

Parasites, Paleoclimate, and the Peopling of the Americas

Using the Hookworm to Time the Clovis Migration

Alvaro Montenegro, Adauto Araujo, Michael Eby, Luiz Fernando Ferreira, Renée Hetherington, and Andrew J. Weaver

School of Earth and Ocean Sciences, University of Victoria, Victoria, BC, Canada V81 3P6 (Montenegro, Eby, Hetherington, and Weaver)/Escola Nacional de Saudo Publica-Fiocruz, Rio de Janeiro, RJ, Brazil (Araujo and Ferreira). 21 IX 05

Paleoparasitological findings and paleoclimate modelling simulations indicate that early peoples migrating via the “Clovis first” route across Beringia into North America could not have traversed the required distance in time to provide a reasonable explanation for the presence of the hookworm in the pre-Columbian Americas. The introduction of the hookworm into the Americas by a land migration at around 13,000 years BP could have happened only under extraordinary circumstances and even then would have required displacement rates that appear to have no parallel in the archaeology of the continent. This implies that while the Clovis people may have been the first migrants to the Americas, they were almost certainly not the only such migrants.

The date and route travelled by the first peoples who colonized the Americas remain unknown. The “Clovis first” theory suggests that the earliest settlers were big-game hunters who travelled across the Beringian land bridge connecting Northeast Asia to North America during the last ice age. This theory further suggests that after reaching the northern regions of North America, the Clovis people continued to follow the ice age megafauna into the interior of the continent via an “ice-free corridor” east of the Canadian Rocky Mountains. They were then thought to have expanded beyond the ice sheets as far as southern South America, leaving discarded Clovis stone tools as evidence of their presence. Radiocarbon dating of Clovis points indicates an age between 11,500 and 11,000 radiocarbon years (Haury, Sayles, and Wasley 1959; Haynes 1969, 1992; Dixon 2001) or approximately 13,500–12,900 calendar years before present (hereafter all dates are converted from radiocarbon years to calendar years according to Fairbanks et al. n.d.).

Geological conditions constrain the possible timing of this terrestrial route. The mollusc and bowhead whale records in the western Canadian Arctic and the submerged peats off the coast of Alaska indicate that the Beringian subcontinent was

submerged by rising sea levels at or shortly before 12,900 BP (Kaufman et al. 2004), thus restricting the last Clovis crossing to this date. The Laurentide and Cordilleran ice sheets that had expanded to cover most of Canada and the northern United States coalesced east of the Canadian Rocky Mountains, precluding the use of the “ice-free corridor” as a viable route between ~24,000 years BP and 14,000 to 12,900 years BP. Jackson et al. (1997) used ^{36}Cl dates on boulders from the Canadian Rocky Mountain foothills erratics train to support an interpretation of continued coalescence of the ice sheets until 12,900 years BP. More recently Dyke (2004) has suggested that the opening of the corridor occurred at 14,700–14,000 years BP, but he considers it unlikely that coalescence remained until 13,500 years BP.

The speed of this southward spread of the Clovis population has been a matter of some consideration by researchers. According to the blitzkrieg theory of Martin (1973), the Clovis population migrated south at a speed of 16 km/yr. Kelly (1990), estimating the rates of population movement between northeastern Asia and sites in North and South America from the distances between dated archaeological sites, suggested speeds between 0.68 km/yr. for 4,200 km and 28.00 km/yr. for 16,800 km, the latter being the rate of population movement from the Nenana Valley in Alaska to southern Patagonia in 600 years.

Here we use paleoparasitological findings, climate data, and paleoclimate modelling to ascertain whether peoples migrating via the “Clovis first” route from areas amenable to the hookworm in Asia across Beringia and into North America could have traversed the required distance in time to provide a reasonable explanation for the presence of the hookworm parasite in the pre-Columbian Americas. Our findings are estimated under the assumptions of what we call the “Clovis first and only” hypothesis, according to which, prior to European contact, all the inhabitants of the Americas, excluding the northernmost portion of North America, descend from a group or groups that migrated into the continent by a terrestrial interior route across the Beringia land bridge at around 13,000 years BP.

