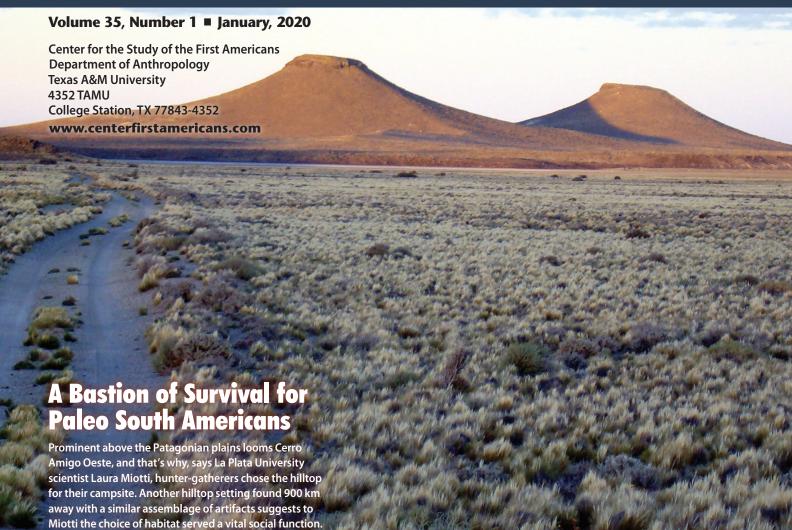


For our story of this remarkable scientist, see page 12.

Photo by Laura Miotti



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Gray wolves, Canis lupus lupus—the parental species for modern dogs, Canis lupus familiaris.

S I TYPE THESE WORDS, a wolf sits beside my chair, begging for treats. With her alert, upright ears, thick fur, powerful jaws, and large feet, she resembles a timber wolf in some ways—though her medium size, red merle coat, and brown eyes don't match the classic description. In fact, she's classified as *Canis lupus familiaris*, variety Mutt, rather than *Canis lupus lupus*—that is, she's a representative of that somewhat mysterious wolf subspecies generally known as "dog."

Why "mysterious"? Because, despite a wealth of research, the who, when, and where of dog origins remains uncertain. We know the what, and have some good guesses about how and why some wolves hitched their wagon to humanity's star. Dogs probably originated in a single wolf population that, unlike most wolves, could digest starch (a significant component of kitchen middens) thanks to a minor mutation. Interested humans selected them for docility, those proto-dogs thrived, and their descendants then spread throughout the world. Eventually, they reached the New World via Beringia.

Early European observers reported that dogs were ubiquitous in Native America—but you wouldn't be able to tell that today

INSIDE

- **5** Confirming the location of the Beringian Standstill by fire proxy Where were the forebears of the First Americans sequestered for thousands of years, western or
 - First Americans sequestered for thousands of years, western or eastern Beringia? Richard Vachula's team put their money on the east, and they back it up with evidence for fires of human agency during the LGM in Alaska.
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17 Examining the peopling of the Americas under a new lens

before 9,000 yr B.P.

What was the homeland of migrants? When did branches split from the mainstream lineage? Geneticists are finding answers in Y-chromosome data.

by looking at the genetic data. According to a paper published in the 28 August 2018 issue of the journal



Science, modern American dogs are descended almost exclusively from European dogs. Commonly referred to as the Ní Leathlobhair study after its senior author (cancer specialist Máire Ní Leathlobhair of Cambridge University Veterinary School), the study identified only one surviving concentration of Native American dog genes: a transmissible cancer, of all things.

Where did they come from?

Dogs probably accompanied the first human immigrants to the New World. The Ní Leathlobhair results indicate the ancestors of pre-contact dogs split from Siberian dogs 17,650–13,700 yr B.P., and were south of the ice sheets by sometime between 16,500 and 13,000 yr B.P. "If dogs weren't with the first wave of human migration, it was possibly the second or third wave," says Greger Larson of Oxford University, who oversaw much of the work published in the Ní Leathlobhair study.

Either way, dogs were well entrenched in Naïve American culture by 9000–10,000 CALYBP, as represented by burials at the Koster Site in Illinois. Four near-complete dog skeletons were recovered from one of the deepest levels of the site, all buried in shallow graves like their human contemporaries. This treatment suggests they were valued members of their community. So far, the Koster dogs are the oldest known indisputably dog remains in the New World.

While some have suggested the First Americans may have domesticated their own dogs from local wolves, that's unlikely. Multiple studies (including Ní Leathlobhair's) have shown that while there was some gene swapping between pre-contact dogs, coyotes, and wolves (MT 24-4, "Big black wolf"), the first American dogs were of Asian descent. Thus, they were just as much immigrants to American shores as humans—and it seems that some dogs (and presumably their people) flowed back in the opposite direction, at least for a while. The Ní Leathlobhair study included a close examination of the Canine Transmittable Venereal Tumor (CTVT) cancer, which retains the full genome of its original "founder dog." Surprisingly, they discovered that this canine, which probably lived in Asia as early as 8225 yr B.P., may

have had some coyote ancestry. Coyotes are indigenous only to North America. Furthermore, the CTVT founder dog is closely related to pre-contact American dogs. The logical conclusion is that the CTVT dog had at least some American ancestors. Indeed, it's possible that CTVT actually originated in America, though that's unlikely.

We may yet discover older dog remains that will help us determine in more absolute terms when dogs and their humans arrived on American shores. The Pleistocene fossil record is spotty in many regions of the New World, even for remains deliberately buried. And as with humans, dog populations would have to reach a certain threshold before we'd find enough remains to find and study. Even in arid, sheltered areas, human remains older than Clovis age are practically nonexistent, though we know for a fact that people



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Many years may pass between the time an important discovery is made and the acceptance of research results by the scientific community. To facilitate communication among all parties interested in staying abreast of breaking news in First Americans studies, the **Mammoth Trumpet**, a science news magazine, provides a forum for reporting and discussing new and potentially controversial information important to understanding the peopling of the Americas. We encourage submission of articles to the Managing Editor and letters to the Editor. Views published in the **Mammoth Trumpet** are the views of contributors, and do not reflect the views of the editor or **Center** personnel.

-Michael R. Waters, Director



Koster **-**:a. 10,000 BP)

were here before Clovis. Their lithic technologies and other indicators have survived at scattered locations throughout the Americas, including Buttermilk Creek in Texas, Monte Verde in Chile, Paisley Caves in Oregon, and Meadowcroft Rockshelter in Pennsylvania. If dog remains were to be found in older Pleistocene sites like these, they might very well help clarify our understanding of the ultimate age and origins of dogs not just in America, but in general.

Zhokhov Island (ca. 9000 BP)

Uyak (2000-200 BP; pre-contact)

with early human migration(s)

Second (potential) introduction

European dogs by European settlers

recent introduction of Husky dogs (Beginning ca. A.D. 1900—during gold rush))

(17,500-13,000 years ago)

First introduction

Arctic dogs by Thule

(1,000 years ago)

Third introduction

Fourth introduction

(Beginning ca. A.D. 1492)

Where did they go?

In historical records of European contact with Native Americans, writers report seeing domesticated dogs in nearly every native village. They were common, serving as pets, hunting companions, beasts of burden, and occasionally dinner. Sadly, most Native American populations were already in decline by the time the Europeans documented them, largely owing to diseases racing

ahead of the colonization front and burning through entire populations. The same was true of their dogs. Some estimates put the pre-contact human population of both continents as high as 112 million, and dogs were almost everywhere humans were. Estimating their pre-contact numbers is impossible, though it was likely in the millions.

The verdict of Ní Leathlobhair et al. is that, with the exception of the CTVT cancer, the genome of the original American dogs is now more or less extinct. According to Larson, this conclusion was unexpected. "In 2013, we began to try to get to bottom of

Zhokhov Island

Aachim
Lighthouse

Port au Choix

Weyanoke
OldTown

dog domestication with ancient DNA. We began working mostly in the Old World, then got some New World material. We weren't going to invest a lot of time in the New World DNA," he admits. "We didn't think it would yield too much. And then it turned out

everything we looked at was radically different from anything we had ever sequenced. Because we had the ancient nuclear DNA, we saw that stuff existed there that didn't exist elsewhere. It vanished when Europeans appeared."

Larson isn't entirely sure why that happened, since we see only the pattern and its product, not what caused it. It seems probable that, like their Native American masters, native dogs

Greenland dogs

Port au Choix

(ca. 4000 BP)

were nearly annihilated by an influx of diseases they had no immunities to, brought in by Europeans and their companion animals. (Ironically, CTVT may have been one of the culprits.) "What we see for the Native American people is largely true for their dogs as well, in terms of disease. We shouldn't be too surprised, as dogs and people

Proposed dog migrations into the New World.

are so conjoined," says Larson. Ultimately, "We suspect it was some combination of disease, deliberate replacement with European dogs by pastoralists, and the fact that they were outcompeted by bigger, heavier European dogs." If the surviving Native Americans adopted interesting new European dog breeds in preference to native dogs, fashion may have been as complicit in their replacement as any disease.

Are they really gone?

