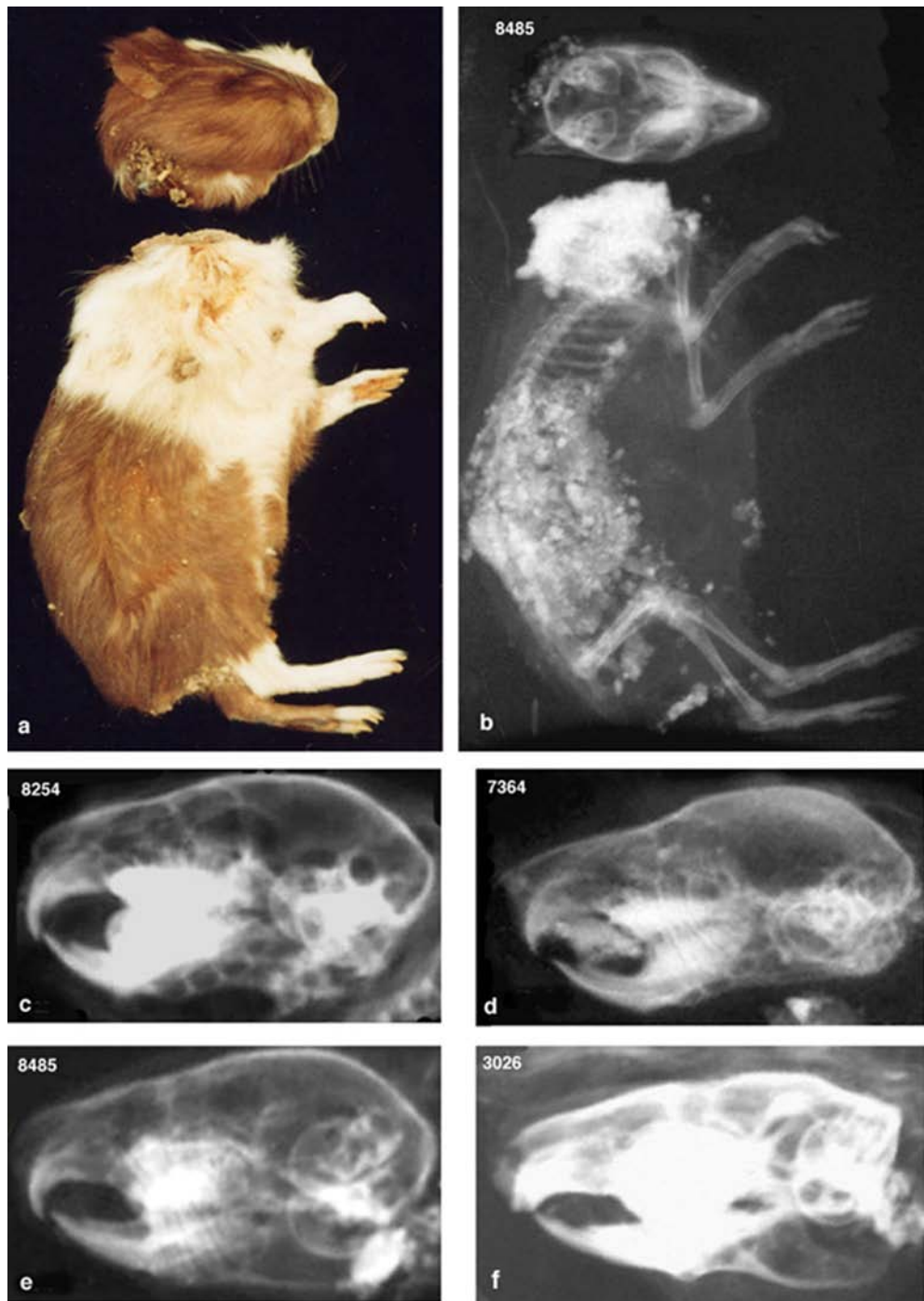
Plate I. Guinea pig mummies from El Yaral, Moquegua, Peru. a) external and b) X-ray of young specimen M8 8485 (see Table 1). c) d) and e) Young specimens. f) Adult M8 3026.

Table 1. Measurements (in grams and millimeters) and skin color of naturally desiccated cuy mummies from the sites of Punta Pichalo, Pisagua (northern Chile, MHN) and El Yaral (southern Peru, site M8, material kept by J. Wheeler), of contemporary domestic cuyes, and wild guinea pigs (LCM). GL = Greatest length. Measurements judged to be underestimations (i.e., dry weights) are in square brackets.

