

NEW PLEISTOCENE CAVE FAUNAS OF THE ANDES OF CENTRAL PERÚ: RADIOCARBON AGES AND THE SURVIVAL OF LOW LATITUDE, PLEISTOCENE DNA

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ABSTRACT

Peruvian citizens have led our team to their discoveries of Pleistocene cave faunas in the central Andes of Perú. These caves (Jatun Uchco, Departamento de Huánuco; Cueva Roselló, Departamento de Junín; and Trigo Jirka, Departamento de Huánuco) preserve numerous carnivorans (*Puma*, a sabercat [*Smilodon populator*], an unnamed large extinct felid, fox [*Lycalopex* sp.], hognose skunk [*Conepatus* sp.]), deer (cf. *Pudu* and cf. *Hippocamelus*), vicuña, an extinct horse (†*Onohippidium devillei*), a chinchillid rodent (cf. *Lagidium*), bats (*Anoura*, *Desmodus*, and *Platalina*), and sloths (†*Megatherium*, †*Scelidodon*, and †*Diabolotherium*). Bats were found only in the lowest cave (Jatun Uchco, 2,150 m), and ungulates were found only at Cueva Roselló—the only cave studied in a region of flat terrain. Trigo Jirka preserved ancient feces of a large animal and the keratin claw of †*Diabolotherium*.

Collagen for radiocarbon dating and DNA for phylogenetic studies have been isolated from bone from Cueva Roselló (3,875 m) and Trigo Jirka (2,700 m). Conventional radiometric ages from Cueva Roselló are $23,340 \pm 120$ and $22,220 \pm 130$ years before present and that of Trigo Jirka is $29,140 \pm 260$. Ancient DNA (aDNA) from †*Onohippidium* of Cueva Roselló (12° South latitude) and †*Diabolotherium* of Trigo Jirka (10° South) is being used in phylogenetic studies. The successful recovery of aDNA suggests that the cool temperatures, low humidity, and the shield from UV radiation of caves at high elevation can permit aDNA studies at low latitudes. Previously, such studies have been limited to latitudes greater than 35° for Pleistocene samples.

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INTRODUCTION

For the greatest part of the Cenozoic (the last 65 million years), South America has been an isolated continent, home to a peculiar endemic fauna that consisted mostly of marsupials, xenarthrans (armadillos, glyptodonts, anteaters, and sloths), and several groups of the now extinct native “ungulates” (Simpson 1980). This “splendid isolation” ended about three million years ago with the formation of the Panamanian land bridge that now connects South and North America (Stehli and Webb 1985). This resulted in a mixing of the faunas of both continents that reached its peak diversity after the beginning of the Great American Biotic Interchange (GABI), but before the late

Pleistocene megafaunal extinctions 10-15,000 years ago.

Recent discoveries of new cave faunas in the Andes of central Perú provide rare opportunities to sample mammals from this post-GABI / pre-megafaunal extinction period (Salas and Stucchi 2005; Anonymous 2006; Shockey et al. 2007; Figure 1). Their location is particularly fortuitous because these caves preserve samples of Pleistocene mammals from low latitudes (from 9° to just over 12° South), whereas much of the knowledge of Pleistocene South America comes from high latitude localities in Argentina (>30°). The drier conditions and cooler temperatures at high elevation negated the usual disadvantage of low latitude Pleistocene fossils—the destruction of organic



Figure 1. *The Discoverers.* The initial discoveries of the cave faunas in this study were accomplished by responsible local individuals: Iván Solano (left) was instrumental in discovering fossils in Jatun Uchco; Gonzalo Roselló (left in center photo) and his crew discovered the cave and fossils at Cueva Roselló; and Don Magno (right) discovered the cave and fossils at Trigo Jirka.

molecules in warm and humid environments (Austin et al. 1997; Wayne et al. 1999). Also, the location of the fossils within the ground provided some protection against damaging ultraviolet radiation.

Most Pleistocene fossils known from the Andes of Perú have come from caves (Pujos and Salas 2004; Salas and Stucchi 2005). Gervais (1855) reported fossils from Sansón-Machay near Cerro de Pasco in the central Andes, and Norden-skiöld (1908) reported and described remains of various taxa from Casa del Diablo Cave located on the Altiplano of southern Perú at 3,819 m. Other Peruvian Andean cave faunas include Santa Rosa, near Celdín, in northern Perú (Pujos 2002); Huargo Cave in the Departamento de Huánuco, central Perú (Cardich 1973); Tres Ventanas in the Departamento de Lima at about 4,000 m, and Pikimachay cave in the Ayacucho Valley at 2,800 m (see Pujos and Salas 2004 for a summary of these and other Andean faunas of Perú). Of these, only a few have been radiometrically dated. These include Tres Ventanas, with a ^{14}C age estimated to be greater than 40,000 BP (Engel 1970); Huargo, cave bed 8, with a ^{14}C age of $13,490 \pm 700$ BP (Cardich 1973); and Pikimachay with ^{14}C age estimates of $14,150 \pm 180$ and $19,620 \pm 3,000$ BP (McNeish et al. 1970). As far as we know, no previous radiocarbon analyses of Andean faunas of Perú were accomplished using accelerator mass spectrometry (AMS).

The purpose of this work is to summarize the results of our field studies of the three caves that contain Pleistocene faunas (a fourth cave that contained remains of a mid-Holocene spectacled bear, *Tremarctos ornatus*, is documented elsewhere [Stucchi et al. 2009]). This summary includes the basic locality data for the caves, a faunal list of taxa recovered with figures of some of the more instructive specimens, results of radiocarbon dating from bone samples from two of the caves, and a list of plant taxa of which pollen or spores were found in sediment or fecal samples. We also provide previews of recently completed and pending ancient DNA studies.