The Hookworm Evidence

The clinical picture called ancylostomiasis or hookworm disease is associated with the presence of *Ancylostoma duodenale* or *Necator americanus* in the human intestine. These parasites can cause blood-loss-induced anemia and currently infect some 1 billion people in tropical and subtropical countries (WHO 1987). Each species can be found alone or associated in the same individual, and both are considered anthrophilic (Rep 1963). The southeastern portion of the Sahara and southern Asia are considered the dispersion centers of human infection by *N. americanus*. *A. duodenale* dispersion came from northern Africa, southern Europe, and southern

Asia. After the improvement of communication in the nineteenth century, the limits of distribution of the two species became less clear (Manter 1967). Some studies suggest that the source of *A. duodenale* in *Homo sapiens* was wild canids and later domesticated dogs (Cameron 1927), while others argue that both species were already associated with hominid ancestors (Fonseca 1972). It has been accepted that *N. americanus* has been associated with humans longer than *A. duodenale*.

Hookworms require a passage through the soil to complete their biological cycle. Eggs are passed with feces by infected human hosts. Soil temperature must remain between 17°C and 35°C for eggs to evolve into infective larvae. Eggs can survive for 30 days under favourable soil conditions. When present in moist, oxygen-rich soils and under optimum temperature conditions, eggs can hatch within 24 hours. Two molts then occur, and infective larvae appear after 5 to 14 days (Chandler and Read 1961; Cox 1982). Infective larvae are active and able to migrate 10 to 15 cm vertically in the soil. They can survive for two to ten months under favourable conditions but perish at temperatures lower than 14°C or if the soil becomes dry (Brumpt 1958). Infective larvae from both species penetrate the host's skin; *A. duodenale* can also become infective through oral ingestion.

Hookworm eggs and larvae have been found in archaeological sites throughout the world (Gonçalves, Araujo, and Ferreira 2003). The oldest dates have been registered in South America, including the earliest recorded date of $7,230 \pm 80$ years BP obtained from human coprolites in Northeast Brazil (Ferreira et al. 1987). Adult hookworms were found attached to the intestinal mucosa of a Peruvian mummy dated to 890–950 years BP (Allison et al. 1974). Eggs and larvae were found in coprolites extracted from mummified bodies from Chile (2,500–2,100 years BP) and Brazil ($3,490 \pm 120$ to 430 ± 70 years BP and 1,200 years BP [Gonçalves, Araujo, and Ferreira 2003; Ferreira, Araujo, and Confalonieri 1980, 1983; Sianto et al. n.d.]). In North America there is one find dated to pre-Columbian times ($2,177 \pm 145$ years BP [Faulkner and Patton 2001]), and another three pre-Columbian finds in North America are consistent with hookworm (Reinhard 1990). In the Old World, hookworm eggs were found in human coprolites and latrine sediments dated 5,600–4,400 years BP in France (Dommelier-Espejo 2001) and 3,600 years BP in the Czech Republic (Sebela, Vojtková, and Vojtek 1990, cited by Aspöck, Auer, and Picher 1999).

Pre-Columbian Hookworm and the Clovis Migration

Under optimum temperature conditions (25–30°C), hookworm eggs can develop into infective larvae in five days. If conditions are suboptimal (e.g., temperatures between 25°C and 17°C), the period of development is longer (Schmidt and Roberts 1977; Cox 1982; Schad and Warren 1990). The analysis we have conducted using present-day and paleoclimate model temperatures indicates that if the minimal conditions

(five days at 17°C) are assumed, any land route between northern Asia and North America intersects an area in which these conditions do not occur or occur very rarely (less than once every 45 years, the length of the present-day climate record examined).

Under the “Clovis first and only” hypothesis, the pre-Columbian presence of the hookworm in the Americas could be explained in terms of the following scenarios: (A) The hookworm populations brought by migrants were different from those of today, with larvae capable of developing at lower temperatures. (B) Migrants made stops and became reinfested in protected sites where ambient temperature was high enough for larvae to develop. (C) Movement across the non-infecting, cold region was fast enough to allow adult worms to survive inside their hosts, with migration occurring within the maximum life span of the adult hookworm, taken here to be eight years (Cheng 1973).