Specimen (together with)	Weight gr	Skull GL	Humerus GL	Femur GL	Molar Row	Diastema	Tibia GL	Dorsum Color	Venter Color	Foot Color	Face Color
MHN 2532	38	54	36	39	16	13	37	gray	yellow	gray	black line
M8-3026	-	65	40	47	18	15	44				
M8-7230	[95.5]	55	34	39	19	12	41	brown	brown	white	brown
M8-7364	-	42	[20]	[24]	12	9	29	orange	orange	white	white
M8-7453	-	-	-	-	-	-	-	brown	brown	brown	white
M8-8033	[80.3]	63	-	-	15	14	-	brown	brown	brown	brown
M8-8085	-	45	[20]	[30]	-	6	[28]	chestnut	chestnut	chestnut	white
M8-8254	-	42	25	29	12	9	30	brown	white	brown	brown
M8-8262	[56.1]	-	-	-	-	-	-	orange	white	white	orange
M8-8263	[31.5]	43	26	29	14	5	30	brown	white	brown	brown
M8-8264	-	50	32	35	13	10	37				
M8-8396 (R236)	[36.8]	44	30	34	13	8	36	orange	orange	white	orange
M8 8485	-	41	25	28	11	10	30	brown	white	white	brown
M8-8849 (R267)	-	43	28	30	12	11	32	chestnut	white	white	brown
M8-8849-2	-	46	29	32	13	10	32				
M8-2208 (Yaral 62)								brown	brown	brown	brown
M8-R193 (Yaral 64, 316)								brown	brown	white	brown

Table 1 (continued).

Cavia porcellus (Andean breed, Arica, Chile)

LCM 3137	743	59	36	45	12	11	46	black
LCM 3135	823	69	41	45	17	18	46	gray
LCM 3136	-	68	41	47	16	17	47	brown
LCM 3138	858	68	41	49	18	13	48	white

black

Cavia tschudii (Lluta, 30 km west of Arica, Chile)

LCM 3081	300	61	45	42	14	13	50	gray agouti
LCM 3080	306	56	36	39	11	12	42	gray agouti
LCM 3110	233	57	43	44	13	12	45	gray agouti
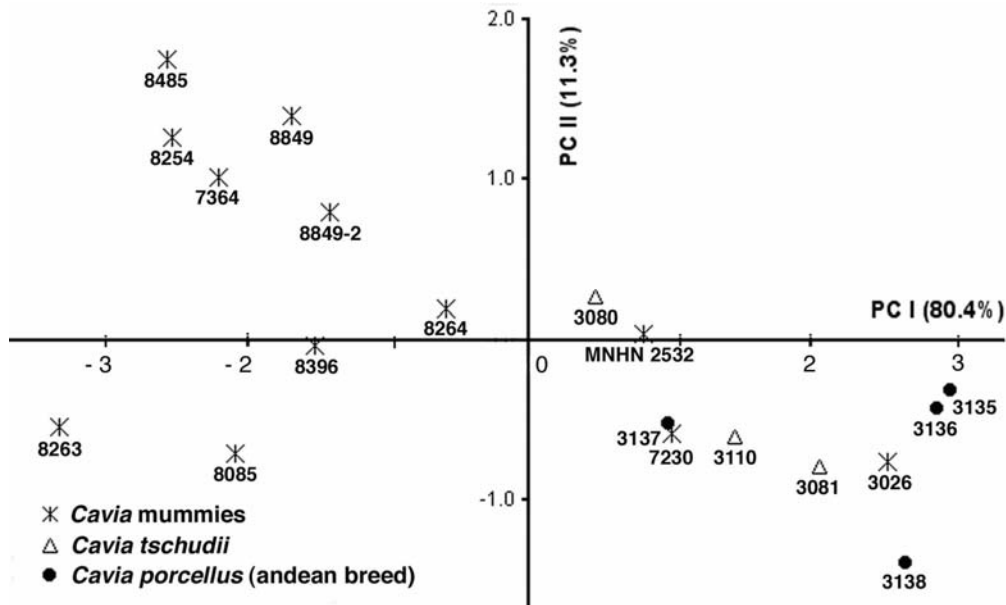
Figure 4. Principal Component Analysis of skeletal measurements from domestic cuyes (Andean breed), mummies and wild guinea pigs (from data in Table 1). Numbers designate collection number of specimens. Percentages are percent of total variance explained by each axis.