Limitations of the present study include the permitting constraints that allowed only surface collections and our desire to avoid disturbing any archaeological material. Detailed analyses regarding particular taxa are deferred for forthcoming studies that involve other investigators.

METHODS

All fossils collected have been accessioned into the Museo de Historia Natural of the Univer-

sidad Nacional Mayor de San Marcos (MUSM) in Lima, Perú. Representative samples from all taxa are being stored in a freezer at the MUSM to preserve organics for future molecular studies. Identification of the fossil vertebrates was accomplished by comparing them to specimens in the mammal departments at the Museo de Historia Natural-UNMSM and the American Museum of Natural History as well as comparative collections in the vertebrate paleontology collections of these two institutions.

Sediment samples from Jatun Uchco and Cueva Roselló and “coprolites” (ancient feces) from Trigo Jirka were submitted for palynological analysis using the palynology collection of the Laboratorio de Palinología y Paleobotánica de la Universidad Peruana Cayetano Heredia under the direction of LH. Angiosperms were identified from pollen, and spores were used to identify ferns and club mosses (i.e., *Lycopodium*).

Beta Analytical (Miami) performed the radiocarbon analyses. Bone samples were washed in de-ionized water, and the outermost layers were removed by scraping. The remaining bone materials were then crushed and washed repeatedly in HCl until the mineral apatite was eliminated. Throughout this acid treatment, the remaining collagen was inspected for rootlets, which were removed if detected. The quality of the bone preservation and quantity of collagen obtained permitted an alkali pretreatment in which the collagen was washed in NaOH to ensure that all organic acids were removed. Accelerator mass spectrometry (AMS) was performed at one of the six *International Consortium of Accelerator Laboratories* (ICAL) on graphite (100% C) that had been reduced from the collagen samples.

In addition to ^{14}C content, stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) were obtained to verify the purity of the collagen and to apply the standard correction to Measured Radiocarbon Age to obtain the Conventional Radiocarbon Age. Dates are reported as radiocarbon years before present (RCYBP, where “present” = 1950 A.D.). Errors (\pm) represent one standard deviation statistics (68% probability) and were based on combined measurements of the sample, background, and modern reference standards. The measured $^{13}\text{C}/^{12}\text{C}$ ratios were calculated relative to the PDB-1 international, standard and the ages were normalized to -25 per mil to yield the Conventional Radiocarbon Age (Stuiver and Polach 1977).

DNA samples from some bones have been isolated in the Australian Center for Ancient DNA,



Figure 2. *Jatun Uchco of Ambo, Perú.* Openings to upper and lower chambers of the caves of Jatun Uchco are indicated on the photo at left. Fossils were obtained by surface collection (right).

the University of Adelaide, Australia, and the McMaster Ancient DNA Centre, Hamilton, Ontario, Canada. A report regarding the horse (\dagger *Onohippidium* = *Hippidion*) of Cueva Roselló is forthcoming (Orlando et al. in press) and that regarding the sloth, \dagger *Diabolotherium*, will be available in a few more months. We are optimistic that other phylogenetic studies will be ultimately accomplished on a number of taxa, particularly those from our highest cave (Cueva Roselló, at 3,875 m), whose fossils appear to be exceedingly well preserved in terms of their organic content.

RESULTS

Jatun Uchco

Geographic and Geological Setting. Jatun Uchco (Quechuan for “The Big Hole”) is a network of caves that penetrates cliffs overlooking the city of Ambo, Perú in the Departamento de Huánuco (South 10° 07' 55”, West 76° 12' 07”) at an elevation of 2,150 m (about 7,050 ft above sea level) (Figure 2). Although residents of the region have known of these caves for centuries, the fossils were only discovered in 2001 (personal communication with Iván Solano, Figure 1). This was accomplished largely by Iván Solano Beteta of Ambo, who (with several friends) explored beyond dangerous passageways into the deeper galleries where he found fossils. He reported his findings to local and national authorities, which then led to our fieldwork.

Prospecting for fossils and mapping (Figure 3) occurred from the lower entrance of Jatun Uchco, which led to the Gran Galería, one of the fossil localities (JU 1). Several narrow passageways extend outward from the Gran Galería. These

include Área del Perezoso (JU 2), which leads to a lower fossil-producing area we refer to as Bajo Área del Perezoso (JU 3). Below JU 3 is a hole that produced fossils of a baby sloth. That area is denoted as Wawawasi (Quechuan for nursery) (JU 4). Still lower, in a remote part of the cave reached by Miguel Custodio Martel and our spelunking specialists (P.B. and J.-L. G), is a fossil producing locale we refer to as Sitio Miguel (JU 5). Another large tunnel leads from the Gran Galería. This hole, named Pozo Hondo, includes the localities Pozo Hondo: Repisa (JU 6), which overlies Pozo Hondo: Zona Principal (JU 7) and Pozo Hondo: Zona Lateral (JU8).

Fauna. The mammal fauna we recovered from Jatun Uchco includes six species of carnivorans (puma [*Puma* sp. cf. *P. concolor*], saber cat [*Smilodon populator*, Figure 5.1-2], a large extinct, unnamed felid allied to jaguar [*Panthera onca*], Andean fox [*Lycalopex* sp.], and skunk [*Conepatus* sp.]), at least three species of bats, and specimens from several individuals of the enigmatic sloth, \dagger *Diabolotherium nordenskioldi*, including associated partial skeletons of two individuals (Figure 4.1-2) from Área del Perezoso (JU-2). Also, a few bird bones were recovered. These bones include those of an owl and a vulture, *Coragyps* sp. (See Table 1, Figures 4-6, and Discussion.)