There is no present indication of cold-tolerant hookworm variants in either Asia or the Americas, making scenario A appear very unlikely. Scenario B requires migrants to have routinely made use of shelters in which temperatures were significantly higher than the surrounding average, especially in the high latitudes. It is unlikely that such conditions would have been provided by caves found in the region; even today, mid- to high-latitude cave temperatures tend to be below 17°C (Poulson and White 1969). Further, there are indications that the Clovis people rarely used caves for shelter (Kelly 1990).

It could be argued that at very small spatial scales, temperatures in living areas could have been increased by the use of fire and/or temporary shelters such as tents. However, we deem it unlikely that migrants would have used these warmed-up portions of the sites for defecation. Also, we assume that they would not have wasted resources and time, especially during the summer, warming large portions of their living spaces above 17°C, a temperature that would probably have been well tolerated by inhabitants of high-latitude regions.

In this study we assume that no reinfection occurred in cold regions (scenario C). We then use temperature data from a paleoclimate model and a present-day reanalysis to estimate the speeds of migration between Asia and North America required to explain the paleoparasitology findings under the “Clovis first and only” hypothesis. Temperature fields are used to identify the areas in which contagion is not viable (hereafter ACNV), and the speed of migration is estimated on the assumption that these areas were crossed within the life span of an adult hookworm. Our procedure takes into account the suggestion of Hawdon and Johnston (1996) that *A. duodenale* larvae could have undergone hypobiosis inside their hosts during the colder periods of the year, later to mature and lay eggs when environmental conditions, especially in coastal areas, permitted larval development and new contagion. In our analysis, even assuming hypobiosis, contagion in ACNVs was impossible because temperatures were too low even during the warmest periods of the year.

Methods

Paleotemperature data were obtained from three simulations (at 15,000, 13,000, and 11,000 years BP) of the UVic Earth System Climate Model (UVic ESCM). The model consists of an ocean general circulation model coupled with a dynamic-thermodynamic sea ice model, a land surface model, a terrestrial vegetation model, and an energy-moisture-balance atmospheric model (Weaver et al. 2001; Meissner et al. 2003b; Matthews et al. 2003). The atmospheric model includes a parametrization of the water-vapour/planetary-longwave feedback, while the radiative forcing associated with changes in atmospheric carbon dioxide is externally imposed as a reduction of the planetary-longwave radiative flux. A specified lapse rate is used to reduce the surface temperature over land where there is topography. The model uses prescribed winds to obtain its present-day climatology, and a dynamical wind feedback is included that exploits a latitudinally varying empirical relationship between atmospheric surface temperature and density. One of the virtues of the coupled model is that we do not need to employ explicit flux adjustments to keep the simulation of the present climate stable. The UVic ESCM has been extensively and successfully evaluated against both contemporary climate observations (Weaver et al. 2001) and paleo-proxy records (Weaver et al. 1998; Schmittner et al. 2002; Meissner et al. 2003a).

Each of our simulations was forced with orbital parameters and atmospheric carbon dioxide appropriate for the particular period. Continental ice sheet thickness and cover were specified according to the Peltier (1994) ICE4G reconstruction. All simulations were integrated to equilibrium for 4,500 years with a resolution of 1.8° latitude by 3.6° longitude. Analyses were performed on the last 10 years of five-day mean model output.

Present-day temperatures were obtained from 45 years of European Centre for Medium-Range Weather Forecasts (ECMWF) ERA 40 reanalysis (<http://data.ecmwf.int.data/>). As the constraint on the hookworm life cycle is related to minimum temperature thresholds, our analysis was restricted to the summer months (June, July, and August). Test analyses using values for the whole year produced results identical to those of analyses of the summer data only. The data have 2.5° by 2.5° spatial resolution and cover the period from September 1957 to August 2002 with four temperature values per day.

To represent the different environments in which hookworm eggs and larvae may be found (Cox 1982), we define T_h as the local mean of near-surface air, soil skin (first few millimeters), and internal soil (0.07–0.21 mm for ECMWF; first meter for UVic ESCM) temperatures. Drawing on the literature (Chandler and Read 1961; Rey 2001), we used two combinations of parameters to define distinct ACNVs: ACNV1, a region in which, during the length of the experiments, the 14-day T_h mean never climbs above 17°C, and

ACNV2, a region in which the 10-day T_h mean is never higher than 20°C.

