we must note that none of the organisms studied so far has a simple dose-response curve with a threshold at $\Omega_{arag} = 1$ (28). Rather, some organisms or life stages respond negatively at higher Ω_{arag}, whereas others can tolerate undersaturated conditions for some time. In addition, organisms living in the California CS may have had the chance to adapt to the naturally low and variable pH and Ω_{arag} conditions that prevailed before the onset of the industrial revolution, making them potentially less vulnerable to the effects of ocean acidification (32). Regardless of these uncertainties associated with the biological response to ocean acidification, our simulation results indicate that the California CS is moving rapidly toward conditions that are well outside the natural range, with frequent or even persistent undersaturation conditions (Fig. 3). Such conditions probably will be challenging to calcifying and other organisms, as well as the fisheries that depend on them (33).

Although we focused our study on the changes in Ω_{arag}, ocean acidification alters all aspects of the carbonate chemistry in the ocean, including pH and the concentrations of dissolved CO_2, bicarbonate, and carbonate (34), each of which can impact physiological processes and, hence, affect marine organisms and ecosystems (35). Yet, the changes in these properties are highly correlated (fig. S7) because they are mechanistically linked through the driver of ocean acidification (i.e., the oceanic uptake of CO_2 from the atmosphere), which increases dissolved CO_2 and bicarbonate but decreases pH, Ω_{arag}, and carbonate with predictable ratios (34). Therefore, regardless of whether the parameter affecting a biological process is Ω_{arag} or the dissolved CO_2 concentration, the changes are unprecedented.

In addition, ocean acidification will not be operating in isolation, but its impact could be potentially worsened with synergistic effects of ocean warming and deoxygenation (35, 36), both of which have been noted to occur in the California CS (37, 38) and probably get more severe with time (39). Thus, specific attention should be given to the development of ocean acidification in this very rich and productive ecosystem, as well as to some of the other Eastern Boundary Current Systems where similar conditions prevail.

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Clovis Age Western Stemmed Projectile Points and Human Coprolites at the Paisley Caves

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The Paisley Caves in Oregon record the oldest directly dated human remains (DNA) in the Western Hemisphere. More than 100 high-precision radiocarbon dates show that deposits containing artifacts and coprolites ranging in age from 12,450 to 2295 ^{14}C years ago are well stratified. Western Stemmed projectile points were recovered in deposits dated to 11,070 to 11,340 ^{14}C years ago, a time contemporaneous with or preceding the Clovis technology. There is no evidence of diagnostic Clovis technology at the site. These two distinct technologies were parallel developments, not the product of a unilinear technological evolution. "Blind testing" analysis of coprolites by an independent laboratory confirms the presence of human DNA in specimens of pre-Clovis age. The colonization of the Americas involved multiple technologically divergent, and possibly genetically divergent, founding groups.

Despite increasing evidence for pre-Clovis sites in North and South America (1–6), debate continues as to whether the technological tradition that led to Clovis was the first to arrive in the Americas. Was Clovis the first in a long, unilinear technological evolution spreading throughout the Americas? Or were other Pleistocene technological complexes involved (6–10)? In the American Far West, the Western Stemmed Tradition (WST) is recognized as the oldest nonfluted lithic technology. Stemmed points were present earlier in East

Asia and Siberia, and the basic form could have arrived in the Americas before Clovis developed (11–15). Like Clovis, the WST is a New World development sharing basic morphological and technological characteristics with Old World forms.

Western Stemmed (WS) projectile points are generally narrow bifaces with sloping shoulders, and many have relatively thick contracting bases (Fig. 1, A to C). They were commonly made on flakes by broad collateral, midline, percussion flaking and finished by pressure flaking. In this, they are morphologically and technologically distinct from the generally broader, concave-based, fluted Clovis points made on large bifacial preforms often thinned by overshot flake technology (16–19) (Fig. 1D). Prismatic blades—long, narrow flakes with triangular cross sections driven from specially prepared cores—are common to Clovis sites outside of western North America (16, 17) and are less common to WST assemblages. Most dated WS projectile points are younger than Clovis, and it has been proposed that they evolved from a single tradition. The possible exceptions are WS projectile points found in strata dated to the Clovis era at the Smith Creek Cave, Cooper's Ferry, and Bonneville Estates Rockshelter sites. The association of the dates with the points at these sites has not been confirmed and is not widely accepted (fig. S1) (13, 20–24). Here, we describe WST assemblages—including human coprolites—at the Paisley Caves and show that these date to between 11,070 and 11,340 radiocarbon years before the present (^{14}C yr B.P.), confirming that they overlap or precede Clovis (20).