Table 2.   Coefficients of each morphological variable on the first 3 PC axes (eigenvalues in parenthesis).

	Axis1 (0.0413)	Axis 2 (0.0058)	Axis 3 (0.0033)
Skull	0.3832	-0.2021	-0.0157
Humerus	0.3928	-0.2832	-0.2594
Femur	0.3664	-0.2811	-0.1213
Molar row	0.2339	-0.3127	0.8995
Diastema	0.6138	0.7785	0.0933
Tibia	0.3648	-0.3099	-0.3161
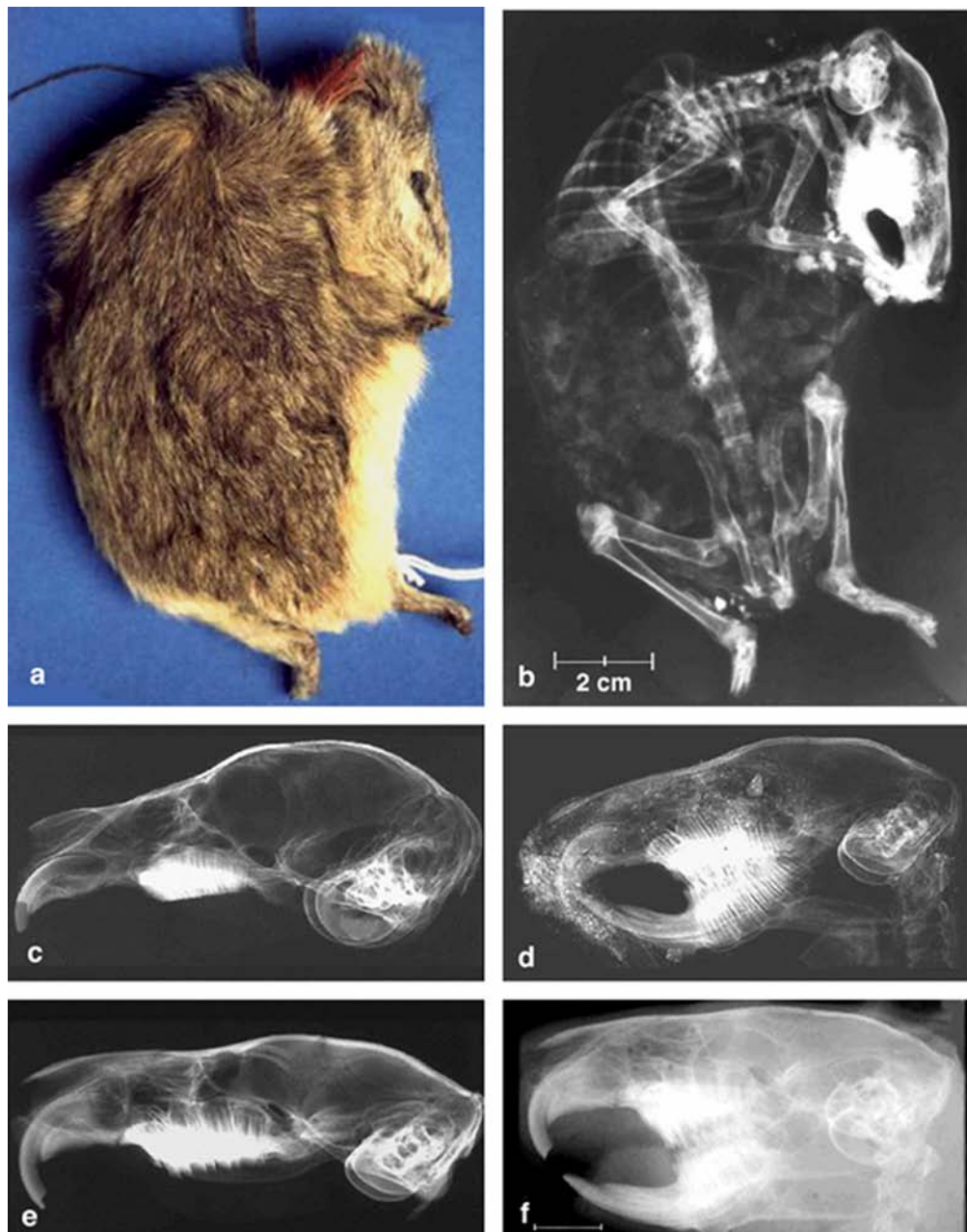
Plate II. Guinea pig mummy MNHN 2532 from Punta Pichalo, Pisagua. Chile and domestic and wild cavies. a) Mummy external dorsal view. Flamingo red feather at the neck tied with camelid brown thread (terminals above). b) X-ray. Intestine portions (arrows). c) Wild *Cavia tschudii* LCM 205, skull X-ray . d) Mummy skull X-ray. e) *Cavia porcellus*, Andean breed skull from Arica, Chile; 91 days age. f) *Cavia porcellus*, laboratory breed skull.