Flora. Analysis of pollen and spores suggests that cacti were the most common plant of the region at the time of deposition. (See Table 2.) Amaryllidaceae (flowering monocots that grow from bulbs, like lilies and daffodils) and Thymelaceae (shrubs and trees of fibrous bark) also were present.

Age. We were unable to obtain collagen of appropriate quantity or quality to obtain reliable radiocar-

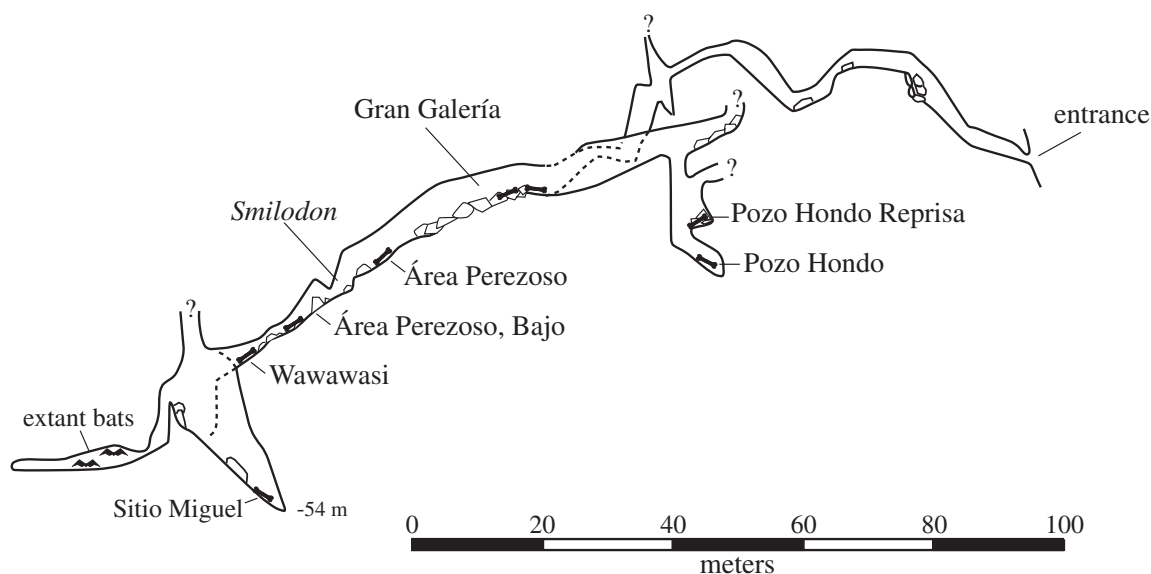


Figure 3. Vertical Section of *Jatun Uchco*. No fossils were encountered in the entrance region. Such were recovered only at the named localities, beyond the vertical tubes, suggesting that there had formally been a natural trap, which is now closed as a boulder choke. Map prepared by J.-L.G. and P.B.

bon ages from any of the bones sampled from *Jatun Uchco*. These included bones from both extinct taxa (e.g., †*Diabolotherium*, †*Smilodon*) and extant (e.g., *Puma concolor*). Thus, we still have no ^{14}C age to report for the *Jatun Uchco* fauna. The presence of the extinct taxa suggests that at least some of the fossils from *Jatun Uchco* are of Pleistocene age.

Cueva Roselló

Geographic and geological setting. Cueva Roselló is located in the Departamento de Junín at South $12^{\circ} 14' 51''$ and West $75^{\circ} 22' 34''$, about 26 km southwest of Huancayo, Perú (but a two hour drive, owing to the terrain) and 5 km southeast of the pueblo of Yanacancha at an elevation of 3,875 m (12,713 ft). The cave was discovered during travertine mining operations when it was fortuitously opened. The general manager of the mine, Gonzalo Roselló, discovered great quantities of fossils scattered about the cave floor (Figure 7) and donated them to the MUSM.

Fauna. The composition of the vertebrate fauna of Cueva Roselló is distinct from that of the other caves discussed in the dominance of ungulates, including vicuña (*Vicugna* sp.) (Figure 7), an extinct horse (†*Onhippidium devillei* = *Hippidion devillei*) (Figure 8), and a couple of deer (cf. *Pudu* sp. and cf. *Hippocamelus*). Remains of carnivorans included several partial skulls and jaws of *Puma* sp., the Andean fox, *Lycalopex* sp. (e.g., Figure 6),

and a jaw of the hognose skunk, *Conepatus* sp. Sloths were uncommon, but a partial skull and jaws of a juvenile †*Scelidodon* sp., postcranial elements of a subadult mylodontid, cf. †*Scelidodon* sp., and fragmentary remains of †*Diabolotherium* sp. were recovered.

We specifically refer the extinct horse to †*Onhippidium devillei*. The mean length and width of our sample of *Onhippidium* metatarsals ($n=4$) of Cueva Roselló was nearly identical to those reported by MacFadden for *Onhippidium devillei* from Tarija, Bolivia, the type locality of *O. devillei* (Gervais 1855, MacFadden 1997). The Roselló horse metatarsals III had a mean length of 191 mm and mean mid-shaft width of 31.7 mm; those from Tarija were 191 mm and 32.4 mm, respectively (MacFadden 1997).