We continued to excavate the Paisley Caves from 2009 through 2011. To resolve the question of stratigraphic integrity, we acquired 121 new AMS (accelerator mass spectrometry) radiocarbon dates on samples of terrestrial plants (e.g., *Artemisia* sp., *Atriplex* sp.), macrofossils from coprolites, bone collagen, and water-soluble extracts recovered from each of these categories. To date, a total of 190 radiocarbon dates have been produced from the Paisley Caves (tables S1 to S9). These are distributed throughout four

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of the caves, although the primary set of high-precision dates represents six dating columns in Caves 2 and 5. DNA analysis has been completed on 65 coprolites from the site. To investigate whether non-endogenous human DNA may have leached into samples, we also tested Camelidae, Felidae, and Caprinae coprolites for the presence of ancient human DNA (25).

Middens of wood rat (*Neotoma* sp.) are common in the Paisley Caves, particularly in the North Block of Cave 5 (fig. S2). To investigate whether excavations by rodents disturbed the stratigraphic integrity of the deposits, we dated two profiles there (Fig. 2A and tables S2 and S3) (25). The dates in each are stratigraphically and chronologically well ordered. Beginning just below a layer of Mount Mazama O tephra—dated to 6790 ± 15 ^{14}C yr B.P. in Cave 2 and ~6850 years regionally (26)—the ages in profiles I and II range from 6980 ± 15 to 12,450 ± 30 ^{14}C yr B.P. WS projectile point 1294-PC-5/6D-47-1 (Fig. 1B), a biface, a polished probable food-processing stone (fig. S3), and eight pieces of lithic debitage were recovered from lithostratigraphic units LU1 and LU2 in the North Block,

which are of late Pleistocene–early Holocene age. Projectile point 1294-PC-5/6D-47-1 was recovered from sifted LU2 [LU1a in (4)] sediments in excavation unit 5/6D (fig. S2) and may date from 11,135 to 11,600 ^{14}C yr B.P. (Table 1) (25).

A trench connecting the North and South Blocks provided continuous stratigraphic exposure across the mouth of Cave 5 (fig. S2). Profiles III and IV, at the intersection of this trench with the South Block, reveal well-stratified, highly indurated sandy sediments (LU2 and LU3) underlain by gravelly LU1 deposits. Ages here range from 7700 ± 20 to 12,410 ± 25 ^{14}C yr B.P. (Fig. 2, B and C, and tables S4 and S5). Organic materials in basal LU1 sediments of profile III date to 12,410 ^{14}C yr B.P. The lower portion of overlying LU2 is dated between 11,070 ± 25 and 12,405 ± 25 ^{14}C yr B.P. and is composed of more organic, loamy, and gravelly sand, varying portions of which are highly indurated. The upper portion is dated between 10,855 ± 30 ^{14}C yr B.P. and ~9500 ^{14}C yr B.P.