To some researchers, whether ancient American genes are re-

ally missing from the modern dog genome is still an open question. Not everyone in the canine research community is convinced by the Ní Leathlobhair study, in part because it directly contradicts previous studies of American dog genetics. Perhaps the most influential was published by Asch et al. in the 7 September 2013 issue of the *Proceedings of the Royal Society B: Biological Sciences*. The title of the study says it all: "Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs,

Locations and rough ages of archaeological dog remains sampled in the Ní Leathlobhair study. Each dot represents one sample.

confirmed by mtDNA analysis." For those not up on their biological terminology, mtDNA comes from mitochondria, tiny energy structures inside cells, and is passed down through the female line only. The Asch study traced the origins of a variety of dogs



from the Americas and Greenland, including far northern Thule dogs, comparing them with extensive Asian samples as well as all the pre-Columbian sequences that had been published at the time. They found no European influences in the genomes of the Thule dogs, and no more than 30% replacement for North and South American breeds.

Peter Savolainen, one of the Asch study's contributors, is known for his "ASY theory," which contends that all modern dogs originated from an Asian wolf population somewhere south

of the Yangtze River approximately 15,000-16,000 CALYBP (MT 25-1, "On the trail of the domestic dog. part I"). Dr. Savolainen asserts that the Ní Leathlobhair study isn't as clear-cut as it should be, arguing in a recent interview with Archaeology magazine that there's still a significant percentage of ancient American ancestry in modern American dogs—and that, based on his own examination of their data, Larson's crew downplayed the American ancestry they observed in some breeds. In addition, he says, they lumped all their modern American samples together, averaging those with ancient American ancestry with 100% European lineages, so that the large number of full European samples overwhelmed the smaller number of samples from breeds with significant native heritage. This drove down the percentage of ancient American dog

The phylogenetic breakdown for the samples from Ní Leathlobhair's study shows that pre-contact American dogs didn't contribute significantly to the modern dog genome.

Peopling of the Americas Zhokhov dogs ca. 15,600 Pre-contact ca. 14,600 dogs Modern dogs Zhokhov dogs Aachim dogs 20,000 10,000 15,000 5,000 yr B.P. Modern dogs Arctic doas

Pre-contact dogs

monophyletic clade," Larson states, meaning that all the pre-Columbian dogs were closely related to one another. "All those dogs we see prior to European arrival are radically different to European dogs. If there was going to be continuity, you would expect the modern dogs to all have a mitochondrial signature that fits the old dogs."

Critics also point out that Thule dogs—like historic Eskimo, Inuit, and Greenland dogs, which arrived about 1000 CALYBP and may have completely non-European genomes—were left

out of the Ní Leathlobhair study. Larson freely admits to this, though he can't say much more, owing to ongoing research. "We have numerous lineages of dogs found in sites from Greenland to Beringia. They're different from pre-Columbian dogs, and seem to be mostly East Asian. How they fit in with the rest of the dogs is something we're working on."

An interesting fact Larsen calls to our attention is that lineages of humans worldwide seem to be associated with the same lineages of dogs for thousands of years. "People and their animals have a very tight connection," het says. "We're happy to let dogs into the house. The evolutionary history of humans is closely tied to the evolution of their dogs: dogs and humans co-evolved."

In the Americas, it seems the two species not only lived together—they also died together, unable to cope with the negative aspects of European

contact. "People and dogs both had distinct lineages in the New World; their resistance to disease and how they were wiped out mirrors each other," Larson explains. Some of the human populations survived, though not without drastic demographic shifts. But if Larson and his colleagues are correct, the original dogs of the Americas never recovered. Barring some scientific miracle, America's lost dogs are gone for good.

-Floyd Largent

genes cited in their study to an insignificant level. Plus, he said, they compared their ancient samples with an incomplete modern collection, while failing to see the ancient component in those lineages.

Larson counters the Asch study's findings (and Savolainen's criticism) by pointing out that the data used in the 2013 study were derived completely from mitochondrial samples. The Ní Leathlobhair study looked at more than just mtDNA, focusing also on more inclusive nuclear DNA. "What [Asch et al.'s] studies are based on is modern samples looking at female descent, which doesn't provide a direct sense of their heritage. They're going from today to the past; we're including an analysis of all the dogs from ancient times and modern—including all of Peter's. Less than .03% of all dogs we have looked at have mitochondrial signals that originate before the arrival of Europeans."

Furthermore, when Savolainen and his colleagues were doing their research, they didn't have access to the 87 samples now available from pre-Columbian sites. "They all form a

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95% highest-probability density

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O PROVE THAT HUMANS were present in a region is easy if you have artifacts—tools, weapons, trinkets, even stones arranged into a hearth and, with luck, accompanied by charcoal. The task is much more difficult when the parcel of land is the size of northern Alaska, the human population comprises only a few individuals, and the hope of finding any tangible evidence of their presence is a pipe dream. If this isn't

complicated enough, the timeframe adds another layer of frustration, for the period of interest is the Last Glacial Maximum (LGM). This is the task Richard Vachula, a Ph.D. candidate at the Brown University Institute for Environment and Society, and his team set for themselves. Their goal was to topple a moribund scientific model and bolster support for its successor.

Time for fresh thinking

An entrenched scientific model, like an impacted wisdom tooth, can be devilishly hard to dislodge. For generations, the model of the peopling of the Americas that dominated anthropologists' thinking was straightforward: At the end of the Pleistocene, Northeast Asians trod across the Bering Land Bridge. The Cordilleran and Laurentide Ice Sheets having conveniently parted, the newcomers, now identified as Clovis and bearing their distinctive fluted projectile point, continued their journey south by way of the Ice-Free Corridor and proceeded to populate the Americas.

Mavericks have been hacking away at the model ever since Junius Bird in 1934 discovered an occupation on the Straits of Magel-

lan at least as old as Clovis (MT 23-4, 24-1, "In the footsteps of Junius Bird"). The discovery of an occupation as early as 18,000 yr B.P. at Monte Verde in Chile threw a monkey wrench into the works (MT 33-3, "Tom Dillehay: The Clovis-First iconoclast"), and human coprolites found in the Paisley Caves

Lake E5

Bluefish

Dawson

in Oregon dating 1,000 years before Clovis (MT25-4, 26-1, "Paisley Caves: What's the scoop on the poop?") convinced even die-hard boosters that Clovis-First was a thoroughly discredited premise.

Almost ready to take the place of the shattered model is the Beringian Standstill Hypothesis (BSH). *Almost*, because one crucial element has yet to be proved to the satisfaction of the scientific community.

The BSH was conceived in response to the startling discovery that *all* Native Americans in

the New World share genetic lineage different from that of Northeast Asians (MT 34-2, "Beringian child's genome reveals the founding population of the First Americans"). But where did this founding population come from? How did it arise? The solution proposed by the BSH is that the first Native Americans came into being in Beringia as a result of immigrants from Northeast Asia being genetically sequestered, isolated for a period long enough

Plumbing the Depths for Human Presence



that they accumulated sufficient genetic diversity to render them distinct from their forebears, a duration geneticists estimate at 2,400–9,000 years. If this newborn population provided the hardy colonizers that ventured south, either by foot or by boat, and populated North and South America in occupations that date

to more than 14,000 years ago, then their period of isolation must have begun quite early, in fact, during the LGM.

This imaginative hypothesis is indeed attracting proponents. They differ, however, in where they place the hypothesized melting pot. Many authorities argue for western Beringia, on or close to the Asian mainland, because of the dearth of archaeological evidence in eastern Beringia. Anthropologist Lauriane Bourgeon of the University of Montreal scored a victory for champions of eastern Beringia when she ascertained that mammal bones found in the Bluefish Caves of the Yukon, near easternmost Beringia, bore cutmarks and therefore registered

human presence as early as 24,000 yr B.P., the onset of the LGM (MT 33-2. "The Bluefish Caves: Proving the Beringian



Standstill Hypothesis"). Mere presence, however, isn't enough to convince western-Beringia adherents. One family of daring hunter-gatherers, they argue, doesn't constitute a founding population.

This is the crucial missing element of the BSH that Vachula and his team, who propose eastern Beringia as the birthplace of the founding population, were determined to produce: proof of the presence of a founding population in eastern Beringia dur-

ing the LGM in the absence of archaeological sites and artifacts.

Lake sediments: A window into the past

Lake E5 is located in the northern foothills of the Brooks Range. In the Quaternary period, the Brooks Range hosted alpine glaciers, which contributed to the geomorphology of the North Slope. Lake

A southward view of Lake E5 with the Brooks Range in the background.

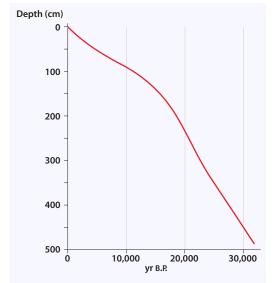
E5, however, sits on an older glacial landscape known as the Sagavanirktok, which escaped glaciation during the last Ice Age. It therefore preserves a record of environmental changes during the LGM. Because it was one of the few sources of freshwater in a predominantly arid region, the Lake E5 watershed may also have attracted temporary or sustained human occupation.

Vachula tells us that his team's essential task was to create a timeline of different depths of the sediment cores taken from Lake E5. "We look at a sediment core and look for pieces of wood

or insects, or any other organic material that we can date. You need quite a bit of carbon to get a good radiocarbon date out of a lake sediment core, and there are difficulties in obtaining enough carbon. Plus, in the Arctic, dates tend to be older because matter has been sitting on the landscape before getting washed into a lake.

"After obtaining a radiocarbon date, we then converted the radiocarbon years

Approximate age vs. depth of the Lake E5 sediment core.



to years-before-present on a calendar, and using that we were able to determine the depth-age relationship of the sediment core. All the analyses we did were based on sediment samples in that same core," Vachula says. "Our age-depth model was one of the best in this region in terms of the number of dates."