sperms within an 18 x 16 mm testes.

Cavy from Punta Pichalo, Pisagua, Chile

This specimen is a very well-preserved body with the full skeleton intact (Plate II). It had a brown thread tied around the neck, probably made of llama or alpaca wool, with a red feather that was identified as belonging to a flamingo (Plate IIa). The body exhibited no externally visible tail, but at least 4 distal caudal vertebrae were clearly revealed in the radiographs, probably Ca4 through Ca7 (Cooper and Schiller, 1975). Skull morphology confirmed that it belonged to a member of the genus *Cavia* (Eisenberg and Redford, 1999). Four digits in the right manus and 3 digits at the right pes were observed, and the corresponding phalanges observed on the X-ray plate (Plate IIb). A few portions of the intestines were still visible, but other internal organs clearly have been removed, probably through the perigenital area, which showed some visible cuts.

The skin color was uniformly gray brown with a yellowish belly, but a remarkable black frontal line 3 mm wide crossed from above the eyes to the nose and mouth. A small black line ran parallel to the frontal line from the internal border of the right eye towards the mouth (Plate IIa), but was less apparent on the left side. The body size of this mummy appeared to be similar to mature wild and domestic guinea pigs (Fig. 4). Its diastema, molar row and femur lengths were similar or higher than those of the wild guinea pig 3081 or the domestic Andean breed 3137 (Table 1).

DISCUSSION

The domestication of guinea pigs in South America has a long history of more than 4 and possibly 7 millennia (Wing, 1986). The process and its steps can be revealed by comparing the biological characteristics from 4 sets of animals: the wild species, the 2 living domestic breeds (Andean and European), and preserved remains from different periods in this process in the Andes. To our knowledge, our study is the first to consider these 4 groups simultaneously. In fact, our data clarify 3 particular issues about the process of cuy domestication: 1. the controversial origins from a wild species, 2. the diversification of living domestic cuyes; and 3. the biological characteristics of some antique mummies when compared with wild and domestic cuyes to evaluate their degree of domestication.

The most closely related wild species of domestic *C. porcellus* clearly seems to be *C. tschudii* rather than *C. aperea*, according to all available molecular data. The present re-analysis of molecular data on published 12S sequences, although weak in supporting the grouping of single specimens of *C. porcellus* with *C. tschudii* (Fig. 2), detected a single substitution exclusive to such a branch. More importantly, the alternative hypothesis of grouping *C. porcellus* with *C. aperea* was clearly rejected by both parsimony and maximum-likelihood methods. These results are consistent with those recently obtained from the analysis of complete cytochrome *b* gene sequences (Spotorno et al., 2004), where all maximum parsimony and likelihood analyses grouped *C. porcellus* with *C. tschudii* rather than with *C. aperea*. This topology also appeared in the cladistic analysis of corresponding amino acids, being supported by 3 amino acid substitutions and a 96% bootstrap (Fig. 5). When the *C. aperea* branch was forced to join *C. porcellus*, the
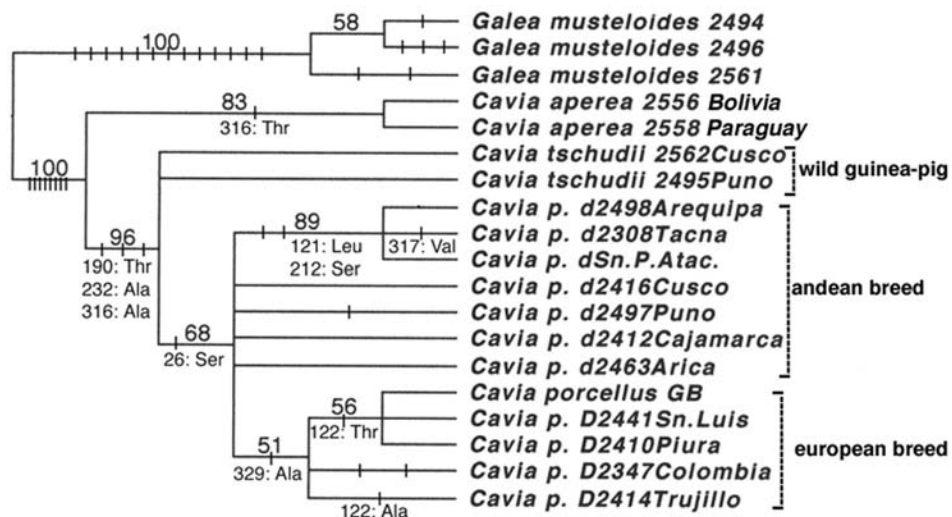
Figure 5. Consensus MP tree based on the inferred 380 amino acids of cytochrome *b* gene (51 were informative). Tree length = 779 steps. CI = 0.802 and RC = 0.72. Characters were ordered according to the outgroup. Bootstrap values (1000 replicates; >50%) over each branch. Site number below, followed by the exclusively shared amino acid substitution. Modified from Spotorno et al. (2004).