Rodent disturbances were traceable as oval voids filled with loose organic sediments intruded into less organic, compact to cemented LU2 sandy-
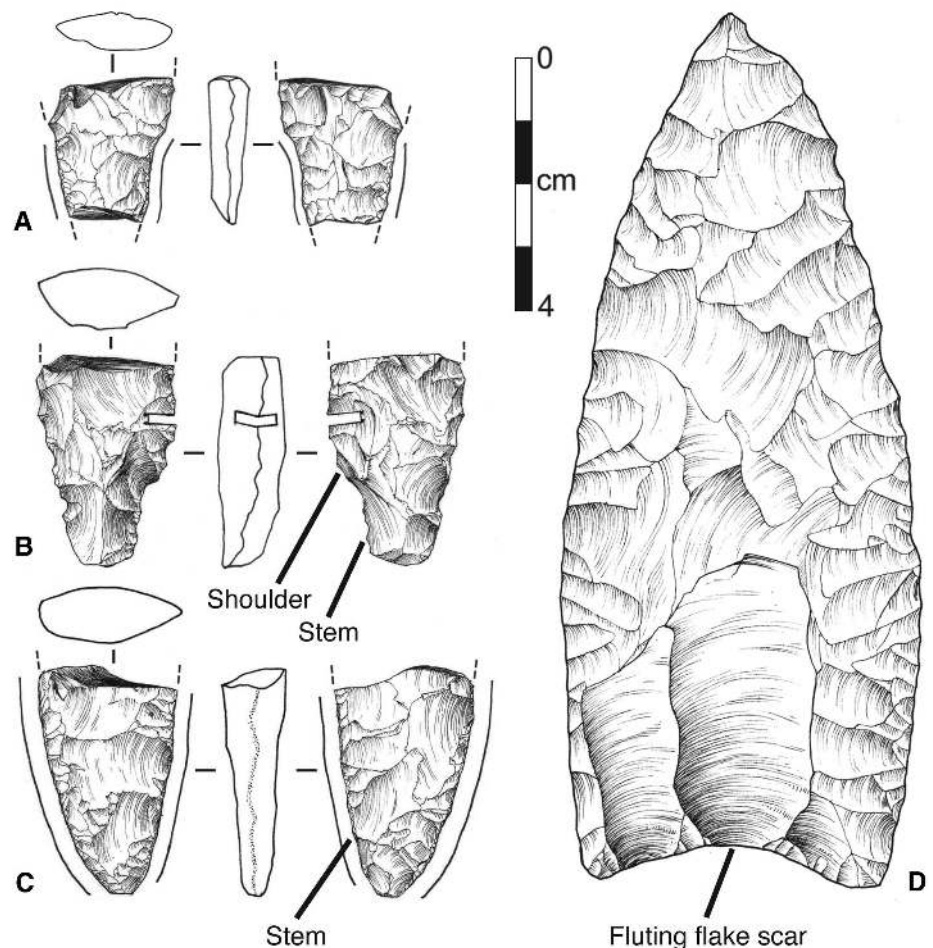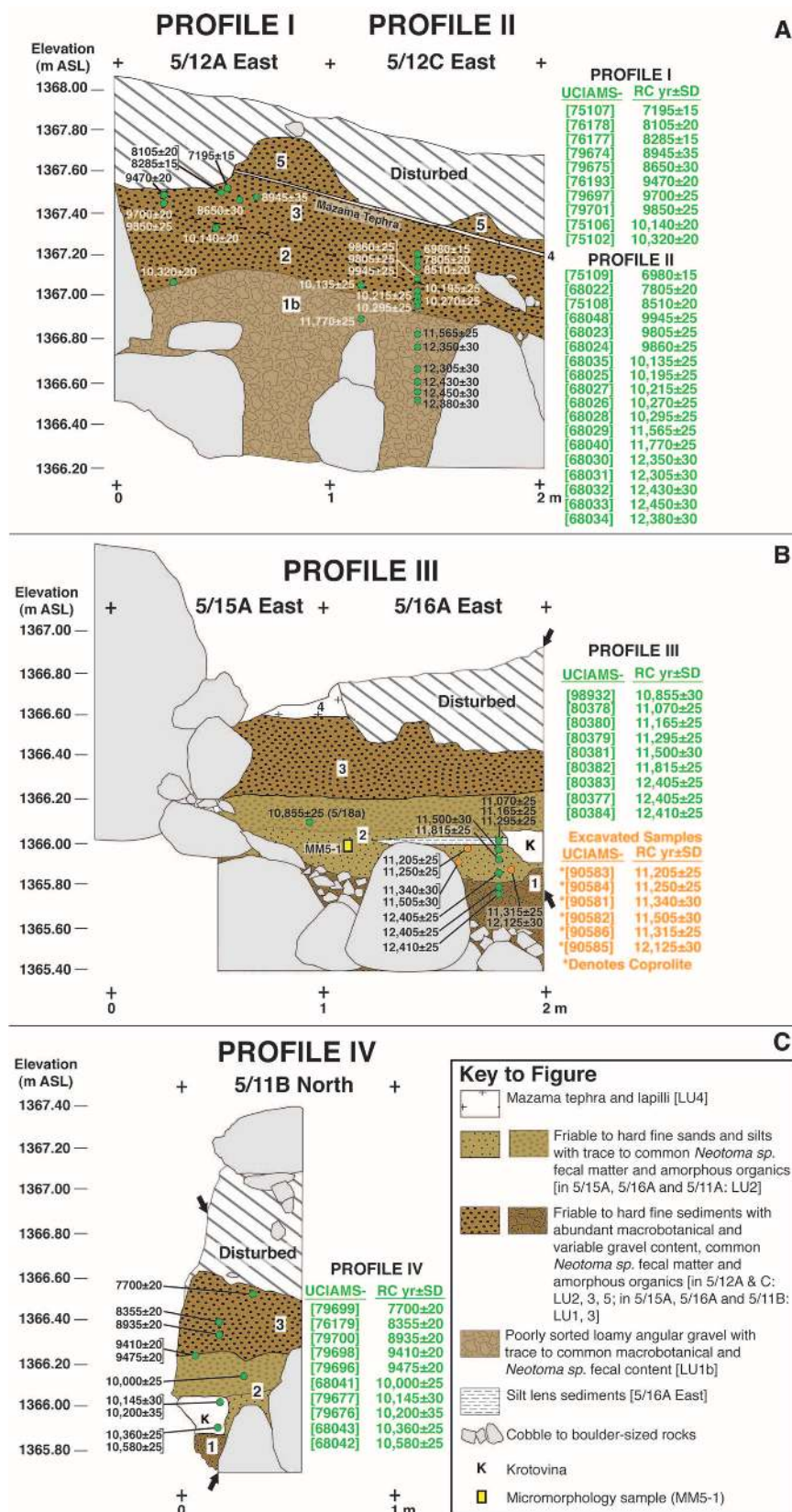