Natural vs. anthropogenic causes of fire

The first approach of the team was to investigate whether the landscape had been altered by fire during the LGM to a degree that could be attributed to human agency.

Humans have altered landscapes around the world for thousands of years through their use of fire. However, the intensity and extent of anthropogenic burning in many regions remains unresolved. Most reconstructions of past fire regimes focus on

variations in the concentration of charcoal particles preserved in the sediments of lakes and other wetlands. Such records reveal the occurrence of fire and variations in the frequency and timing of biomass burning, but fail to determine the agency of ignition, natural or human.

To distinguish naturally caused fires from those started by hu-

mans is a challenge. Instances where the quality of vegetation and climatic conditions make naturally caused fires unlikely are often offered as indirect evidence for anthropogenic burning. Identifying human presence in ancient watersheds relies on archaeological data, but few archaeological sites yield evidence for local fire use. Consequently, linking past changes in vegetation and fire with human activity is largely inferential.

Sparking an interest

Vachula recalls in 2007 a huge fire occurred in the tundra of northern Alaska. "It was unprecedented and larger than anything anyone had observed, so that spurred a lot of scientific interest into how these fires occur and what impact they have on ecosystems."

At Brown University, Vachula is working to reconstruct the fire history of ecosystems from charcoal particles found in sediments from lakes that span the Holocene (about the last 10,000 years). Although most lakes in Alaska date to the Holocene, the Lake E5 record spans about 32,000 years, "a rare glimpse into that period of time in terms of sediments." His team's goal was to determine whether the incidence of fires corresponded to climate changes associated with deglaciation. The Pleistocene–Holocene transition was a period of severe fluctuations in climate: Toward the end of the last glacial period,

the Allerød oscillation (about 13,900–12,900 yr B.P.), a warm and moist global interstadial, raised temperatures; the succeeding glacial Younger Dryas (about 12,900–11,700 yr B.P.) was followed by the present warm Holocene. What Vachula's team found was evidence for fire predominantly in the LGM.



Sources of ignition

Vachula's team was surprised to discover that in the Alaskan Arctic, fires occurred more frequently during the cooler LGM than during deglaciation and into the Holocene. Surprising, because one would expect burning to decrease with cooler temperatures.

Researchers Eisner and Coinvaux in their 1990 study interpreted aridity as the principal cause of pronounced LGM burning. But it's important, Vachula cautions, to consider the role of temperature. He notes that the huge fire in 2007 on the North Slope of Alaska occurred during a warm, dry summer. Warmer temperatures increase evaporation, which further dries out

the landscape. Concerning tundra fires, warmer temperatures are accompanied by drier conditions, which increase the flammability of tundra. What's involved is a temperature-driven moisture balance.

Vachula's colleagues are preparing to publish temperature and hydrology records from the same Lake E5 sediment core. Vachula mentions published data that suggest that the climate during the LGM was colder and drier. "That's one of our biggest uncertainties," he admits, "whether we control for the role of aridity in promoting burning. But ev-

erything we know about tundra fires, at least in the Holocene, would suggest that colder temperatures actually *decrease* the likelihood of fires *by natural causes*. We see that warmer and drier temperatures promote burning in tundra at least within observational records. Temperature is the most important factor relative to aridity."

It's significant that at the time of Eisner and Coinvaux's 1990 study, it was assumed that humans couldn't survive in Arctic Glacial climate conditions, an assumption that has since been refuted by genetic evidence. At that time, Vachula emphasizes, "scholars didn't even consider human populations as a potential ignition source for Arctic fires."

Decreased lightning frequency

Lightning strikes are the principal agent in most regions for non-anthropogenic fire ignitions. North of the Brooks Range, however, the frequency of lightning strikes is among the lowest observed on Earth. Although tundra fires are relatively frequent in lower-latitude regions of Alaska, the North Slope Foothills and Coastal Plain hosted only 11% of the total number of observed Alaskan tundra fires over a 74-year period. Here the

arid conditions of the LGM, which increased the likelihood of ignition, were offset by decreased frequency of lightning strikes.

To fathom the effect of these conflicting agents, Vachula's team looked at the FAMOUS climate model simulation. "It was run using earth system characteristics over the last 120,000 years," Vachula explains. "We just looked at our region. We were trying to figure out the amount of convective energy available for lightning strikes." A rough estimate of what they could expect can be inferred from present conditions, which have produced very few lightning strikes in the past 30 years. As expected, the model indicated a low Convective Cloud Fraction (CCF), an index of thunderstorm and lightning activity. This low CCF value, cou-

pled with low temperatures, low evaporation rates, and low frequency of lightning strikes, "eliminated the background climate as the source of those ignitions, which suggests even more that humans were responsible." Vachula says.

For Vachula and his team, the greatest challenge of this project was identifying humans as the cause of the multitude of fires in northern Alaska during the LGM. Given the prevailing climate, naturally occurring fires couldn't have produced the substantial quantity of charcoal and the high levels of polycyclic aromatic hydrocarbons (PAHs)

Paleolimnologic data from Lake E5 sediment core. A, charcoal density used to calculate fire events. B, frequency of fires; points on baseline register events falling in the 90th percentile. C, coprostanol:stigmastanol ratios; the purple line indicates the ratio corresponding to mammoth feces (van Geel et al., 2011).

Copr:Stig

0.8

0.6

0.4

0.7

Fire freq. (fire/kyr)

3

B

2

1

0

Charcoal (cm²/yr)

2.5

2

A

1.5

1

0.5

0

30

25

20

15

10

5

0

preserved in the sediments at Lake E5. (PAHs are a residue of the incomplete combustion of organic matter. The principal source of PAHs in today's environment is human-initiated burning of wood, dung, and crop remains.)

What was needed now was confirming evidence, direct or indirect, that humans were indeed present. For that, the team turned to analyzing biomarkers in the sediment cores.

A lengthy record of defecation

Fecal sterols, produced in the guts of mammals as they digest plant and animal sterols, such as cholesterol, are familiar to scientists. Different mammal species produce varying ratios of sterols, and they have been used by archaeologists to determine whether ancient farmers used manure on their fields and to pinpoint the location of ancient latrines. Modern environmental scientists use them to detect sewage contamination in deltas and estuaries.

No one, though, seemed to have looked for sterols in a sediment core until Rob D'Anjou, a graduate student in geoscience at the University of Massachusetts Amherst, published his research in *Proceedings of the National Academy of Sciences* in



2012. Analyzing two narrow columns of silt, mud, and other sediment cored from the bottom of Lake Liland in Arctic Norway, he recognized chemical compounds that turned out to be human fecal sterols.

It's now possible to detect human presence and early human migration by analyzing trends in soil and sediment accumulation of fecal sterols, chemical compounds which are crucial in human physiology. Human fecal presence is indicated by a distinct ratio of coprostanol:stigmastanol of 2.22–5.5, at least an order of magnitude higher than that of woolly mammoth.

The biomarkers Vachula measured reflect a composite mix-

ture of all fecal inputs of the Lake E5 sediment. Since 94% of animal biomass (mammoth, horse, and bison) in the paleontological record of pre-Holocene Alaska would provide fecal inputs with coprostanol:stigmastanol ratios of less than 0.18, deviations of sedimentary assemblages above this ratio indicate a human fecal contribution. Vachula tells us the team only considered stanols, which are sterols containing no double bonds between the carbon atoms, as these are more resistant to diagenesis (physical and chemical changes occurring during the conversion of sediment to sedimentary rock) than sterols, which contain double bonds.

Omnivores could have contributed

Climatologic data modeled by FAMOUS. **A**, anomalies of precipitation minus evaporation calculated from evaporation (**B**) and precipitation (**C**). **D**, temperature. Anomalies are calculated relative to mean pre-Industrial values (AD 850e1850).

coprostanol to the assemblages, but their biomass would have been negligible relative to the megafauna of the mammoth steppe, so they wouldn't have altered the coprostanol: stigmastanol ratios. "Coprostanol is found only in human feces or omnivore feces. Based on the animals that were out there during this time, chances are there were some omnivores, but it was predominantly herbivores, so humans would have been the biggest contributors of comprostanol," Vachula says.

Values exceeding the 0.18 value of mammoth dung therefore most likely reflect human fecal input. And coprostanol:stigmastanol values consistently exceed the 0.18 threshold after ca. 18,000 yr B.P., which may represent either more permanent human settlement or a decline in the herbivore population relative to humans. The takeaway message: Fluxes of both coprostanol and stigmastanol are greatest during the LGM at Lake E5, and elevated fluxes of coprostanol:stigmastanol have been interpreted to reflect human presence.

"When we measured fecal sterols, that became the smoking

gun of human presence," says Vachula. "Evidence of human presence was coincident with evidence of fire. That was a big surprise! We measured the fecal sterols after we measured everything else, because we couldn't figure out what had happened. We needed that line of evidence."

Early human arrival in eastern Beringia

Human fecal sterol presence coincident with numerous fires demonstrates that humans were present in eastern Beringia as early as 32,000 yr B.P. Humans therefore occupied eastern Beringia at the same time they inhabited Siberia, and by use

of fire they altered Arctic landscapes during the LGM. This early date of entry into eastern Beringia also signifies that humans coexisted with megafauna for a substantial period of time.