resulting trees were consistently longer, less likely, and with fewer defining characters than the best tree. If there is a living sister species to *C. porcellus*, molecular data point to the western *C. tschudii* (Eisenberg and Redford, 1999).

Based on all available data therefore, the most probable original region of cuy domestication was southern Peru and northern Chile. Concordantly, the oldest archeological site with cuy remnants is Ayamachay, in central southern Peru (Fig. 1). However, a similarly old site is located farther north, at Tequendama, near Bogotá, Colombia (Sandweiss and Wing, 1997). Examination of these remnants may provide further resolution.

The diversification of living domestic cuyes has not been studied in detail. The existence of morphological differences in at least 2 different lineages, the Andean (called "criollos" in Perú (Chauca, 1997)) and the European breeds are evident in our geometric morphometry comparisons of skull shapes (Fig. 4). Such differences were clearly documented also with cytochrome *b* gene sequences and their correspondent amino acids, where 5 European specimens clustered in a branch defined by an exclusive alanine at site 329 (Fig. 5), and supported by a 84% bootstrap in the more reliable maximum likelihood analysis of original DNA sequences (Spotorno et al., 2004). By contrast, the 7 Andean specimens studied did not cluster in a single group, although a distinct southern Perú/northern Chile lineage emerged in all analyses; it had 2 exclusive amino acid substitutions (Fig. 5) and was supported by a 99% bootstrap in maximum likelihood analyses. Thus, these data show that the Andean lineage is diverse, most probably the actual descendants of pre-Columbian lineages, and clearly distinct from the European breed. Further morphological and molecular studies of worldwide samples might detect other lineages of *C. porcellus*, in particular the old

pre-Columbian lineages still raised in many rural houses throughout the Andes. Unfortunately, the commercial dissemination of improved cuyes (Chauca, 1997) and the actual urbanization and acculturation processes acting on Andean indigenous peoples (Archetti, 1997) are increasing the mixing and loss of many of these ancient genomes.

The process towards the domestication of a mammal species appears to follow a universal pattern, producing the so-called "domestication syndrome" (Thorpe and Smartt, 1995). It is characterized by increase in body size and fertility, pelage polymorphisms, changes in the color and size of eyes, ears, and face, reduction of brain size and dentition, redistribution of body fat, and behavioral changes, among others. In the case of cuyes, the rather numerous well-preserved mummies provide the intermediate material linking the wild species to the living domestics. Now that the ancestral wild species is known, a better evaluation of the degree of domestication degree in such mummies can be performed.

Although the mummies from El Yaral and Pisagua studied here belong to a rather late pre-Columbian period (Fig. 1), they seem to be fully domesticated, according to some of the above criteria. At least 2 of them (3026 and 3137) have similar or larger sizes than mature wild *C. tschudii* and Andean *C. porcellus* (Fig. 4); the Pisagua mummy is also similar in size to adult wild *C. tschudii*. Moreover, most of them show skins with evident color polymorphisms (El Yaral, Table 1 and Plate Ia) or particular hair designs (Pisagua, Plate IIa). Finally, most of them seem to have reduced brains, judging from the low neurocranial heights of their skulls (Plates I and II), with the exception of juveniles such as 8254, 7364, and 8485 (Plate Ic, d and e, and Table 1).