Fig. 1. Western Stemmed projectile point fragments. (**A**) 1961-PC-5/18a-10-1. (**B**) 1294-PC-5/6D-47-1. (**C**) 1895-PC-5/16A-24. (**D**) Clovis point from Dent site, Colorado. Edges of (A) and (C) are intensely ground, as indicated by lines paralleling edges and stippling in edge-on view. The notch in (B) is an obsidian hydration cut. [Illustrations by Eric Carlson and George T. Jones]

Fig. 2. (**A**) Dating column profiles I and II in North Block, Cave 5. (**B**) Dating column profile III. (**C**) Dating column profile IV.

silt or low organic gray sandy-gravelly LU1 sediments. Dated artifacts, charcoal, and the KOH-soluble fraction from the charcoal within stratigraphic disturbances indicate that they occurred between 9500 and 10,250 ^{14}C yr B.P. (table S10).

Three additional WS projectile point fragments were recovered from LU2 sediments with a chert flake tool and 165 pieces of lithic debitage (Fig. 3A) (25). Point 1895-PC-5/16A-24 (Fig. 1C) was found in situ laying horizontally, solidly encased in a compact silt lens formed by a brief pooling of water on the cave floor (Fig. 3, fig. S4, and table S11). This projectile point was on the cave floor when the lens formed and remained undisturbed until discovery (25). *Atriplex* sp. and *Artemisia* sp. twigs sampled in the east wall of unit 5/16A ~40 cm east of point 1895-PC-5/16A-24, at elevations 1365.97, 1365.93, and 1365.89 m, were dated to 11,070 ± 25, 11,500 ± 30, and 11,815 ± 25 ^{14}C yr B.P., respectively. Two human coprolites at elevations 1365.91–.96 and 1365.88 in unit 5/16A were dated to 11,205 ± 25 and 11,340 ± 30 ^{14}C yr B.P., respectively. Projectile point 1895-PC-5/16A-24 was dated between 11,070 and 11,340 ^{14}C yr B.P. (Figs. 2B and 3B, fig. S4, and table S11).

WS projectile point 1895-PC-5/16A-23-6a (not illustrated) was recovered with 37 pieces of lithic debitage sifted from organic sediments directly overlying the silt lens. Bracketing dates for this projectile point are 10,855 ^{14}C yr B.P. (1366.05 to 1366.00 m) and 11,070 (1365.97 m). WS projectile point 1895-PC-5/18a-10-1 was recovered ex situ from sifted sediments in excavation unit 5/18a—located 75 cm from projectile point 1895-PC-5/16A-24 (Fig. 3) (25)—between 1366.10 and 1366.05 m and is bracketed between dates 10,200 and 10,855 ^{14}C yr B.P. (Table 1).

A Camelidae coprolite was recovered in situ below the silt lens at 1365.85 m (table S11). It produced a macrofossil age of 12,125 ± 30 ^{14}C yr B.P.; however, the age of its water-soluble extract was 11,315 ± 25 ^{14}C yr B.P. This is the only instance of fractions differing by hundreds of years between macrofossils and their extracted solutes in 12 such tests (25). Three coprolites containing ancient human DNA (aDNA)—results from two of which were replicated by laboratories in Copenhagen and York in blind testing and found to relate to mitochondrial DNA founding haplogroup A (25)—were recovered in close horizontal proximity. Dates on the macroflora and solute fractions, respectively, from these three coprolites were 12,265 ± 25 and 12,260 ± 30 ^{14}C yr B.P.; 12,165 ± 25 and 12,050 ± 25 ^{14}C yr B.P., and 11,205 ± 25 and 11,250 ± 25 ^{14}C yr B.P. (tables S1 and S12). The two oldest of these were recovered lower in the deposits of adjacent excavation unit 5/11B (fig. S2). Presumably, they would have been contaminated in the manner of the Camelidae coprolite had water reached them. Their concordant ages indicate that the effects of water were limited spatially, stratigraphically, and in volume. The new human aDNA

Table 1. Western Stemmed projectile point proveniences and their bracketing radiocarbon dates. Two independent laboratories provided the dual dates for specimen 1294-PC-5/6D-47-1.