Flora. No pollen was found in sediment samples of the Cueva Roselló. However, spores of the club moss *Lycopodium* were fairly common (Table 2).

Age. Collagen was extracted from two bone samples from Cueva Roselló and submitted for AMS radiocarbon dating. The bone sample of metacarpal III of †*Onhippidium devillei* yielded a conventional radiocarbon age of $23,340 \pm 120$ BP (Table 3). That of a metacarpal of *Vicugna* sp. yielded a conventional radiocarbon age of $22,220 \pm 130$ BP (Table 2), which significantly extends the record of vicuña in the Altiplano by over 10,000 years. (Previously, vicuña were thought to have migrated to

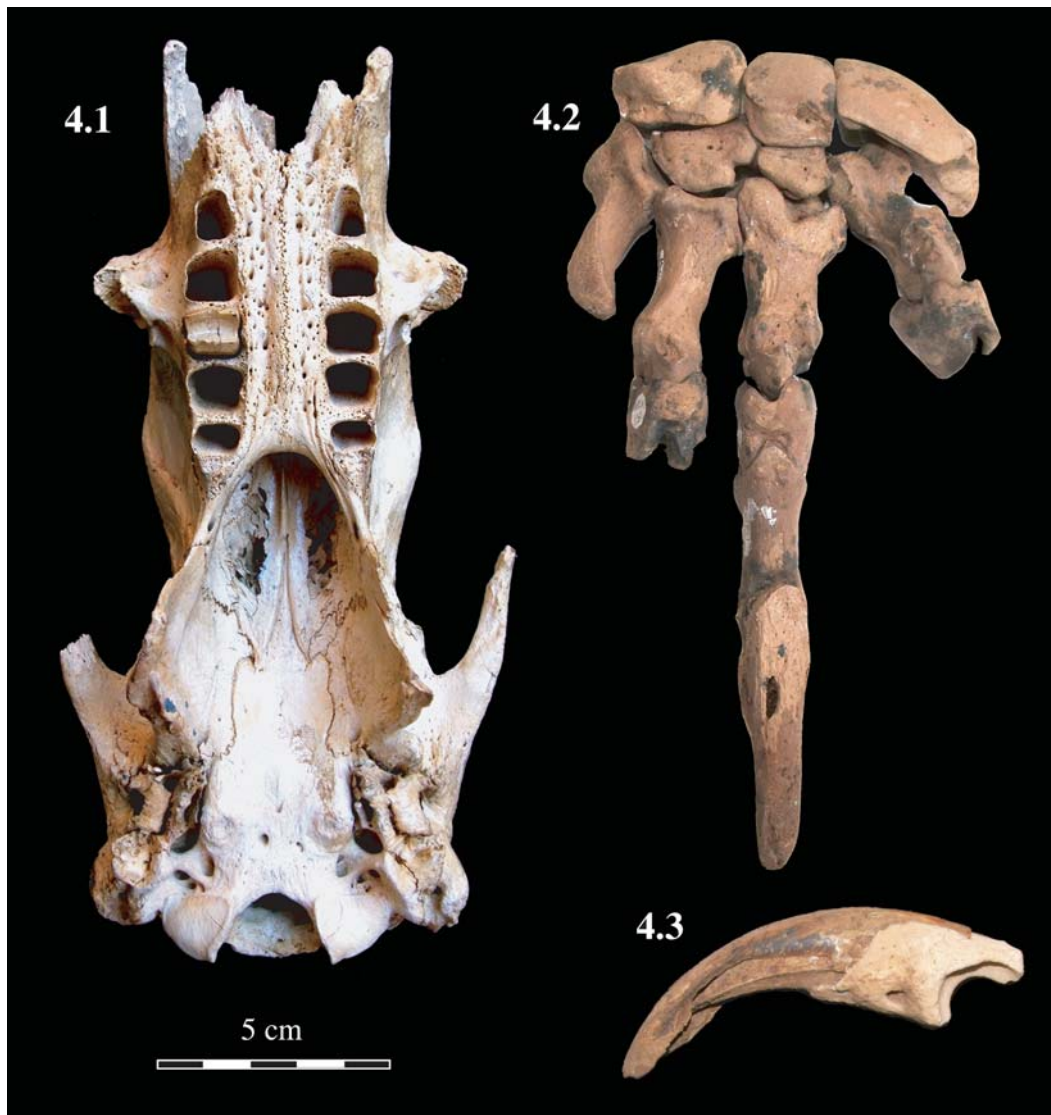


Figure 4. †*Diabolotherium nordenskioldi*. 4.1, Ventral view of skull (MUSM 1017) from Área Perezoso (JU 2) of Jatun Uchco; 4.2, nearly complete manus (MUSM 1381), also from Área Perezoso, Jatun Uchco; and 4.3, Manual claw with keratin (MUSM 1678) from Trigo Jirka. Collagen from this claw of Trigo Jirka was used for ^{14}C analysis. It yielded a conventional radiocarbon age of $29,140 \pm 260$ BP. Ancient DNA was also obtained from MUSM 1678.

the Altiplano around 12,000 to 9,000 years ago [Marin et al. 2007 and references within.]

Trigo Jirka

Geographic and geological setting. Trigo Jirka is a large opening of shallow depth in cliffs about 300 meters above the Río Marañón (Figure 9), near Huacaybamba, Departamento de Huánuco, South $9^{\circ} 7' 36''$, West $76^{\circ} 47' 48''$ at an elevation of 2700 m (8,868 ft). Fossils in this shallow cave were first discovered by Don Magno (Figure 1), who brought these fossils to the attention of R. S.-G.