Vachula's data weigh heavily in the debate regarding whether humans or climate change caused megafauna extinction. "Some people say it's both at the same time. Our findings offer a new view on that." Although megafauna and humans coexisted in Beringia since at least 32,000 yr B.P., the paleontological record shows that megafaunal extinctions in the northern foothills of the Brooks Range didn't begin until 13,000 yr B.P. This means that, during the Pleistocene, humans practiced sustainable megafauna hunting in Beringia for nearly 20,000 years. That late-Pleistocene extinctions in eastern Beringia coincide with

ΔPrecip.
ΔPrecip.
(kg/m²/s)
2E-06

-4E-06

ΔEvap.
(kg/m²/s)
1E-06

ΔP-E.
(kg/m²/s)
1E-06

severe changes in the climate and environment argues for climate change as the dominant agent in megafauna extinctions.

In support of the Beringian Standstill Hypothesis

Vachula's study indicates humans were present in eastern Beringia well before they became genetically isolated from their Asian ancestors. Vachula explains, "We know there was some kind of genetic isolation happening between these three groups: Asian peoples, Beringian peoples, and Native American peoples. Now we have a place where this can be inferred. We just need to work out the timing, which relies on genetics."

The Yana River sites in northern Siberia (**MT 19-3, -4, 20-1,** "Yana River, Siberia: Implications for the peopling of the Americas") verify human presence in western Beringia at 32,000 yr B.P.; the Bluefish Caves site confirms human presence in eastern Beringia during the LGM, by at least 24,000 yr B.P., thus supporting the BSH. The paucity of archaeological

continued on page 17



Dung Fungus and Megafaunal Extinctions



N THE LAST SIX DECADES OR SO, researchers have become increasingly clever in their efforts to glean knowledge about the past from the most unusual sources, clarifying our view of the ancient world a bit more with each breakthrough. Arguably, the trend began with dendrochronology, the study of tree rings; later came radiocarbon dating, the Holy Grail for dating relatively recent organics. Then we learned how to tease data out of what had formerly been discarded as useless. Burnt earth and rock can now be roughly dated with thermoluminescence; archaeomagnetic dat-

dated with thermoluminescence; archaeomagnetic dating allows us to find true north at the time a feature was formed; and the parasite load and pollen content of human feces have made coprolites priceless indicators of ancient lifeways and environments. The microscopic evidence has proven surprisingly rich. Some of this evidence is indirect, in that specific organisms, elements, or natural objects associated with our subjects (but not *part* of them) provide evidence of what happened to those subjects—be they human beings, megafauna, or an entire hemisphere. These clues are known as microproxies.

For those who study megafauna extinctions, dung fungi have recently emerged as prized microproxies. Numerous types have been studied, their spores isolated from well-dated sedimentary cores for analysis. The brightest star in this category is *Sporormiella*, a fungus that grows on the dung of herbivores. It's prized for its ubiquity and sensitivity to the fluctuations of large-herbivore populations. Nowadays, one of its most dedicated researchers is Angelina Perrotti, who recently obtained her doctorate from the Department of Anthropology at Texas A&M University, the current base of operations for the CSFA. In

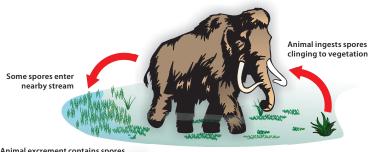
conjunction with Eline van Asperen of Durham University, UK, Dr. Perrotti published a landmark paper in the 6 June 2018 issue of the journal *Vegetation History and Archaeobotany*, "Dung fungi as a proxy for megaherbivores: Opportunities and limitations for archaeological applications." During their research, Perrotti and van Asperen combed the mycological literature for research on 10 dung fungi taxa, and their value as megaherbivore proxies.

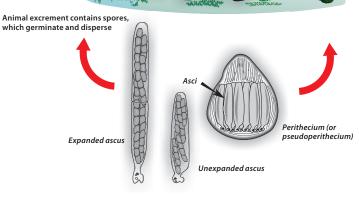
Why dung fungus is so useful a proxy

The end of the Pleistocene was a chaotic period for the Northern Hemisphere. That was when humans first entered the New World, though we're still not sure precisely when, since the date keeps getting pushed back in time by new discoveries. At the end of the epoch, about 30 genera of large animals died out, most likely due to relatively abrupt habitat change, the introduction of new diseases, and, possibly, a coup de grâce by human hunters.

For the last decade, we've probably been less certain about when and how humans arrived in the New World than we were during the previous 30+ years. Back then, Clovis-First seemed reasonable and obvious to most researchers . . . but evidence for earlier occupations was already available, and

it just kept piling up until the First Americans paradigm had no choice but to change. We've chronicled that shift and its effects in the pages of this magazine many times (MT 20-4, "Early Americans in Western Beringia: Pre-Clovis traces at Swan Point", MT 22-3, -4, "Clovis dethroned," and MT 25-4, "Paisley Caves, Part I"). But it remains a mother lode ripe for discovery, and the out-of-the-traditional-box thinking of researchers like Perrotti and van Asperen is still smelting the ore of it, helping to refine the truth.





FROM PERROTTI AND VAN ASPEREN, 2019



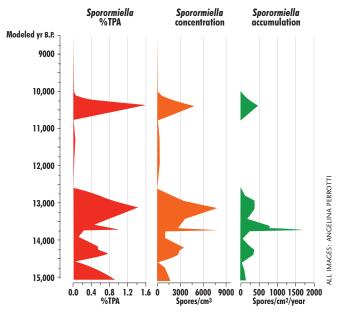
The dung-fungus connection began in the 1980s, when Owen K. Davis observed high levels of *Sporormiella* in historic sediments *and* in Pleistocene sediments at six of seven sites in the American West, and their rarity during the 10,000 years in between. This led him to propose that the high frequencies of *Sporormiella* reflected the reintroduction of large herbivores in the past few hundred years—and the presence of megaherbivores before they died out approximately 11,000 RCYBP (about 13,000 CALYBP). He proposed examining dung fungus frequencies as one way to detect the prehistoric abundance of megaherbivores when macrofossils were lacking, and that researchers use their absence as a marker to estimate the local timing of megaherbivore extinctions.

The idea took a while to take hold, but in a study published in 2009, Jacquelyn Gill, Jack Williams, and colleagues used it to pinpoint the date range of mammoth and mastodon extinctions

in New York and Indiana by examining lakebed sediments. They employed a paleoecological and palynological approach to compare the relative frequencies of *Sporormiella* and other microproxies in sediments from a series of well-dated deep cores.

But why use dung fungus, and *Sporormiella* in particular? Largely because they're dung-dependent, especially *Sporormiella*. It subsists on the undigested organic matter in herbivore dung, so researchers don't have to worry about

Sporormiella concentrations from Page-Ladson, Florida.



mixing up carnivore "signals" with those of herbivores. And one thing's for sure: In ancient North America, proboscideans produced more dung for fungus to colonize than any other herbivores, mega- or otherwise. In addition, *Sporormiella* spores are common and easily identifiable, and as Perrotti points out, "It's typically well preserved in sediments, even when other indicators of megaherbivore abundance are absent." All this provides a handy index of large-herbivore abundance. Ultimately, with its presence in sediments across North America, *Sporormiella* helps fill in gaps in the fossil and geological record. It's also easily linked to changes in vegetation regimes via associated pollen and plant macrofossils, as well as to absolute dates determined by other means.

Perrotti started working with *Sporormiella* in 2014 at the Page-Ladson site on the Aucilla River in Florida, a rich trove of archaeological and paleontological treasures. The *Sporormiella* record from local cores revealed that humans occupied the area for approximately 2,000 years *before* megaherbivores like mammoths vanished around 12,600 CALYBP (MT 32-2, "The opposite of overkill: *Sporormiella* evidence from the Page-Lad-

son site"). She reports, "It was actually Jacquelyn Gill's work that prompted those of us working at Page-Ladson to consider using it at the site. It proved to be a really interesting approach to take at Page-Ladson, since there are so many megaherbivore remains preserved in the Aucilla River."

In some parts of the world, however, researchers have been quick to blame humans alone for megafauna extinctions based on *Sporormiella* studies. For example, in one study published in *Nature* in 2017 tracing the *Sporormiella* record of southwestern Australia from 150,000 years ago forward, the researchers reported substantial changes in vegetation and fire regimes about 70,000 CALYBP. During this period, *Sporormiella* frequencies remained high. They also observed a sharp decline in *Sporormiella* frequencies 45,000–43,100 years ago. The researchers noted that this occurred within 4,000 years of human dispersal throughout Australia, which began about

47,000 years ago. Based on their own studies, however, Perrotti and van Asperen assert that *Sporormiella* is an unreliable proxy for initial human occupation of a region—and the 4,000-year overlap between humans and megafauna in Australia suggests they are correct.

Treading carefully

While useful, *Sporormiella* isn't the be-all-and-end-all of dung-fungus proxies. "In our paper, we discussed 10 commonly encountered dung fungi taxa, and how obligate each taxon is to herbivore dung," Perrotti explains. "I'm including all 10 in my current research, which is a survey of dung-fungal spores across multiple end-Pleistocene records across the eastern U.S. Researchers should

actually expand their analyses to include other dung fungi taxa in addition to *Sporormiella*." She cites *Coniochaeta* as a fungus sometimes used as a megaherbivore indicator, although it sometimes grows on decaying wood and plant remains.

Nor is *Sporormiella* infallible as a proxy; it too sometimes grows on dead wood or in soil. Meanwhile, *Podospora*, another common fungus, grows almost exclusively on dung, as do other taxa like *Delitschia* and *Ascodesmis*. Furthermore, "It's important to consider all of the other factors that influence *Sporormiella* reproduction," Perrotti notes. "*Sporormiella* should be used as a piece of the puzzle, rather than the whole story. We outlined many factors that can contribute to the formation of a fungal-spore record in addition to herbivore abundance, so these should all be taken into consideration when interpreting the data."