Specimen no.	Unit	Elevation (m)	Upper bracketing age and elevation (m)	Lower bracketing age and elevation (m)
1294-PC-5/6D-47-1	5/6D	1366.06 to 1366.01	10,050 ± 50 (1366.40 to 1366.35) 10,965 ± 50	12,140 ± 70 (1365.91 to 1365.86) 12,260 ± 60
1895-PC-5/16A-24	5/16A	1365.93	11,070 ± 25 (1365.97)	11,340 ± 50 (1365.88)
1895-PC-5/16A-23-6A	5/16A	1366.01 to 1365.96	10,855 ± 30 (1366.05 to 1366.00)	11,070 ± 25 (1365.97)
1961-PC-5/18a-10-1	5/18a	1366.10 to 1366.05	10,200 ± 35 (1366.09)	10,855 ± 30 (1366.05 to 1366.00)

results (table S12) confirm our previous findings that humans with DNA founding haplogroup A had occupied the site in pre-Clovis times (3).

In Cave 2, dates for profiles V and VI, beginning at the base of the Mount Mazama tephra, range between 6790 ± 15 and 12,320 ± 35 ^{14}C yr B.P. (Fig. 4 and fig. S5). All Cave 2 dates between 10,980 ± 20 and 12,425 ± 30 ^{14}C yr B.P. come from LU1 and LU2, both of which are easily distinguished from LU3 by their low organic, sand, and gravel content. LU1 contains water-rounded boulders and sandy gravels. It is covered by up to 30 cm of brown gravelly sand (LU2). The LU2 sands are partially capped by a thin alluvial silt lens with a mean age of 11,035 ^{14}C yr B.P. *Artemisia* charcoal from the surface of hearth 2/6-4 at elevation 1365.48 m was dated to 10,020 ± 30 ^{14}C yr B.P., whereas *Artemisia* charcoal recovered at lower elevations—1365.40 m and 1365.35 to 1365.30 m from within the hearth depression—was dated to 11,005 ± 30 and 11,055 ± 35 ^{14}C yr B.P (Fig. 4B and table S1). Because the younger sample was taken from the LU2-LU3 stratigraphic boundary where charcoal is common, and LU2—into which the hearth was excavated—is an incombustible, low-organic matrix, the 10,020 ± 30 ^{14}C yr B.P. sample is interpreted as younger charcoal associated with LU3. We accept the age of 11,005 ^{14}C yr for this hearth. The hearth was surrounded by obsidian debitage and burned bone. Stone artifacts in undisturbed LU2 deposits at and below the hearth include 228 pieces of lithic debitage, a biface, a polished and chipped probable food-processing stone (fig. S6), and a flake tool. The pre-Clovis context of the probable food-processing stone at elevation 1365.28 m (not associated with the hearth) is established by dates on an Artiodactyla rib (11,930 ± 25 ^{14}C yr B.P.) and an *Equus* sp. maxilla (11,740 ± 25 ^{14}C yr B.P.) found below and above it at elevations of 1365.25 and 1365.31 m, respectively. LU2 transitions abruptly upward into more organic LU3 sediments that are rich in bat guano and are dated between 6790 ± 15 and 10,585 ± 30 ^{14}C yr B.P. (table S1).