Fauna. Remains of two extinct sloth species were recovered from Trigo Jirka. These are referable to †*Diabolotherium nordenskioldi* and †*Megatherium* sp. Remarkably, a ungula phalanx of *Diabolotherium* retains the protein keratin covering, despite its relatively great antiquity (see below).

Flora. Over 20 species of plants were identified from pollen and spores recovered from the ancient dung, possibly that of a large sloth (Table 2). Most of the pollen is that of *Alnus* sp., the Andean alder of the birch family, Betulaceae. There were also many spores of club moss (*Lycopodium*), ferns, and fungi.



Figure 5. Felids of Jatun Uchco. Jaws (5.1) and left humerus and radius (5.2) of †*Smilodon populator* and skull (5.3) of *Puma* sp., cf. *Puma concolor*. Scale bar = 5 cm.

Age. Accelerator mass spectrometry of collagen recovered from a distal phalanx of the sloth †*Diabolootherium* (Figure 4.3) yielded a conventional radiocarbon age of $29,140 \pm 260$ BP (Table 3).

Due to the presence of human and other archaeological remains at Trigo Jirka, we limited our field studies to making preliminary superficial examinations of trenches that had already been dug by locals. The profiles of these trenches showed a thin superficial layer of fine sediments that covered a deeper layer that contained plant material, including maize. Underlying the plant layer was a layer of dung that was a half-meter deep in places. Some of this dung retained a form that suggested it came from a very large animal. The vertical nature of the surrounding terrain

makes it unlikely that a proboscidian was the source of the half-meter deep layer of defecations (even us less climbing challenged humans had some difficulty getting to the cave), so we suspect that a large sloth may have been the source of the feces.

Excepting those remains that had been previously recovered by locals and left upon the surface, all sloth fossils we encountered were below the level in which the maize was observed. Señor Magno had previously recovered a claw of †*Diabolootherium* and he indicated that it, too, came from below the archaeological level. Its radiocarbon age of $29,140 \pm 260$ BP is consistent with Señor Magno's recollection of its level of occurrence.

Table 1. Faunal summary and physical factors of caves

FAUNAL Members		Jatun Uchco	Cueva Roselló	Trigo Jirka
Xenarthra:	† <i>Diabolotherium</i>	X	X	X
	† <i>Megatherium</i> sp.	--	--	X
	† <i>Scelidodon</i> sp.	--	X	--
Chiroptera:	<i>Anoura</i> sp.	X	--	--
	<i>Desmodus</i> sp.	X	--	--
	<i>Platalina genovensium</i>	X	--	--
Rodentia	cf. <i>Lagidium</i>	--	X	--
Carnivora	† <i>Smilodon populator</i>	X	--	--
	<i>Puma</i> , cf. <i>P. concolor</i>	X	X	--
	†Indeterminate large felid	X	--	--
	<i>Lycalopex</i> sp.	X	X	--
	<i>Conepatus</i> sp.	X	X	--
Artiodactyla:	<i>Vicugna</i> sp.	--	X	--
	<i>Pudu</i> sp.	--	X	--
	cf. <i>Hippocamelus</i> sp.	--	X	--
Perissodactyla:	† <i>Onohippidium devellei</i>	--	X	--
Ciconiiformes:	<i>Coragyps</i> sp.	X	--	--
Strigiformes:	Indeterminate owl	X	--	--
TOTAL TAXA		11	10	2
Elevation of cave		2,150 m (7,050 ft)	3,875 m (12,713 ft)	2,700 m (8,860 ft)
Terrain around cave		Cliffside	Flat	Cliffside
Latitude (S)		10° 07' 55"	12° 14' 51"	9° 07' 36"
Longitude (W)		76° 12' 07"	75° 22' 33"	76° 47' 48"
Age (ybp)		--	23,340 ± 120 22,220 ± 130	29,140 ± 260

DISCUSSION

Environmental Contexts

The three caves noted above occur in environments that differ in terms of elevation, the surrounding terrain, and the actual physical structure of the caves (Table 1). Jatun Uchco and Trigo Jirka are located within cliffsides, whereas Cueva Roselló is in a flat region. The opening to Trigo Jirka is broad and singular for this simple depression in the cliff, whereas Jatun Uchco has numerous deep and sometime steep passageways. "Boulder chokes" in Jatun Uchco block former, steep openings that may have served as natural traps.

One of the most conspicuous features regarding the remains recovered from Cueva Roselló was the non-stochastic representation of the elements of the skeleton. For example, of the hundreds of bones found, less than 10 were ribs or vertebrae. Distal limb elements far outnumbered proximal elements (e.g., whereas there were several metacarpals of †*Onohippidium*, no humerus of this animal was found) and forelimbs of vicuña far outnumbered hindlimbs (there were 30 adult *Vicugna* metacarpals, but only three complete metatarsals).

We propose the provisional hypothesis that this skewed representation of skeletal elements in Cueva Roselló occurred via predation selection and concentration (e.g., by the *Puma* and/or *Lycalopex*) rather than hydrodynamic sorting. This predator selection hypothesis is weakly supported by tooth marks on some of the specimens, but these are few and generally ambiguous (e.g., the puncture in the ascending ramus of the *Onohippidium* [MUSM 613] jaw seen in Figure 8).

Elevation, terrain, and physical structures of the caves likely influenced the composition of the fauna preserved within. Some of these factors are considered in our discussions of the faunal components below.