In some cases, erosion by wind and rain, or concentration in a drainage basin, could conceivably affect *Sporormiella* frequencies. And it's possible that, say, a rabbit population explosion might result in a false signal for megaherbivores, though several factors militate against that possibility. First of all, it takes a *whole* lot of rabbits (and even more field mice!) to produce the same



volume of dung as one mammoth or mastodon. Second, such a population explosion would be so brief that it might not even be noticeable in the pollen record; predators and carrying capacity would soon suppress populations to normal levels. Meanwhile, Sporormiella populations remained high for thousands of years.

And that's not all. "The fact that Sporormiella declines at the end of the Pleistocene in sediment records across North America is a striking relationship, which I think is very meaningful," Perrotti says. "However, looking at a spore decline at an individual site can be tricky. There are many factors that can influence spore abundance in a sediment core, such as changes in hydrologic conditions, including water level at a coring site, environmental fluctuations that provide a more or less favorable environment for fungal reproduction, and the presence of other coprophiles such as insects or other fungi."



Palynology has long since proven itself invaluable, and dung fungus proxies offer the potential to firm up our understanding of a period currently in scientific turmoil. Knowing that humans and mammoths coexisted for two millennia on the Aucilla River in Florida provided a steadying hand; the Perrotti and van Asperen paper in Vegetation History and Archaeobotany offers another. Unfortunately, Sporormiella and its relatives can only take us so far back into the past of North America. It would be wonderful to check the North American

Perrotti in the field in Alaska, summer 2018.

Microdetectives and the future of archaeology

There was a time when archaeologists tossed coprolites out of dry cave sites like Frisbees, not knowing what they were literally throwing away. When potsherds were common

at a site, the extras might be discarded in great heaps (see videos of Snaketown from the 1930s), or used as poker chips in casual evening games. Few thought to collect soil samples for posterity, or to search for microscopic clues in that soil-and there are many, from pollen to nanodiamonds. Luckily, it's standard practice to leave at least part of a significant site unexcavated, just in case future researchers invent new investigative methods. They have indeed done; in many ways, they've exceeded our

fondest hopes. The fact that researchers are now taking the literal minutiae of archaeological sites seriously as such specialization becomes possible is a boon for the field. It's made us better researchers. It's made it easier for us to date sites, both relatively and absolutely—and we're starting to tease out the answers to questions that have haunted the discipline for centuries, including the true origins of the First Americans and their dispersal through the New World. We still have much to learn, but now we understand that for years, we were laboring under the burden of not knowing what we didn't know. We're starting to get some glimmer of the truth; and if it's causing some tremors in the field, well, isn't that how science works?

Pleistocene for earlier extinctions or *Sporormiella* declines, but it's difficult to find dung fungal-spore records from earlier than the Last Glacial Maximum (LGM). Sediment records older than 20,000 years are rare in North America. However, "There actually are a few North American sediment records that extend ear-

lier than the LGM, for which dung fungal spores have been analyzed," Perrotti says, "including research by me, not yet published. This is a question I'm really

off most of the American megafauna? Or did sharp population declines also occur earlier in the Pleistocene, before humans ever found the Americas? Right now, there's no way to know for sure. But if we could get our hands on the right

interested in." Are humans really to blame for killing

Common dung fungi: A, Arnium sp.;

B, Arnium imitans; **C**, Apiosordaria;

D, Cercophora; E, Coniochaeta;

F, Podosopora; **G**, Sordaria;

H-I, Sporormiella; J, Trichodelitschia.

deep-time sediments, we might soon be able to answer these and other pressing research questions.

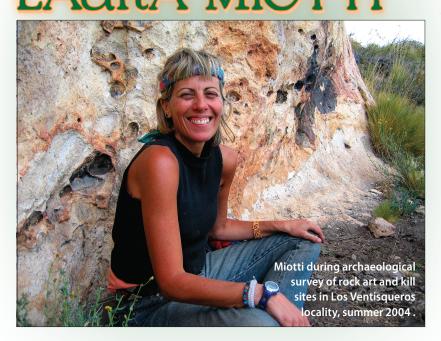
-Floyd Largent

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The Peopling of the Pampas and Patagonia



ONSIDER SOUTH AMERICA, a continent so vast it could swallow the United States twice over. Even today, only natives have ever set foot on some inner reaches. Indeed,

Native Americans have colonized every clime and exploited every ecological niche in a process that began when Northeast Asians crossed the Bering Land Bridge and, after a layover of some thousands of years, set out on foot or in watercraft in search of greener pastures to the south. These bold explorers share the same genetic lineage as other Native Americans who colonized North America (MT 34-2, "Beringian Child's genome reveals the founding population of the First Americans"). Now, more than 10,000 years later, Laura Miotti has set for herself and her colleagues a staggering task: To determine how South America was colonized.

Born in La Plata, Argentina, in 1956, Laura Miotti earned a degree in Anthropology and became a Doctor of Natural Sciences (anthropology orientation) in 1990. Currently a professor of Anthropology at the University of La Plata, her studies of hunter-gatherer societies in the Pampean and Patagonian regions of Argentina have enriched the understanding of their adaptive strategies and

paleoenvironments. "My interest has always been focused on Patagonia," Laura says. "This region is magic for me like the Galapagos or Svalvard Islands. Its name evokes distance, temporal and geographical, that inspires my research in pursuit of human variability."

Her research hasn't gone unnoticed. "Laura is a great colleague and one of the best in South America studying past hunter-gatherer societies," says colleague Tom Dillehay of Vanderbilt University. "Her work is judicious, interdisciplinary, and trustworthy."

Discarded, the Clovis-First model

Miotti scrutinizes both new and previous findings with an eye to developing alternative models that explain the peopling of the Americas. She notes that South America is a continent marked by enormous contrasts. Large regions are covered by rain forests laced with long, wide rivers, high chains of parallel mountain ranges, vast plains, and plateaus. Such a rich environmental mosaic would have offered first colonizers multiple migration routes—and that's not counting water-borne avenues.

These widely diverse potential routes into the South America continent—we must also consider terrain occupied by glaciers during the LGM—have persuaded Miotti that some previous models of the settlement of South America are too simplistic and mechanical. "Today, more and more groups of archaeologists working in South America are

demonstrating that the Clovis-First model doesn't seem to be the only way to explain the peopling of the Americas," Miotti tells us. She challenges us to imagine specialized hunters of mam-

Southern Cone

Paraguay

Bolivia

Argentina

Paso Otero

La María Cerro Tres Tetas

El Ceibo

Peru

moth and bison confronting dense rain forests. "Greater complexity and variability of the early archaeological record than previously thought and the usefulness of testing a variety of possible interpretations have been evident for some time in South American studies."

A meeting convened by Mexican scholars in November 2010 in La Plata, Argentina, was the fifth in a series of international symposia that focused on the late-Pleistocene peopling of the Americas. The CSFA publication *Southbound*, a product of these meetings, presents evidence from Miotti and her colleagues that fills salient gaps in research on the early peopling of South America.

An important lesson Miotti has learned is that *both* cultural heritage and academic traditions can powerfully influence a researcher's work. "In the past,"



she explains, "archaeological science in Latin America related to the peopling of the New World has been strongly influenced by its colonial past and by the Native and African-American peoples that compose a large part of the population." Although

these can enrich studies of postcontact cultures, they may introduce a misleading bias when studying ancient hunter-gatherers, a subject in which Laura Miotti is a recognized authority.

Networking is the magic bullet

First Americans research has grown quickly in volume and scope in recent years, and national meetings now regularly include sessions focused on the dispersal of humans in South America. To understand the early colonization of the Western Hemi-

sphere, Miotti believes scientists must be aware of the information produced in numerous countries and published in English and other languages. Formerly, the language barrier prevented sharing vitally important information. Research well known in a scientist's own country may be unknown elsewhere—North American archaeologists, for example, don't have ready access to information and ideas published in Latin America. "Poor communication among different countries," Miotti argues, "remains an obstacle to science and is sorely in need of further improvement."

Rethinking early objects and landscapes

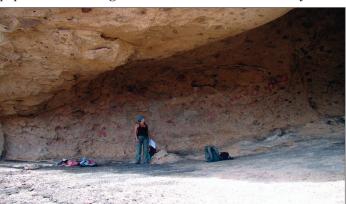
Analysis of two sites, Cerro El Sombrero and Cerro Amigo Oeste, has convinced Miotti and her colleagues, mainly Nora Flegenheimer, that people living in Patagonia and the Pampas during the Pleistocene-Holocene transition shared cultural meanings and had more in common than technical knowledge and design. The sites are similar in two respects: their hilltop locations, and the kinds of objects discarded there by settlers. Both sites revealed discoidal stones, small spheres, and broken fishtail points. The fishtail point is ubiquitous throughout the Southern Cone, which includes territory in Argentina,

Chile, Uruguay, southern Brazil, Ecuador, and Bolivia. So widespread is its appearance, in fact, that it has achieved the same icon status for early South American hunter-gatherers as the fluted point for the North American Clovis culture.

To Miotti, it's no coincidence that occupants of these two sites, Cerro El Sombrero and Cerro Amigo Oeste, separated by more than 900 km, chose a hilltop for their campsite and fashioned the same lithic objects. She believes these choices

served social functions and played an important role in communicating among people. The people living in these widely dispersed regions, she is convinced, shared common social values.