DNA can be carried through sedimentary deposits by water (rain, sheet wash, capillary fringe solutions) and urine (3, 27). We initially (3, 28–30) addressed the question of DNA leaching by testing sediment around the coprolites, as well as *Neotoma* fecal pellets, for human aDNA; however, no human aDNA was detected. *Neotoma* sp. (wood rat) aDNA was extracted from *Neotoma* fecal pellets, and *Callospermophilus lateralis*
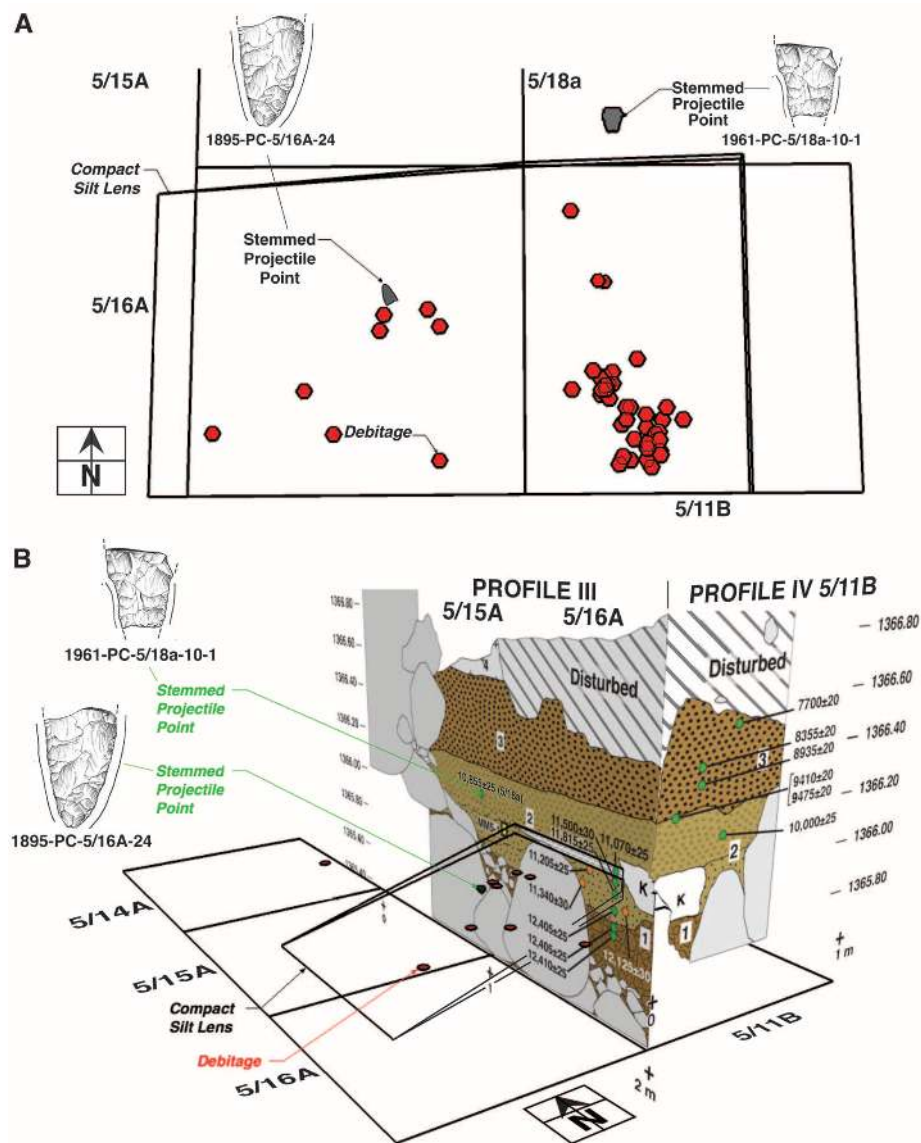

Fig. 3. (A) Horizontal distribution of Western Stemmed projectile points and in situ lithic debitage in excavation units 5/16A and 5/18A. **(B)** Vertical distribution of artifacts relative to acceptably dated coprolites and dating column samples.

(golden-mantled ground squirrel) aDNA was obtained from rodent bones near the coprolites, demonstrating that endogenous DNA survives in the material and the aDNA extraction techniques were producing reliable results (3, 28). Further tests were undertaken to investigate for potential leaching of modern DNA or aDNA

by attempting to extract human aDNA from dry *Neotoma* urine and from *Neotoma*, pronghorn, and mountain sheep fecal pellets. Again, no human aDNA was detected.