Fauna

Xenarthra. Sloth remains were found at all three of these new cave localities (Table 1). †*Diabolotherium nordenskioldi* was the only sloth present at Jatun Uchco, but fragmentary remains of larger sloths (†*Megatherium* and a †mylodontid) were recovered at Cueva Roselló and Trigo Jirka. †*Diabolotherium* was present at all three localities, but abundant material of this peculiar beast was recovered at Jatun Uchco. Unfortunately, we were

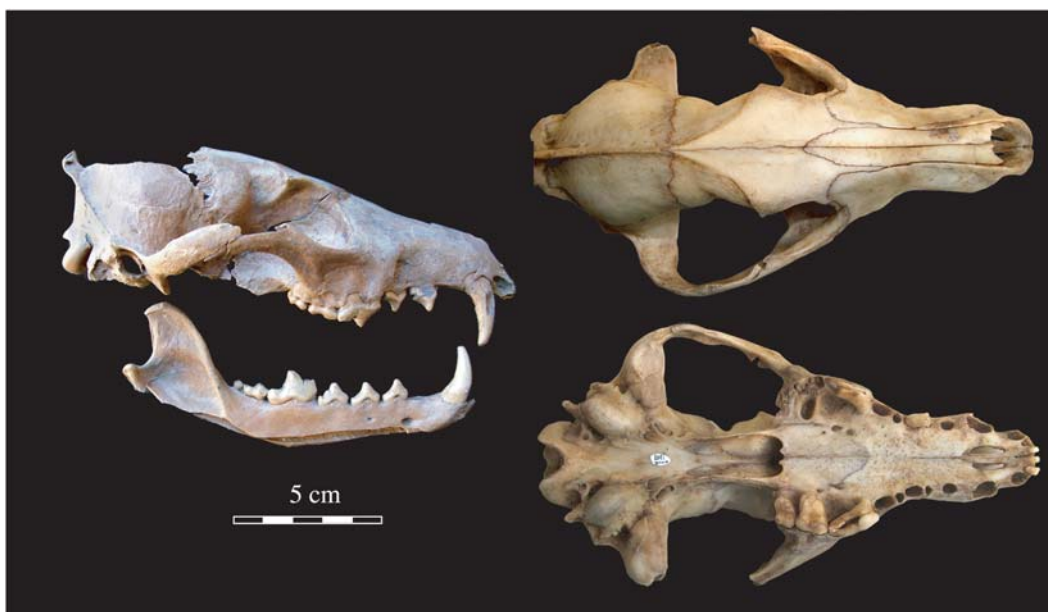


Figure 6. *Zorros*—Andean foxes. Skull of *Lycalopex* sp. of Jatun Uchco (left MUSM 679) in lateral view and one from Cueva Roselló (right, MUSM 1383) in dorsal and ventral views.

unable to obtain collagen from †*Diabolotherium* specimens of Jatun Uchco (or any other samples attempted from that locality), but organics were recovered from a Trigo Jirka specimen of †*Diabolotherium*.

Kraglievich (1926) originally placed the species now known as †*Diabolotherium nordenskioldi* in †*Nothropus*, but a recent analysis by Pujos et al. (2007) showed that it is quite distinct from †*Nothropus* species and thus assigned it a new generic name. Morphologically, †*Diabolotherium* is best described as a mosaic of primitive and derived features. Pujos et al. (2007) noted characteristics similar to Santacrucean forms (e.g., †*Hapalops*), †megatheriids, †megalonychids, and extant tree sloths (*Bradypus* and *Choloepus*). Based upon their phylogenetic analysis, they referred it to the †Megalonychidae.

Preliminary findings from the McMaster Ancient DNA Centre, based upon MUSM 1678 (Figure 4.3), suggest that †*Diabolotherium* is indeed a megalonychid. This Trigo Jirka specimen provided short nuclear amplifications for the PLCB4 gene (94 base pairs) and the CREM gene (120 base pairs). These showed no variation from the two genera of mid-Holocene Greater Antillean sloths under study, but differed from those genes of *Choloepus*, suggesting that †*Diabolotherium* was more closely related to the extinct, West Indian megalonychid taxa than to the extant, two-toed

Choloepus. Repeat sampling is in process to rule out the possibility of contamination.

No cingulate xenarthrans were found in any of the three caves. Considering that a single armadillo specimen could have produced numerous osteoderms, in addition to the usual skeletal elements, we suspect that the absence of evidence, in this case, may actually represent evidence of absence.

Chiroptera. Bats were recovered only from Jatun Uchco. These were commonly encountered and included specimens of the vampire, *Desmodus* sp., a fruit bat, *Anoura* sp., and the nectarivorous, *Platylina genovensium*. A few bats currently reside in Jatun Uchco, so it is possible that many of the bones are Recent, but we note finding some bat specimens beneath bones of extinct taxa (e.g., †*Smilodon*), suggesting that some of the bats are Pleistocene in age.

Although Cueva Roselló yielded a large sample of mammals, no bats were recovered. When one considers the elevation of Cueva Roselló (3,875 m [12,713 ft]) and the fact that bat diversity declines as elevation increases and are scarce over 3,200 meters (Graham 1983), the absence of bats is not surprising. Bats were also absent at the lower elevation Trigo Jirka, however. This may be a reflection of the small sample of fossils recovered to date from Trigo Jirka, but we also failed to detect any evidence of living bats at that shallow cave.