Miotti in Cave 10 of Los Toldos when registering rock art of the locality, summer 2015.



Among sites with shared traits, those with fishtail points are the most conspicuous. Faunal evidence of human exploitation shows regional variation among sites with fishtail points, and the people who produced them have fascinated South American scientists since the 1970s. Sites in Patagonia and the Pampas record that hunter-gatherers had lived there for many millennia before the Spanish Conquest. A record number of researchers from different cultural backgrounds and perspectives are currently at work on sites with early dates.

They have an enormous list to choose from: Miotti can name at least 70 sites that date older than 9,000 yr BP.

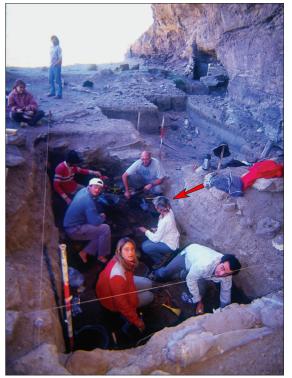
Archaeology in North vs. South America

The current model for the peopling of South America posits an exploring phase, followed by a colonizing phase. The length of time between the two phases depended on the intensity of early land use and the material culture colonizers hoped to introduce. Some authors favor a slow advance, others a faster one. Interdisciplinary teams composed of archaeologists, geologists, palynologists, and paleontologists often publish jointly and attend the same meetings and fieldwork. This pooling of knowledge is yielding detailed

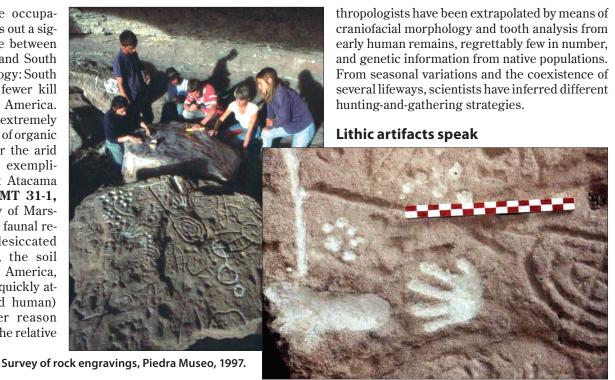
Miotti (arrow), with Natalia Carden, Martín Vázquez, Darío Hermo, Mariano Bonomo, Juan Pera, and two local visitors, excavating at AEP-1 in Piedra Museo, summer 1997.

reconstructions of the paleoenvironmental and paleoclimatic contexts of early sites, especially campsites and special-activity sites in the Southern Cone.

Most of the information gathered from South American sites



comes from cave occupations, which points out a significant difference between North American and South America archaeology: South America has far fewer kill sites than North America. One reason is the extremely rapid rate of decay of organic matter. Except for the arid western regions exemplified by the great Atacama Desert of Chile (MT 31-1, "The archaeology of Marson-earth"), where faunal remains become desiccated and mummified, the soil in most of South America. moist and acidic, quickly attacks faunal (and human) remains. Another reason that accounts for the relative



paucity of kill sites in South America is the nature of its Pleistocene and early-Holocene fauna. North America was home to great herds of megafauna—mammoth, mastodon, and the greatest herd animal of all, bison. South American megafauna, by contrast, were generally solitary animals like the guanaco, megatherium, glyptodont, and macrauchenia (MT 29-2,

"Footprints of the pampas: A past worth saving"). Their kills were infrequent events, and their remains (for as long as they

lasted before decomposing) were thinly distributed over the landscape. Nowhere in South America do we find evidence for hunting strategies like bison jumps (MT 31-4, "Inside the complex mind of the Paleoindian bison hunter"), where bison were stampeded over cliffs, or caribou drive lanes (MT 32-1, "Archaeology under the Great Lakes"), which channeled caribou on their semi-annual migrations past lurking hunters. The reason doesn't credit North American Paleoamericans with superior ability compared with their South America counterparts. Rather, it's that Pleistocene South America lacked herd animals conducive to stampeding. Although South American hunters were denied great herds of prey animals, abundant evidence of collective hunting during the late Pleistocene and early Holocene is being found at sites in Pampa and Patagonia like Piedra Museo

and Paso Otero by Miotti and colleagues María Gutiérrez and Gustavo Martínez.

Migration models hypothesized by South American bioan-

If Miotti's work is hampered by a dearth of human remains, she has a voluminous source of information in lithic artifacts. By focusing on the lithic technology of fishtail points—manufacturing sequence, resharpening, recycling, and bifacial thinning—she and her colleagues have found a wealth of clues about their use in hunting megafauna and other prey, particularly guanaco.

In the Pampas, a long-term research program undertaken in the rockshelters and small caves of 21 sites scattered about the





Cueva Maripe lies in a closed ravine in one of the headwaters of the zanjones system that feeds the paleolake of Piedra Museo. The first ephemeral occupations, around 9500–8500 RCYBP, coincide with the second occupational pulse of Piedra Museo. The principal activity was processing guanacos. No remains of extinct fauna have been found. The lithic set

consists mainly of brushes and scrapers.



upper sections of the Tandilia Range shows considerable intersite variability. Radiocarbon dates range from 9640 to 11,150 CALYBP. Hilltop sites Cerro El Sombrero and Cerro Amigo



CERRO AMIGO OESTE





and mountains 60 km distant.

Discoidal artifacts and small ocher-brushed sphere.

The Somoncura Plateau, a hilltop surface site, yielded 15 whole fishtail points and fragments of bifaces, large unifacial tools, and bifacial carvings. The predominant toolstone is chalcedony.

possibly from the Anekén quarry 15 km distant. Visible from the site are at least 6 bodies of water

Fishtail points and fragments.

Oeste contain many discarded and broken tools (90% are broken). Also present are objects of unknown function, spheres and discoidal stones, one of which is decorated.

The density of artifacts discarded at both hilltop sites indicates specialized activities carried out routinely. Abundant broken stems from fishtail points suggests the sites were workshops used for retooling and repairing hunting tools. Toolmakers probably brought blanks or preforms to these sites for final

shaping. If, while reworking fishtail points, toolmakers in other regions also observed the practice of always discarding broken objects in certain places, this custom may have skewed the overall archaeological record. It takes a sharp-eyed researcher to spot a possible aberration in a database.

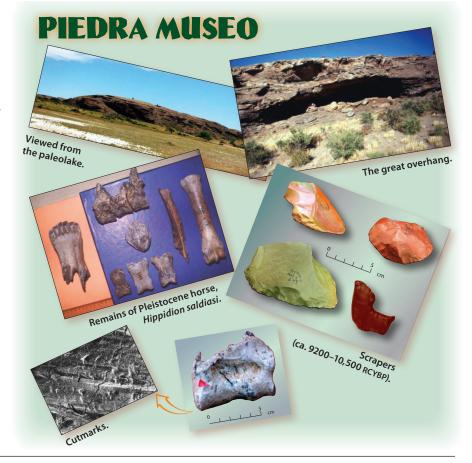
In Patagonia, the geographic distribution of early human occupations is very limited. Two separate clusters of human occupation have been identified that date older than 9000 yr B.P. A detailed study of toolstone suggests social networks were established among people in the Argentinean and Uruguayan Pampas for the purpose of sharing raw materials. As usual, answers spawn more questions. For Miotti, "Important regional questions need further investigating. What routes or paths did first settlers take? How did they find the routes that connected places? Did the first colonizers have social networks for communicating?" She still has plenty of work ahead of her.

Rock art paints a picture of archaeofaunas

The changing face of the prehispanic South American landscape and how it affected colonizers' perception of the land and the creatures that inhabited it are depicted in the rock art of the Deseado Plateau region of Patagonia.

For Miotti and colleagues, spatial and temporal changes recorded in rock art panels are changes to the "archaeological landscape." To correlate rock-art panels with stratigraphic layers and establish relative chronologies is a complex task. Colonization landscapes (societies with hunter-gatherer economies) strongly emphasize hunting guanacos and, in smaller proportions, megamammals and medium-sized birds. This is during the Pleistocene/Holocene transition (13,000-9000 yr B.P), a time of epochal environmental changes. Megamammals were disappearing, and the first colonizers were faced with a volatile landscape rocked by volcanic activity that could collapse rockshelters. Rock art from this period depicts simple and complex circular figures and a few schematic animal tracks.

To systematize the analysis of rock art depicting animals and humans. Miotti and colleagues compiled a descriptive database. Other types of rock-art figures weren't included, since Miotti's purpose was to study the relation between animal and human figures and the archeofaunas of each stratigraphic context. Although problems arose in instances of more than one occupational component, the study was a useful first step toward understanding the archaeological relationships be-





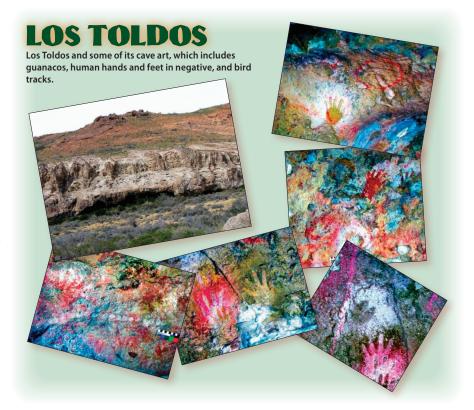
tween humans and animals from a symbolic perspective.