We conservatively define the migration distance as the shortest path, via land, across a specific ACNV. Paths are allowed to cut across ice sheets and other topographic features. For the 13,000 years BP experiment, paths that avoid the ice sheets and pass through the ice-free corridor between the Cordilleran and Laurentide ice sheets are also estimated.

Compared with the dimensions of a hunter-gatherer camp, the model's spatial resolution is coarse. At 60° N, for example, it is approximately 200 by 200 km. Because of spatial variability not resolved by the simulation, an area whose mean temperature is below the threshold could still harbour localities where contagion was viable. To address this possibility we used a high-resolution (~3.67 by 1.83 km at 60° N) topographic data set (National Geophysical Data Center 2-Minute Gridded Global Relief [<http://www.ngdc.noaa.gov/mgg/global/global.html>]) to estimate the maximum temperature within each model grid cell. This is done by adding ΔT to the mean model solution, with ΔT given by $\Delta T = \Delta h L_r$. Δh is the difference between UVic model grid cell mean altitude and the observed minimum altitude. L_r is a lapse rate of 6.5°C/1,000 m. The same lapse-rate adjustment is conducted using present-day reanalysis data.

To account for the effects of high-frequency temporal variability and extreme events, a set of ACNVs is estimated using ECMWF data cooled down to 13,000 years BP values. Cooling is space-dependent and based on the difference between present-day (1950–2000) and 13,000 years BP average temperature fields as obtained from the equilibrium simulations of the UVic ESCM. Differences are calculated for air, soil skin, and internal soil. The lapse-rate adjustment is also calculated to obtain a very conservative estimate (biased toward high values) of maximum temperature within each cell. A last set of ACNVs is obtained by assuming that the model underestimates temperatures in all simulations and for all points by 3°C. This is done by adding 3°C to the lapse-rate-adjusted temperature fields.

The dependency of the hookworm larvae on soil moisture is not considered. We opted to leave it out because the uncertainties associated with modelling soil moisture are greater than with temperature, making our results more robust. Furthermore, because larval development ceases below threshold temperatures independent of soil moisture levels (Cox 1982), the inclusion would only enlarge the temperature-only estimated ACNVs.

Results

The ACNVs for the 13,000 years BP simulation and the cooled-down present-day simulation and the approximate routes through these areas are presented in figures 1 and 2, respectively. Routes are traced as a series of straight lines along the shortest path connecting areas where contagion is possible. Paths were traced in this way for all experiments and used