Table 2. Pollen and spores were identified from sediment samples from Jatun Uchco and Cueva Roselló and from a fecal sample from Trigo Jirka

Plant Family	Taxon	Jatun Uchco sediment	Cueva Rosello at 3.8 m	Cueva Rosello at 10.5 m	Trigo Jirka "coprolite"
Betulaceae	<i>Alnus</i>				159
Amaranthaceae	<i>Althernanthera</i>	1			
Amaryllidaceae	Amaryllidaceae	35			
Asteraceae	Asteraceae 22.5um				36
Asteraceae	<i>Bacharis</i>				20
Asteraceae	<i>Bidens</i>				18
Bignoniaceae	Bignoniaceae				2
Rubiaceae	<i>Borreria</i>				11
Cactaceae	Cactaceae	150			
Convolvulaceae	Convolvulaceae				1
Ericaceae	Ericaceae				3
Euphorbiaceae	Euphorbiaceae				29
Fabaceae	<i>Faboidea</i> 20um				3
Fabaceae	<i>Faboidea</i> 30um				19
Clusiaceae	Clusiaceae				2
Gentianaceae	<i>Gentiana</i>				1
Loasaceae	Loasaceae				7
Myricaceae	<i>Myrica</i>				1
Poaceae	Poaceae				47
Polygalaceae	Polygalaceae				1
Rosaceae	<i>Polylepis</i> 25um				19
Solanaceae	Solanaceae 30um				18
Solanaceae	Solanaceae 37um				10
Thymelaceae	Thymelaceae	25			
Typhaceae	<i>Typha</i>				5
	ind periporado 25um				3
	ind tricolporado 40um				1
	Total pollen	211	0	0	416
	<i>Lycopodium</i>	48	1500	2539	500
	Fern spores	0	0	0	209
	Fungal spores	0	0	0	14

Carnivora. Carnivorans were commonly encountered at Jatun Uchco and Cueva Roselló. Both localities yielded several specimens of *Puma* (c.f. *P. concolor*) and Andean foxes (*Lycalopex* sp.). Two felids discovered at Jatun Uchco are not known from Cueva Roselló. These included †*Smilodon populator* and a partial jaw of another large felid that is not referable to any taxon that we have compared it to (e.g., *Puma*, †*Smilodon*, jaguar [*Panthera onca*]), but may be an extinct species related to jaguar (Martin, personal commun., 2006).

Work in progress suggests that the *Lycalopex* specimens from Jatun Uchco and Cueva Roselló

are close to, but morphometrically distinct from, the extant zorro Andino (*Lycalopex culpaeus*) and from the much larger extinct fox †*Lycalopex peruanus* from Casa del Diablo (southern Perú).

Both Jatun Uchco and Cueva Roselló had a single specimen of a "hognose" skunk, *Conepatus* sp. Otherwise, mustelids were not recorded at any of our localities.

Ungulates. Artiodactyls and perissodactyls were only recovered at Cueva Roselló. Their absence at Jatun Uchco and Trigo Jirka is no surprise when one considers the terrain surrounding the cave entrances there. Few ungulates, especially larger bodied forms, would have been capable of climb-



Figure 7. *Cueva Roselló*. Photo (left) of the floor of cave illustrates the concentrations of fossils. Most shown are those of *Vicugna* sp. (Photo by Gonzalo Roselló.) Jaw of *Vicugna* sp. (right, MUSM 1387).

ing such cliffs and the elevations of the entrances would have made it difficult for carnivores to carry prey items to such heights along steep rock surfaces. *Cueva Roselló*, however, is located on the Altiplano, the high plains between the eastern and western ranges of the Andes. Such relatively flat terrain would have allowed ungulates close proximity to the cave. As previously mentioned, we think

that the ungulate remains were carried into the cave by predators, either puma, fox, or both.

The smallest of the ungulates was a diminutive deer, assignable to cf. *Pudu* sp. or possibly a very small species of *Mazama*. Fragmentary remains of a larger deer, apparently *Hippocamelus*, also were found.

The most common remains of any mammal at *Cueva Roselló* were those of vicuña (*Vicugna* sp.)



Figure 8. Extinct horse *Onohippidium devillei*. Mandible (left), (MUSM 613) and metapodials. (The metacarpus shows where sample was removed for radiocarbon dating.)



Figure 9. *Trigo Jirka.* Our camp (left) on the ledge beside the mouth of the cave at Trigo Jirka. The cave is about 300 m (about a 1,000 ft) above the Río Marañón (right, a view from mouth of the cave). The Marañón is a major tributary of the Amazon River.

(see Figure 7). Previously, it had been thought that vicuña did not migrate into high elevation regions of the Andes until less than 12,000 years ago (Wheeler et al. 1976; Hoffstetter 1986; Marín et al. 2007). However, our calibrated radiocarbon age of $22,220 \pm 130$ BP from bone sample of vicuña along with that of $23,340 \pm 120$ BP from a nearby (coeval or nearly so) †*Onohippidium devillei* specimen strongly suggest that vicuña migrated to the central Andes about 10,000 years earlier than previously thought.

In addition to providing organic molecules for radiocarbon dating (collagen), the †*Onohippidium devillei* specimens of Cueva Roselló also provided aDNA for a molecular phylogenetic study. Morphologically, the †*Onohippidium* of Cueva Roselló is indistinguishable from †*O. devillei* from Tarija, but it is distinct from the South American horses, †*Hippidion principale*, †*H. saldiasi*, and †*Equus insulatus* (see MacFadden 1997). How closely related †*Onohippidium* is to †*Hippidion*, and whether spe-

cies of †*Onohippidium* should be included within the priority genus †*Hippidion*, is a matter of dispute (see MacFadden 1997; Alberdi and Prado 1998). Morphological studies have not resolved this debate, but a recently completed molecular study (Orlando et al. in press) is providing more data for the analyses and discussion.