Rock art at these sites most vividly depicts how humans perceived the creatures around them.

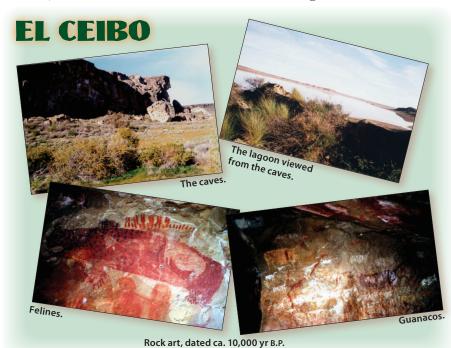
- Piedra Museo Pleistocene occupations recorded scenes of processing prey species (guanacos, ostriches, geese, partridges, foxes, and pumas). Holocene hunters concentrated on guanaco, other prey species having disappeared. Human figures consist of a few hands and feet carved on boulders, and of positive and negative hand paintings.
- Los Toldos Two different stages of human occupation were studied. Rock art showed a large number of hand negatives and positives, geometrical signs, a foot negative, and negatives of guanaco and ostrich-like feet.
- El Ceibo Rockshelters house great concentrations of paintings. Camelids predominate, along with birds, canids, and felids. Felines (including an extinct jaguar), which preside over central locations in the panels and caves, are much larger than the other figures. Miotti and her colleagues therefore

conclude that the caves served ritual purposes and that the feline figures were sacred.

■ La Maria This is the most important site in the Central Plateau in terms of the quantity and diversity of rock art. About 50 caves and rockshelters house the greatest collection of paintings. Taxonomic richness is expressed by birds, felines, guanacos, and humans. Camelids are the most abundant figures.



■ Cerro Tres Tetas Rock-art scenes include two guanacos in profile and six small anthropomorphic figures. Another scene, with a preponderance of young guanacos and human representations and an absence of projectile points, has been interpreted by some authorities as evidence for the incipient domestication of guanacos during the middle Holocene; Miotti and her colleagues don't subscribe to this interpretation.



The rock art of the Central Patagonian Plateau is a continuum of magnificent tableaux, which confirm that animals never lost their importance within the symbolic worlds of hunter-gatherer societies.

Looking ahead

Laura Miotti can boast of many publications in both Spanish and English, and her enthusiasm hasn't waned. On the contrary, she's delighted that scientific methods and theory have progressed to the point that "we can now dig deeper into more sophisticated questions about social and symbolic topics related to First Americans."

What's still missing? How could her task be made easier? "We need ample radiocarbon dates and DNA studies to establish migration routes and identify the affinities of different groups of human colonizers. We need to find new localities with solid repeatable dates. We need to conduct taphonomic studies that will tease more information



from fossilized bones and perishable artifacts." We wish you good luck, Laura.

We asked Miotti's colleagues and professional acquaintances for their opinion of Laura Miotti as a person and as a scientist. María Gutiérrez, Professor of Taphonomy at Universidad Nacional del Centro da la provinca da Bueno Aires, weighs in with this celebration of a scientist who values people: "Working with Laura is always an opportunity for a great deal of learning. Laura taught me the value of patience because the time she spends is always warranted. She knows how to travel in the academic and personal world without fretting about time spent on the road. Her wonderfully disengaged attitude frees her to do what she considers important, not what others expect her to do. I cherish above all Laura's humanist view of the past. For her, people remain humans and are never objects. She never loses sight of human beings. Thanks, Laura, for your legacy. ¡Laura va!"

From Argentinian colleague Luis Borrero of the University of Buenos Aires comes an accolade that any scientist would be proud of: "It is thanks to Laura Miotti, whose dedication and persistence are well known, that we have well-researched and -published records of Piedra Museo and Cerro Amigo Oeste, two crucial sites for the study of the peopling of South America. Of course, she studied many more sites with her team, but those two will be referenced over and over again.

"I have known Laura for many years, and always found it fascinating to discuss our mutual interests with her. This is a refreshing experience, because she is always ready to tackle any issue from as many perspectives as possible, and the inevitable result is that you learn something. Even more important, I recall when she was interviewed years ago by a popular Argentine magazine, and the reporter was more interested in something personal rather than her theories or excavations. She took the occasion to express her fondness for the Rolling Stones. I thought, 'Well, Patagonian archaeology is heading in the right direction!'"

-Martha Deeringer

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Suggested Readings

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Plumbing the Depths for Human Presence

continued from page 8

evidence for LGM occupations in both western and eastern Beringia itself suggests the standstill population must have been quite small, which is confirmed by genetic data, which estimate that the female population numbered only about 1,000–2,000 individuals. Indeed, the total standstill population didn't exceed a few tens of thousands of people. Researchers say the size of this population is thought to have increased after the LGM, leading to dispersal into the Americas, probably either by the coastal route or the Ice-Free Corridor (MT 34-1, -2, "Along the coast or down the Ice-Free Corridor—How did the First Americans get here?").

The impact on Native American communities

Vachula's research group's future studies will focus on the Seward Peninsula region of western Alaska, whose lakes may be hundreds of thousands of years old. He hopes to collect sediments from the previous Glacial period. "This would have been a similarly cold and arid period," he says, "but before any chance of humans being on the scene. So if we can look at this as a baseline for whether there was any burning, and to what extent, it would be a good way to tease out or further prove that

this was human-induced ignition and not just human burning imprinted on natural burning."

As part of this project, he'll be engaging in community outreach and visits to museums. At Kotzebue, Alaska, a Native American community maintains a park service and museum. He says he looks forward to "talking to the community and sharing our results there in the coming years. One of the great things about Alaska and its archaeology and paleoclimate is that we don't know a lot about it, so every new discovery is really exciting."

-Katy Dycus

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Suggested Readings

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Part 1: Eurasian origins and the Beringian Standstill

ANY PEOPLE will have heard of the so-called "mito-chondrial Eve" and may even be familiar with the mito-chondrial DNA haplogroups, or lineages, that represent the founding mothers of Native Americans. These are A, B, C, D, and X. The designations for the Y-chromosome haplogroups, which represent the founding fathers of America, may be less familiar, but they are by no means less important for understanding the entire story of the human expansion into the Western Hemisphere. The study of the Y chromosome provides insights into human history that complement studies of the X chromosome. We consider a number of recent studies in this 2-part series.

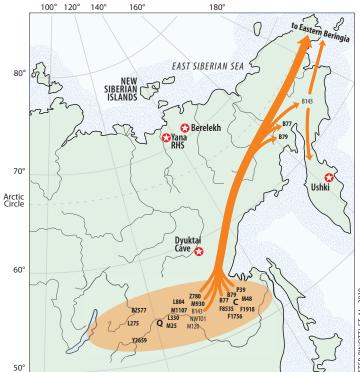
Toomas Kivisild, a geneticist with the Department of Archaeology and Anthropology at the University of Cambridge, reviewed what we know about variation in the human Y chromosome over time and across space in 2017 in the journal *Human Genetics*. Using data from analyses of modern Y-chromosome variants as well as the increasing number of studies of ancient Y chromosomes.

The greatest variability in Y chromosomes is found in Africa, which reflects the fact that Africa is our ultimate homeland and thus af-

he examined human history

from the perspective of men.

Proposed paternal origin of Paleoamericans in Siberia.



forded much more time for mutations and other genetic processes to create diversity across the continent. Kivisild notes that the modern variation in all the other continents combined "is mainly restricted to three branches of the M168" haplogroup. Haplogroups are simply alternative branches of the human family tree that possess certain shared sequences of DNA that differentiate them from other branches. These three branches can all be traced back to a single founding lineage that split from its African ancestors between 40,000 and 60,000 years ago. Kivisild notes that this is consistent with the Out of Africa dispersal model, which proposes that modern humans arose in Africa during this period and then rapidly expanded throughout the rest of the world,

ultimately supplanting descendants of previous migrations out of Africa, such as the Neanderthals in Europe and the diminutive "Hobbits," or *Homo floresiensis*, from the island of Flores in Indonesia.

The emergence of Paleoindians

Kivisild describes the Y-chromosome haplogroups of contemporary native America as "a mixture of haplogroups that derive from pre-Columbian dispersals from Siberia and more recent gene flow from Europe and Africa." Even so, the haplogroup diversity is limited to only two founding lineages within haplogroup Q, along with one, possibly two, within haplogroup C3-M217.

Haplogroup C3-M217, the most common Y haplogroup in modern northeastern Siberia, is only a minor haplogroup among contemporary Native Americans. Haplogroup Q is the most common lineage in North and South America. It's also common in middle Siberia today, which suggests that this region was an important source of probable multiple independent migrations into the Americas.

A rare group of lineages of C3-M217 identified in Ecuador has been interpreted as evidence for a secondary wave of migrations from East Asia, Japan in particular. It seems more likely, however, that such rare, now isolated groups are actually surviving remnants of a formerly more widespread, but still



rare, lineage that has disappeared elsewhere due to genetic drift. Kivisild notes that the study of ancient DNA has shown that "the loss of rare lineages in post-contact Native Americans is not unusual."

Haplogroup Q has two ancient sublineages that appear to be the source of the "overwhelming majority" of modern Native American Y chromosomes. The Anzick Child, who was associated with artifacts related to the Clovis culture (MT

29-2, "Clovis child answers fundamental questions about the First Americans"), has the relatively rare Q1b-M971 haplogroup, whereas Kennewick Man (MT 31-3, "Kennewick Man's DNA reveals his ancestry") belongs to the more common Q1a-M3 haplogroup. Other rare Q sublineages also appear, such as Q3-L275, which was the Y haplogroup of Shuká Káa, from On Your Knees Cave (MT **33-2.** "Genetic insight into the First Americans"). Isolated pockets of this haplogroup exist today in Europe, central and south Asia, and Siberia.