Domestication traits in pre-Columbian cavies have rarely been reported. The coat color of 5 mummified young guinea pigs from Lo Demás (Fig. 1) is said to be varied (Sandweiss and Wing, 1997). Three cavies from a pre-Columbia site at Ancón, Perú "had quantities of adhering white and/or pure brown hairs" (Gilmore, 1950). The predominance of juvenile mummies usually precludes an easy detection of size increase. Nevertheless, the traits of El Yaral and Pisagua mummies described above demonstrate that guinea pigs were already domesticated between AD 300 and 1000, well before the Spaniards arrived to the Americas in the XVI century.

The domestication of guinea pigs might be briefly described as a 3-step process. The major or first domestication, from the wild species to the fully domestic pre-Columbian cuy, occurred in the western Andes. The local indigenous peoples produced there a larger, heavier, polymorphic, and smaller brained (Fig. 3c) animal than its wild ancestor. They continued to breed the Andean (or "criollo") breed or breeds for another 500 years. A second stage involved Europeans, who took a small sample from the Andean breed, and transformed it into the worldwide laboratory/pet guinea pig through a new selection regime. They produced a larger, heavier, more polymorphic, more prolific (Kunz, 2003), and smaller brained (Huckinghaus, 1961) animal than its Andean domestic ancestor. The European breed should also have less genetic diversity than its direct Andean ancestors, considering its historically documented origins (Wagner and Manning, 1976) and its molecular identity (Fig. 5). Finally, a third and more recent stage involved a modern selection regime (Chauca, 1997) to obtain a large, heavy, and prolific "improved" animal for meat production, extensively used by local restaurants along Central and South America (Morales, 1995).

About 50 years ago, in his splendid revisionary work, Gilmore (1950:460) concluded: "Hence, the rarity of the domesticated cavy in Peruvian archaeology is a

mystery and a paradox, and may be considered weighty evidence against the theory that the cavy was domesticated in the Peruvian area. However, the morphologic and genetic evidence points to the Andean Highland area, or its immediate environs, as the home of the domesticated cavy." Using new material and data, we have provided further support for an Andean origin of domestication, with *C. tschudii* being the likely ancestral form. The results presented herein appear to resolve this paradox. Nevertheless, much more work remains to be done on the biology and evolution of this gracile and useful mammal.

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APPENDIX 1: COLLECTION LOCALITIES

Collection localities of specimens examined for geometric morphometry (names follow Woods (1993); collection and number in parenthesis; acronym LCM = Laboratorio de Citogenetica de Mamiferos, Universidad de Chile, Santiago, Chile; MHN = Museo de Historia Natural, Santiago, Chile; HZEGA = Horacio Zeballos personal collection, MUSA = Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Peru.) were as follows:

Cavia tschudii. CHILE: Lluta, I Región (LCM2567, MHN371, MHN372, MHN377). PERU: Islay, Arequipa (HZEGA2, HZEGA3); Sabandia, Arequipa (MUSA104); Socabaya, Arequipa (MUSA203); Majes, Arequipa (MUSA214, MUSA217); Chiguata, Arequipa (MUSA221, MUSA237, MUSA93); Islay, Arequipa (MUSA678); Sachaca, Arequipa (MUSA88); El Cural, Arequipa (MUSA98).

Cavia porcellus. Andean creole breed. CHILE: Arica, Agromarket (LCM2477, LCM2479, LCM2489, LCM2490, LCM2506, LCM2515, LCM2524, LCM2526). PERU: Apacheta, Arequipa (MUSA100, MUSA101, MUSA219); Majes, Arequipa (MUSA215), El Cural, Arequipa (MUSA99).

Cavia porcellus European laboratory breed. CHILE: Pirbright breed, Instituto de Salud

Pública, Santiago (LCM2510,LCM2514, LCM2516, LCM2517, LCM2525, LCM2530, LCM2532, LCM2534, LCM2535, LCM2553); Criadero Lampa, Santiago (LCM293, LCM295); Criadero Florida, Santiago (LCM544). COLOMBIA: Palmira market (LCM2347).

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