High Altitude Caves as a Refugium for Ancient DNA

DNA decay. Heat, humidity, and intense solar radiation are physical features typically associated with low latitudes. These factors contribute to the degradation of DNA (Austin et al. 1997; Wayne et al. 1999). Thus, ancient DNA (aDNA) studies at tropical latitudes have been seriously constrained. In their recent survey regarding the survival of aDNA, Karanth and Yoder (in press) found a positive relationship between latitude and successful aDNA studies. The more removed the locality is from the equator the more likely aDNA could be recovered.

Table 3. Summary data for Accelerated Mass Spectrometry (AMS) radiocarbon ages for Cueva Roselló and Trigo Jirka. All analyses were performed by Beta Analytical Lab, Miami, FL. Ages are given in years before present (BP).

Locality	Bone Sample ID N°	Taxon Sampled	Element Sampled	Measured Radiocarbon Age (BP)	$^{13}\text{C}/^{12}\text{C}$ Ratio	Conventional Radiocarbon Age (BP)*
Cueva Roselló	Beta-227440	<i>Onohippidium devillei</i>	Metacarpal III	$23,250 \pm 120$	-19.6 ‰	$23,340 \pm 120$
Cueva Roselló	Beta-237786	<i>Vicugna</i> sp.	Metacarpal	$22,110 \pm 130$	-18.2 ‰	$22,220 \pm 130$
Trigo Jirka	Beta-227438	<i>Diabolotherium</i>	Distal phalanx	$29,090 \pm 260$	-22.2 ‰	$29,140 \pm 260$

*Corrected for isotopic fractionation. Ages with 1σ laboratory standard error.

Aside from one study of domestic dogs less than 1,500 years old (Leonard et al. 2002), no aDNA had been successfully recovered from bone specimens from localities less than 20° from the equator. The lowest latitude from which aDNA had been recovered from a Pleistocene taxon was 36° (Poulakakis et al. 2002). The results of the Karanth and Yoder study suggested that aDNA could not be obtained from samples collected between 18° North and 16° South. They did, however, provide a caveat for their somewhat pessimistic conclusion—high altitude caves.

Andean Caves: cool, dry, and shielding. Although heat, humidity, and intense solar radiation are associated with tropical latitudes, these physical factors may be limited by local conditions. For example, Karanth and Yoder (in press) noted that aDNA was successfully recovered from a 3,300 ± 60 BP sea eagle of Hawaii at about 20° North latitude that had been recovered from a cave that was at an elevation of 1,463 m (Fleischer et al. 2000). They speculated that the relatively cool temperatures at the high altitude and the blockage of UV radiation by the eagle's presence within the cave facilitated the aDNA preservation.

At greater elevations, caves of the Andes provide opportunities for more extreme preservation. If indeed our radiocarbon age (over 29,000 BP) of the †*Diabolotherium* claw of Trigo Jirka is close to its actual age, then the preservation of its organic compounds (keratin, collagen, and DNA) from a specimen that old and from such a low latitude (10° South) is remarkable. Greater potential lies with the Cueva Roselló fossils. These are from a higher elevation, in a more arid region, and it includes a greater number of taxa. Extra protection against the elements may have been afforded by the fact that the cave had been naturally sealed until its accidental discovery during mining operations.

SUMMARY AND CONCLUSIONS

Recently discovered caves in the central Andes of Perú have yielded numerous fossils that provide clues regarding life in that region during the Pleistocene. Many of the specimens are well preserved and are providing a wealth of morphological and even molecular data for works in progress. Our initial results may be summarized as follows:

- Over 100 Pleistocene mammal fossils have been recovered from three caves in the Peruvian Andes and are cataloged into the research collection of MUSM, Lima, Perú. This includes the largest collection of fossil

vicuña that we are aware of, a few other ungulates, as well as bats, a chinchillid rodent, three genera of sloths, and numerous specimens of rare carnivorans. This also includes a collection of frozen bone samples that will be available for future molecular studies.

- Radiocarbon ages have been obtained for two of the Pleistocene cave faunas. Conventional radiocarbon ages from bone of a horse (†*Onohippidium devillei*) and *Vicugna* from Cueva Roselló yielded conventional radiocarbon ages of 23,340 ± 120 BP and 22,220 ± 130 BP, respectively and a †*Diabolotherium* specimen of Trigo Jirka had a radiocarbon age of 29,140 ± 260 BP (Table 3). Prior to our work, only three Pleistocene cave faunas from the Andes of Perú had been dated via radiocarbon analyses (Huarzo Cave [Cardich 1973]; Tres Ventanas [Engel 1970]; and Pikimachay [McNeish et al. 1970]. Our work is the first to use accelerator mass spectrometry to date Andean Pleistocene faunas of Perú.
- We document the oldest occurrence of vicuña in the Altiplano, extending the record from under 12,000 BP (Marín et al. 2007) to at least 22,000 BP, almost doubling the known age of this taxon in the region.
- The successful acquisition of aDNA of sufficient base pair lengths from fossils over 20,000 years of age and from latitudes less than 20° indicates that high elevation caves can be a source of material for molecular studies from low latitude Pleistocene localities. Cool dry conditions frequently encountered at high elevations can delay the degradation of DNA. Caves also shield fossils from damaging UV radiation.

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