Kivisild concludes his review with the observation that further studies of the Y chromosome have great potential to add to our understanding of the First Americans, including where in Asia they came from, the routes they followed to get here, the number of migrations, and whether the genetic history of early American men differs

from that of women. But he adds that to get to these detailed answers, we will need many more genetic studies of ancient Americans from across the two continents, as well as studies of many individuals from the same geographic region at different times. This last point is especially important, because, as Kivisild notes for the ancient DNA evidence from west Eurasia, in particular, "inferences made from present-day genetic variation about the time and place of origin of Y chromosome haplogroups can be imperfect."

Siberia was the homeland of First American ancestors

Shuhua Xu, a geneticist with the Shanghai Institutes for Biological Sciences as well as other affiliations, and Hui Li, a professor of Anthropology at the MOE Laboratory of Contemporary Anthropology at Fudan University, along with a team of 14 other scientists from China, France, Russia, and the United States, studied sequences along the Y chromosome from Eurasian populations that are known to be related to paternal lineages documented in the Americas and especially North America.

The team had two main objectives. First, they sought to determine the "most closely related lineage of each Native American paternal lineage in Eurasian populations"; and second, they attempted to estimate when each lineage split from its Eurasian ancestors. The overarching goal of their work was to ascertain how the founding group of original Native Americans emerged from the various ancestral Eurasian groups and, in particular, to reexamine the Beringian Standstill Hypothesis

from the perspective of the Y chromosome. According to this model, Native Americans developed genetic diversity while isolated in a sort of Beringian incubator. Isolation was the result of Pleistocene glaciers, which blocked entry into the lower latitudes of America.

Xu, Li, and their colleagues first collected Y-chromosome DNA data obtained from previous studies of both Native American and Eurasian groups. They also selected samples already held in their lab for additional Y-chromosome sequencing. Finally, they obtained Y-chromosome sequences from 15 men through Family

from 15 men through Family

Founding paternal lineages of

Paleoamericans and their most

closely related lineages among

Eurasia populations.

Tree DNA. Of these men, 6

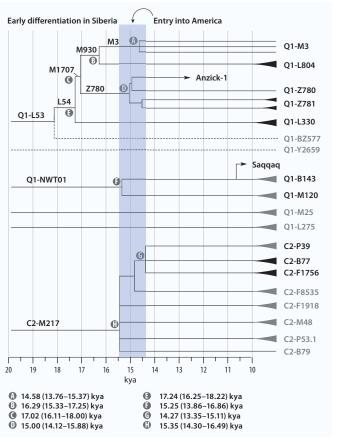
had Eurasian ancestry and 9 had Native American ancestry. The study included a total of 132 samples, with 56 from Native Americans. All participants signed informed-consent agreements, and the study was approved by the ethics committee for biological research at the School of Life Sciences at Fudan University in China.

A Y-chromosome family tree for Native Americans

The haplogroups, or ancestral lineages, were determined for each individual, and when each branch split off was calculated based on the number of accumulated genetic differences that distinguished each Y-chromosome lineage. The various Y-chromosome haplogroups are designated by a unique sequence of letters and numbers.

Xu, Li, and colleagues identified several Y-chromosome haplogroups in Eurasian samples that were closely related to the founding paternal lineages represented in Native American samples. They also identified a number of previously unknown sublineages.

Haplogroup C3-M217, for example, included a number of





sublineages in both Siberia and America. When these diverged worked out to 14,300–15,300 years ago.

Haplogroup Q1-Z780 is found only in Native American populations; the Anzick Child belongs to a sublineage of his haplogroup. Xu, Li, and their team determined that the most recent common ancestor of "all available Q1-Z780 samples" lived around 15,000 years ago.

Haplogroup Q1-M3 is the most common Y-chromosome lineage in Native Americans. Xu, Li, and their team's calculations established that the most recent common ancestor of all available Q1-M3 samples lived around 14,580 years ago. They also determined that this lineage diverged from Q1-L804, a lineage restricted to Northwest Europe, around 16,290 years ago.

Support for the Solutrean hypothesis?

Xu, Li, and their coauthors suggest that the fact that the Native American Y-chromosome lineage Q1-M3 appears to have diverged around 16,000 years ago from Q1-L804 might appear to offer support for the Solutrean hypothesis. This is the controversial idea that one of the routes followed by the First Americans was along the edges of the sea ice of the Pleistocene North Atlantic from Spain and France (MT 28-2, "Do Clovis origins lie in Paleolithic Spain? Part 1," and MT 28-3, "Alternative views of the Solutrean theory. Part 2"). Xu, Li, and their colleagues caution, however, that the Q1-L804 lineage in Northwest Europe may be a now isolated "relic of a prehistoric migration from South Siberia" that occurred in parallel with the migration of another segment of that Siberian population into America. Alternatively, they propose that the Northwest European population may have descended from "an unknown male from Asia in recent history." Xu, Li, and their colleagues conclude that "more ancient DNA analyses from remains of Solutrean culture are needed to falsify or verify the direct connection between ancient Solutrean and Paleo-Indian populations."

Differentiation and diffusion in Siberia

Xu, Li, and their team deduce from their genetic analyses, in conjunction with the current geographic distribution of various sublineages, that the population that gave rise to the First Americans separated from related populations in Siberia in the short period of 14,300–15,300 years ago. They link this period of population differentiation with climatic changes associated with the Last Glacial Maximum. These climate changes also may be responsible for a "strong bottleneck effect" that Xu, Li, and their team identified in their genetic analysis. For example, of at least 10 sublineages of haplogroup Q-M242 extant in Siberia before 15,000 years ago, only 3 migrated toward Beringia, and only 2 found their way into the Americas before 14,000 years ago.

The timing of the split between the founding Y-chromosome lineages of Native Americans and the most closely related lineages in Eurasia establishes that humans first arrived in the Americas no earlier than 15,000–16,000 years ago. To determine the lower limit for this pivotal historic Rubicon, the team analyzed the expansion in America of the uniquely Native American Y-chromosome Q1-Z780 and

Q1-M3 lineages. Their analyses indicate a narrow timeframe of 15,300–14,300 years ago for the human entry into the Americas. Their estimate, they note, is consistent with both the estimates obtained from mitochondrial DNA, or mtDNA, the mostly female genetic legacy recorded in the DNA of the mitochondria in our cells, and the best current archaeological evidence (MT 32-2, "A high-resolution timeline for the peopling of the Americas").

The Y-chromosome perspective on the Beringian Standstill hypothesis

The work of Xu, Li, and their team provides a "Y-chromosome perspective" on the Beringian Standstill hypothesis, which proposes that the Eurasian ancestors of Native Americans were sequestered for some time in Beringia by the glacial ice sheets that covered much of northern North America before they were able to migrate into the lower latitudes of America. This is thought to be where and when the founding mitochondrial lineages of Native Americans arose (MT 33-2, "The Bluefish Caves").

According to Xu, Li, and their colleagues, a standstill indeed occurred, but they believe it was shorter in duration than previous estimates have suggested. They conclude that the founding Y-chromosome Native American lineages diverged from their ancestral Siberian lineages 17,000–14,000 years ago. Moreover, they think the diversity in the founding Y-chromosome Native American lineages developed in southern Siberia, not Beringia, and that these various lineages arose separately 50,000–17,000 years ago. They conclude, therefore, that a "short-term Beringian standstill" began sometime after 18,000 years ago and lasted for less than 3,000 years.

-Brad Lepper

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Observations concerning the Cerutti Mastodon Site, Ruth Gruhn

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Late-Glacial Hunter-Gatherers in the Central Alaska Range and the Role of Upland Ecosystems in the Peopling of Alaska, John C. Blong

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Sankakuyama), Hokkaido (Japan): Refining the Chronology of Small Flake-based Assemblages during the Early Upper Paleolithic in the Paleo-Sakhalin-Hokkaido-Kurile Peninsula, Masami Izuho, Dai Kunikita, Yuichi Nakazawa, Noriyoshi Oda, Koichi Hiromatsu, and Osamu Takahashi

The Keystone Dune Site: A Bølling-Allerød Hunting Camp in Eastern Beringia, François B. Lanoë, Joshua D. Reuther, Caitlin R. Holloway, Charles E. Holmes, and Jennifer R. Kielhofer

A First Look at the Terminal Pleistocene/Early Holocene Record of Guano Valley, Oregon, USA, Derek J. Reaux, Geoffrey M. Smith, Kenneth D. Adams, Sophia Jamaldin, Nicole D. George, Katelyn Mohr, and Richard L. Rosencrance



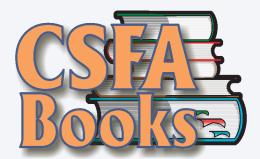
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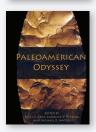
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Ted Goebel, Hiroyuki Sato, and Akira Ono. 2014. 230 pages/ Hardback (ISBN 978-1-62349-276-2).

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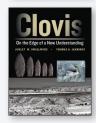
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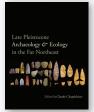
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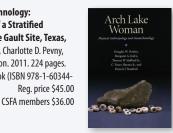
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