DNA moving in rainwaters or urine could contaminate underlying coprolites with younger DNA. To detect DNA translocation, we made
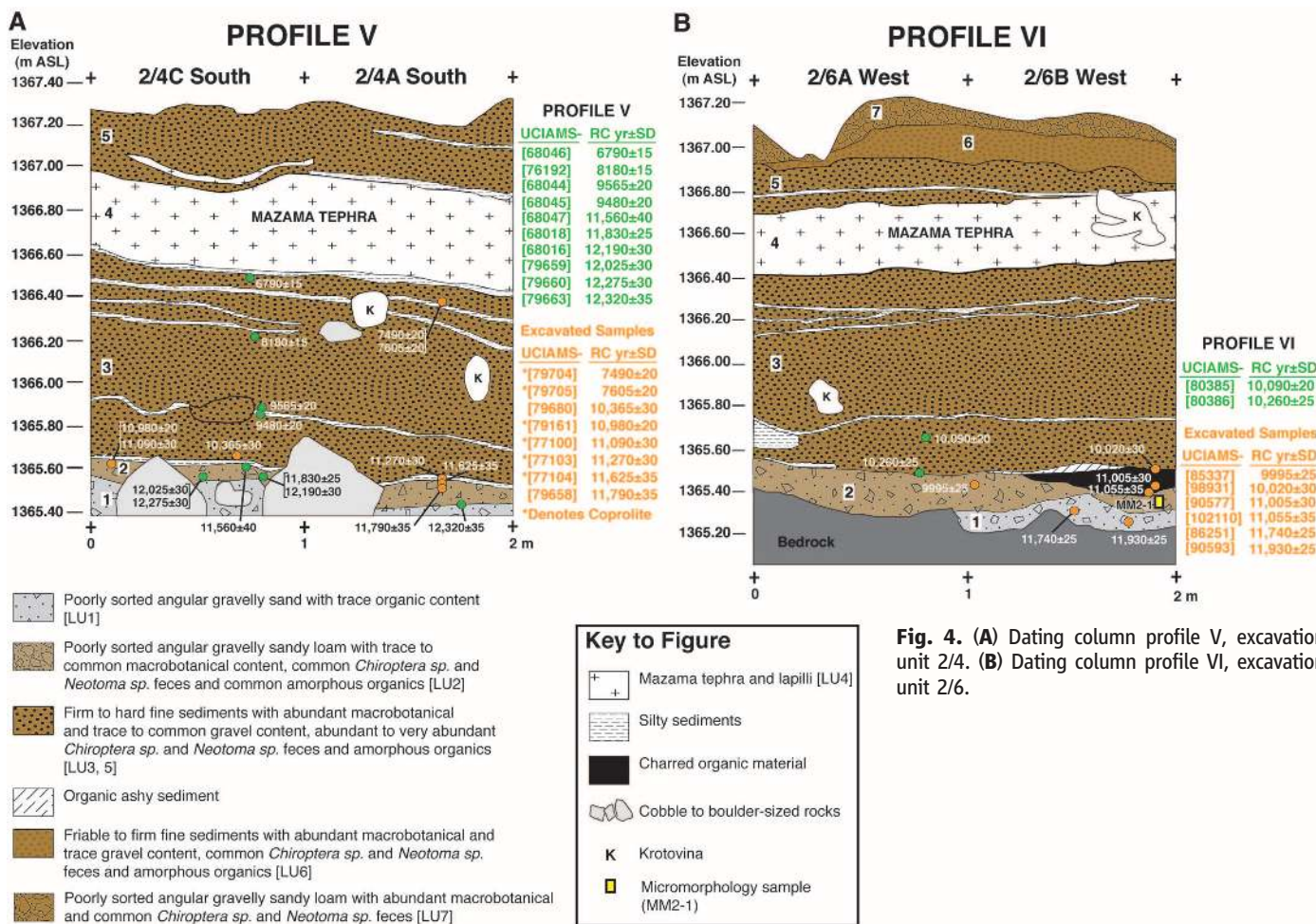
Fig. 4. (A) Dating column profile V, excavation unit 2/4. **(B)** Dating column profile VI, excavation unit 2/6.

26 ^{14}C measurements on paired macrofossils and water-soluble fractions on nine coprolites and three 1-cm-thick sediment samples. Younger solutes would indicate potential DNA contamination from younger overlying strata (table S9).

In seven coprolites, paired fractions had statistically similar ages. Another coprolite's solutes were 165 ^{14}C yr older than macrofossils, and a camelid coprolite's solutes were 810 ^{14}C yr younger than macrofossils. Sediment solutes and macrofossils exhibit differential dating of 85 to 180 ^{14}C yr. Urine-cemented sands accumulating at ~1 cm per 50 to 80 years have time-averaging problems, whereas instantaneous deposits such as coprolites enable accurate solute-macrofossil interpretations.

Radiocarbon data, mummified macrofossils, and struvite accumulations are evidence that the Paisley Caves rarely experienced wetting events that could transport aDNA into older strata. Radiocarbon measurements detect nanograms of carbon contamination, but a few hundred exogenous DNA base pairs—femtogram and smaller amounts—could be present and not detectable by ^{14}C dating. Younger DNA contamination is not indicated but could exist.

Deposition in the caves is generally rapid, normally burying human-size (diameter 2 to >3 cm)

coprolites below the penetration depth of surface water or urine within 225 radiocarbon years. If human DNA were introduced into nonhuman coprolites, it was most likely within a few hundred years of deposition, not thousands of years. Previous DNA findings of mitochondrial founding haplogroup A were confirmed by obtaining matching sequences from coprolites in blind test experiments at two independent laboratories, of which one (1830-PC-5/11B-33-101) is dated to a pre-Clovis age (12,165 ± 25 ^{14}C yr B.P.), one to about Clovis times (11,205 ± 25 ^{14}C yr B.P.), and one to the mid-Holocene (5750 ± 15 ^{14}C yr B.P.). The Paisley Caves' archaeology, geoarchaeology, and DNA analyses all indicate initial human occupation of the northern Great Basin by at least 12,300 ^{14}C yr B.P. (3, 28).