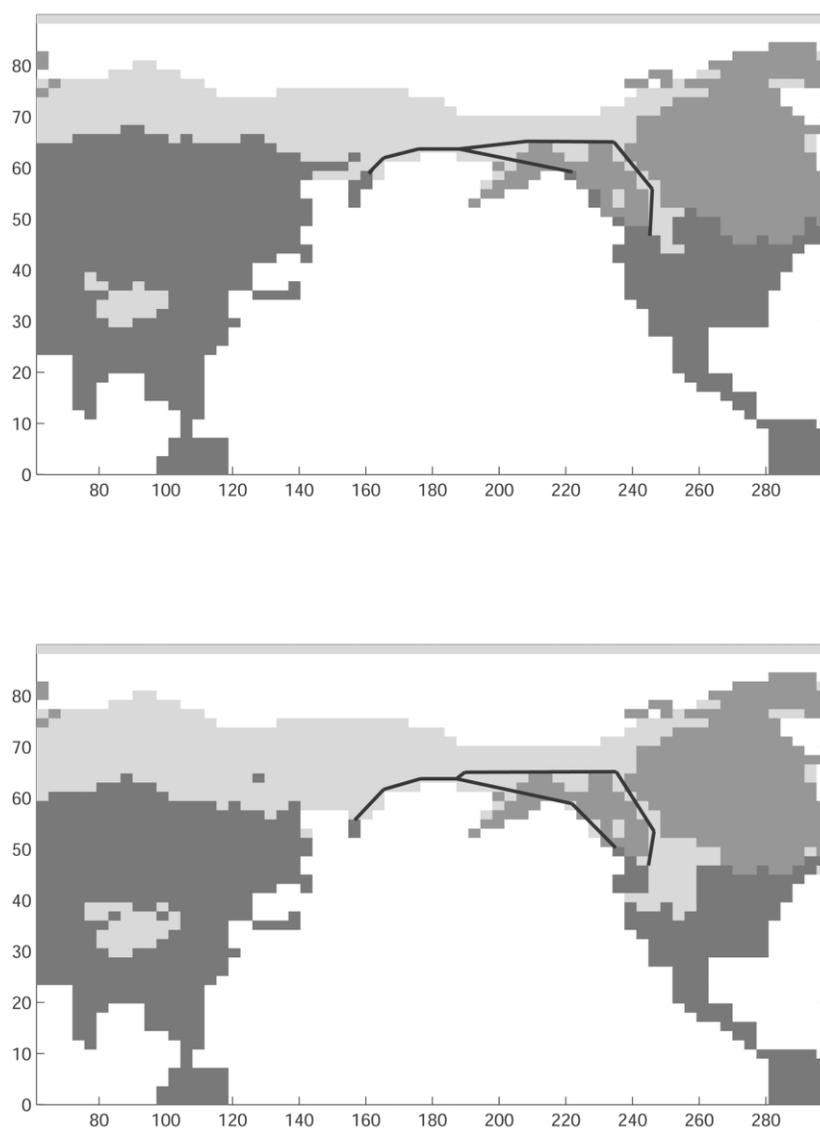


Figure 1. Results of the UVic model 13,000 years BP simulation. *Light grey*, area where contagion is not viable (ACNV); *dark grey*, area where contagion is viable; *intermediate grey*, continental ice sheet; *white*, water. Black lines represent trajectories (both shortest and ice-free) through ACNV used to calculate distances and speeds in table 1. *Top*, ACNV1 (17°C/14-days) adjusted for lapse-rate effects and with arbitrary 3°C temperature increase. *Bottom*, same as above for ACNV2 (20°C/10-days). Numbers in margins refer to latitude and longitude.

to calculate the values presented in table 1. The length of routes across ACNVs decreases from 15,000 years BP to the present. ACNV1s tend to be smaller than ACNV2s, and the effects of climate variability are significant, with the ACNVs estimated for ECMWF values cooled to 13,000 years BP conditions markedly smaller than the model results for the same period. The inclusion of the lapse-rate adjustments decreases ACNVs, as does the addition of the 3°C offset.

For the UVic model output, the shortest/slowest crossing occurs in the UVic ACNV1 11,000 years BP+LR+3°C simulation, where the 14-day temperature mean never climbs above 17°C, the temperature fields are lapse-rate-adjusted, and the 3°C offset has been added. Under these conditions, and assuming a maximum 8-year hookworm life span, migrants would have to have migrated at a minimum speed of 348 km/yr. to bring the hookworm with them into the Amer-

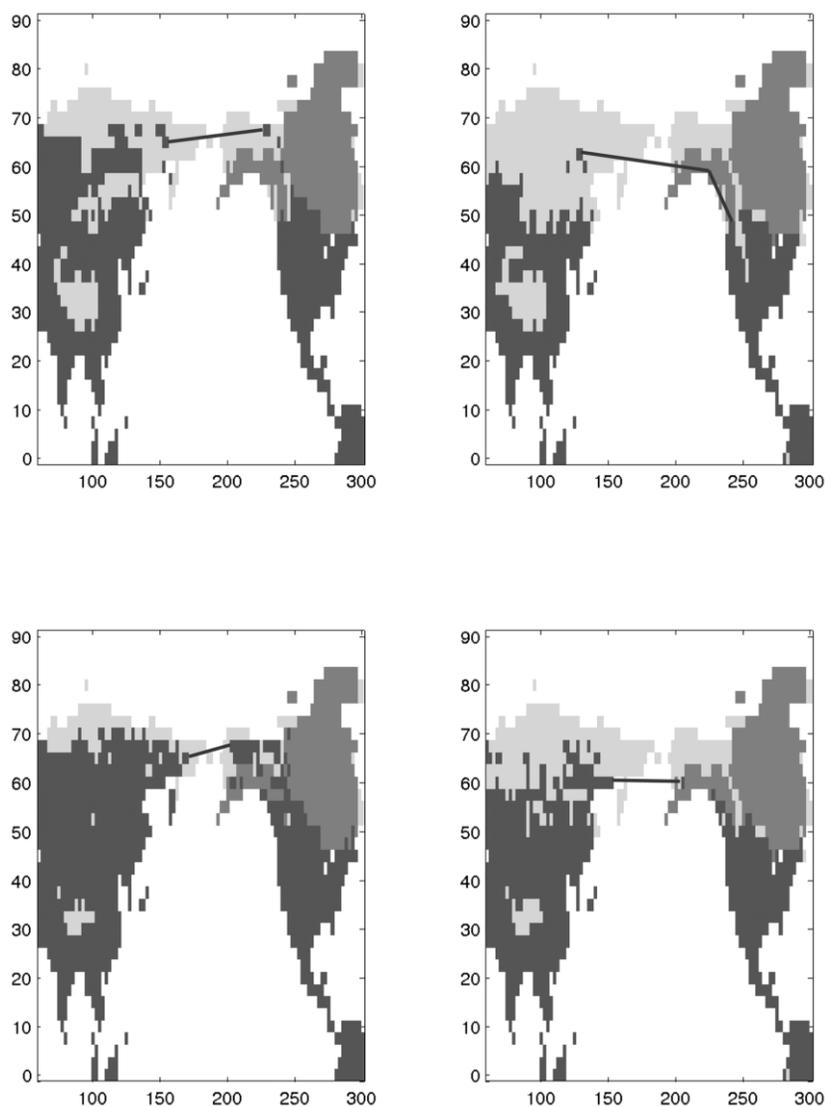


Figure 2. Results of the ECMWF reanalysis data cooled down to 13,000 years BP levels. *Light grey*, area where contagion is not viable (ACNV); *dark grey*, area where contagion is viable; *intermediate grey*, continental ice sheet; *white*, water. Black lines represent trajectories through ACNV used to calculate distances and speeds in table 1. *Top left*, ACNV1 (17°C/14-days); *top right*, ACNV2 (20°C/10-days); *bottom left*, same as top left but with temperatures lapse-rate-adjusted; *bottom right*, same as top right but with temperatures lapse-rate-adjusted. Numbers in margins refer to latitude and longitude.

icas. The minimum speeds based on the average life span of *N. americanus* (4 years) and *A. duodenale* (1.5 years) under the same simulation scenario are 696 km/yr. and 1,856 km/yr. respectively. At 15,000 years BP the slowest speeds (based on routes that cut across the Cordilleran ice sheet) range between 465 and 681 km/yr.

The distances and speeds most relevant to our “Clovis first

and only” hypothesis come from the ice-free-route model results at 13,000 years BP and from the present-day data cooled to 13,000 years BP levels. In the model experiments, the minimal migration speed is 739 km/yr., and in the cooled ECMWF the slowest speed is 183 km/yr. This last value, the lowest migration speed for all experiments at 13,000 years BP, is more than six times faster than the proposed 26 km/yr.

Table 1. Migration Distances and Speeds for All Experiments

Experiment	Speed							
	Distance		<i>N. americanus</i>		<i>A. duodenale</i>		Maximum	
	ACNV1 (km)	ACNV2 (km)	ACNV1 (km/yr.)	ACNV2 (km/yr.)	ACNV1 (km/yr.)	ACNV2 (km/yr.)	ACNV1 (km/yr.)	ACNV2 (km/yr.)
ECMWF	819	1,463	205	366	546	975	102	183
ECMWF + LR	819	2,903	205	726	546	1,935	102	363
ECMWF@13 kyrBP	3,070	6,118	768	1,530	2,047	4,079	384	765
ECMWF@13 kyrBP + LR	1,463	2,558	366	640	975	1,705	183	320
UVic 11 kyrBP	7,137	8,880	1,784	2,220	4,758	5,920	892	1,110
UVic 11 kyrBP + LR	4,417	6,077	1,104	1,519	2,945	4,051	552	760
UVic 11 kyrBP + LR + 3°C	2,784	4,416	696	1,104	1,856	2,944	348	552
UVic 13 kyrBP	8,306	9,054	2,077	2,264	5,537	6,036	1,038	1,132
UVic 13 kyrBP + LR	5,304	6,862	1,326	1,716	3,536	4,575	663	858
UVic 13 kyrBP + LR + 3°C	3,467	5,325	867	1,331	2,311	3,550	433	666
UVic 13 kyrBP IF	9,559	10,336	2,390	2,584	6,373	6,891	1,195	1,292
UVic 13 kyrBP IF + LR	6,609	8,353	1,652	2,088	4,406	5,569	826	1,044
UVic 13 kyrBP IF + LR + 3°C	5,911	6,678	1,478	1,670	3,941	4,452	739	835
UVic 15 kyrBP	8,467	9,217	2,117	2,304	5,645	6,145	1,058	1,152
UVic 15 kyrBP + LR	5,593	6,896	1,398	1,724	3,729	4,597	699	862
UVic 15 kyrBP + 3°C	3,721	5,447	930	1,362	2,481	3,631	465	681