The only chronologically diagnostic late Pleistocene technology at the Paisley Caves is related to the WST. We have firmly dated two WS projectile points to Clovis (10,800 to 11,050 ^{14}C yr B.P.) (31) and earlier times (Table 1) and stratigraphically dated a third to about the same or even earlier times. There is no evidence of diagnostic Clovis technology in the site assemblage (25).

Although stemmed points and seaworthy watercraft were present in late Pleistocene Asia

thousands of years before the Paisley Caves were occupied, there is no direct correlate for WST technology in Asia. The Paisley Caves evidence suggests that the WST and Clovis complexes were contemporaneous and parallel—not unilinear—North American technological developments (18, 19). The Paisley Caves evidence supports the hypothesis that the WST was an indigenous development in the far western United States, whereas Clovis may have developed independently in the Plains and Southeast (11, 19).

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Extinction Debt and Windows of Conservation Opportunity in the Brazilian Amazon

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Predicting when future species extinctions will occur is necessary for directing conservation investments but has proved difficult. We developed a new method for predicting extinctions over time, accounting for the timing and magnitude of habitat loss. We applied this to the Brazilian Amazon, predicting that local extinctions of forest-dependent vertebrate species have thus far been minimal (1% of species by 2008), with more than 80% of extinctions expected to be incurred from historical habitat loss still to come. Realistic deforestation scenarios suggest that local regions will lose an average of nine vertebrate species and have a further 16 committed to extinction by 2050. There is a window of opportunity to dilute the legacy of historical deforestation by concentrating conservation efforts in areas with greatest debt.

In recent decades, there have been unprecedented rates of habitat loss, fragmentation, and degradation, especially in the species-rich tropics (*1*), leading to estimates of resulting species extinctions that are rarely less than catastrophic (*2*). Extinction does not, however, immediately follow changes in habitat extent or quality. Instead, a process of time-delayed community "relaxation" usually occurs (*3, 4*), where species progressively disappear over time. The term "extinction debt" (*5*) refers to any future biodiversity losses that current or past habitat destruction will incur but which have yet to be realized because of time delays in extinction. This time delay offers a window of conservation opportunity, during which it is possible to restore habitat or implement alternative measures to safeguard the persistence of species that are otherwise committed to extinction.

The Brazilian Amazon harbors some 40% of the world's tropical forest (*6*) and a substantial proportion of global biodiversity (*7*) but has also been host to the majority of tropical deforestation that has occurred in recent decades (*1*). There has been much debate over the future of the Brazilian Amazon and especially the prospects for biodiversity in the region (*6, 8, 9*). Quantitative estimates of resulting species loss have rarely been made (*10*), although we know that the number of threatened bird species in the Amazon is likely to triple over the coming decades because of the continued process of deforestation (*11*).

To address this problem, we built a modeling framework that expands on the species-area relationship (SAR) (*12, 13*). SARs provide a powerful way of estimating the final, equilibrium level of extinction caused by habitat losses (*14, 15*) but provide no information on the timing of extinctions or on the extinction debt remaining at a given time. Our improved framework gives estimates of extinctions and debt remaining at all times during and after a sequence of habitat destruction events.

Assume that at time $t = 0$ we have a patch of uniform habitat of area $A(0)$ and initial equilibrial species richness $S(0) = S_{eq}(0) = cA(0)^z$. Here, z is the exponent of the SAR and c is a constant (*12*). The patch is subjected to a subsequent pattern of habitat destruction, so that the remaining area $A(t)$ at time t is less than $A(0)$. If $S_{eq}(t) = cA(t)^z$ is the equilibrium number of species that would eventually remain if habitat destruction ceased at time t, then we assume, following empirical (*16*) and theoretical (*3, 17*) expectations, that the rate of community relaxation to this equilibrium is proportional to the difference between current richness, $S(t)$, and equilibrium richness:

$$\frac{dS}{dt} = -k(S - S_{eq}) = -k(S - cA^z) \qquad (1)$$

Here, k is a relaxation rate constant (*10*). The solution to this is

$$S(t) = S(0)e^{-kt} + e^{-kt}\int_0^t kcA(\tau)^z e^{k\tau}d\tau \qquad (2)$$

which can easily be computed numerically for any temporal pattern of habitat destruction $A(t)$.

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