Note: ACNV1, distances and speeds across areas of contagion not viable defined by the 17°C/14-days threshold; ACNV2, distances and speeds with 20°C/10-days as a limit; *N.americanus*, speeds based on 4-year average life span of adult *N. americanus*; *A.duodenale*, speeds based on a 1.5-year average life span of adult *A. duodenale*; Maximum, speeds based on an 8-year adult life span of the parasites; ECMWF, results from present-day reanalysis; ECMWF@13kyrBP, reanalysis values cooled to 13,000 years BP levels; LR, lapse-rate adjustment; UVic, model results; IF, routes that avoid ice sheets.

migration speed suggested for the displacement between Central Alaska and Patagonia (Kelly 1990) and at least six times faster than the estimated pace of the Thule migration across the Canadian Arctic at around 1,000 years BP (15–30 km/yr. [McGhee 1978]) Migration speeds into the Americas on the order of hundreds of km/yr. have been suggested (West 1996), but these refer to movement within the “ice-free corridor,” where displacement would have been constrained laterally by the ice sheets. This would not have been the case here, where the ACNVs occupy the expanses of northwestern Siberia, western Alaska, and Beringia.

The 183-km/yr. migration rate assumes that migrants moved in a straight line and briefly inhabited only the warmest sites possible, even during summer. It is also based on an adult hookworm life span that has been conservatively set more than five times the expected value for the more cold-tolerant *A. duodenale*, which is also the only species that exhibits hypobiosis. For the same experiment, the migration speed based on average temperatures and an 8-year life span would be 384 km/yr. Speeds based on adjusted maximum temperatures but calculated using the average life span of the organisms would be 366 km/yr. (*N. americanus*) and 975 km/yr. (*A. duodenale*).

Summary

Within the constraints of our present knowledge of the climate system and hookworm biology, these findings suggest that the introduction of the hookworm into the Americas by a group migrating through the interior of Beringia could have happened only under extraordinary circumstances and even then would have required very rapid displacement rates, rates that appear to have no parallel in the archaeology of the continent. Unless humans were able to migrate at speeds much greater than we assume, the “Clovis first and only” hypothesis does not provide a convincing explanation for the presence of the hookworm in the pre-Columbian Americas.

It is important to stress that these experiments were designed to test the “Clovis first *and only*” and not the “Clovis first” hypothesis. The Americas might very well have been originally inhabited by humans moving along an interior land route across Beringia at around 13,000 years BP; however, our research indicates that the Clovis people were unlikely carriers of the hookworm, and this suggests that the parasites were introduced by some alternative mechanism. Alternative mechanisms include the possibility that the parasite entered the Americas by an interior route via Beringia during a period of lower sea level but with regional temperatures significantly

higher than at 13,000 years BP. The archaeological literature offers a number of possible nonterrestrial routes, including transoceanic contacts between Japan and Central America (Meggers 1975) and coastal routes along the North Pacific (Heusser 1960; Fladmark 1979; Hetherington et al. 2003) and the North Atlantic (Bradley and Stanford 2004). Pointing to paleoparasitological findings, Araujo, Ferreira, and Confalonieri (1981; Araujo et al. 1988) have discussed the possibility of a trans-Pacific introduction. This suggestion has been criticized (Hawdon and Johnston 1996; Kliks 1982; Fuller 1997), but strong arguments based on parasite biology and infection dynamics have been presented by paleoparasitologists supporting an alternative route for parasite introduction (Ferreira and Araujo 1996; Reinhard et al. 2001; Reinhard 1992). Whatever the source, our analysis strongly suggests that while the Clovis people may have been the first migrants into the Americas, they were almost certainly not the only such migrants.

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