



The Pre-Columbian Peopling and Population Dispersals of South America

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Abstract

This paper summarizes the current archaeological, physiographic, demographic, molecular, and bioarchaeological understanding of the initial peopling and subsequent population dynamics of South America. Well-dated sites point to a colonization by relatively few broad-spectrum foragers from northeastern Asia between ~13,000 and 12,000 cal BC via the Panamanian Peninsula. By ~11,500–11,000 cal BC, a number of regional, specialized bifacial technologies were developed, with evidence for the seasonal scheduling of resources and the colonization of extreme environments. Restricted mobility, landscape modification, and the cultivation of domesticates were underway by ~8000 cal BC. The early migration routes followed by colonists resulted in a broad east-west population structure among ancient South Americans. Genetic, demographic, and skeletal morphological data indicate that a subsequent demographically driven dispersal into South America largely replaced preexisting central Andeans ~5000 BC, due to increased fertility associated with the shift to agriculture. Beyond the Andes, however, there is little evidence of impact of these later expansions on foragers and horticulturists of the Amazon and Southern Cone who were largely descended from Paleoindians and early Holocene populations.

Keywords Paleoindians · Colonization · Demic diffusion · Western Hemisphere

Introduction

The peopling of the Western Hemisphere has interested scholars since de Acosta (1604) argued that Native Americans came across a yet-to-be-discovered land bridge with Asia. Subsequent archaeological (Braje et al. 2017; Dillehay 2000, 2009; Goebel et al. 2008; Meltzer 2009; Potter et al. 2017), skeletal and dental

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morphological (Hrdlicka 1923; MacCurdy 1923; Turner 1985), and genetic data (Llamas et al. 2016; Moreno-Mayar et al. 2018; Posth et al. 2018) all point to an Asian ancestry for Native Americans who arrived during the Late Pleistocene via the Bering Land Bridge. Numerous attempts have been made to reconcile the discrepancies between and within the different datasets (Dillehay 2004; Fiedel 2017a; Goebel et al. 2008; Greenberg et al. 1986; Hoffecker et al. 2016; Meltzer 2009; Morrow 2017). Although the archaeological record indicates a relatively late and rapid colonization from Beringia, either during the amelioration (~15,000–13,500 BC), or immediately following the end of the Last Glacial Maximum (LGM) (~17,000 BC), the timing, routes, and origins of the earliest Native Americans remain under debate (Braje et al. 2017, 2018; Potter et al. 2018).

Similarly, these same persistent questions are unresolved for the peopling of South America despite more than a century of scholarly inquiry (Dillehay 2009). Archaeological evidence provides a minimum age for the initial entry into South America, while the results of molecular and bioarchaeological research contribute to our understanding of the origins and subsequent population dynamics of the earliest South Americans. They also shed light on how these later prehistoric population dynamics relate to climatic, environmental, and cultural changes and adaptations. Because the peopling and subsequent population dynamics of South America are part of the broader colonization of the Western Hemisphere, I couch this discussion in terms of broader debates. Yet there were unique factors related to South America's physiography and the mobility, subsistence strategies, and biology of the initial colonizers that impacted how they subsequently dispersed and responded to later changes in South America's climate, environment, and resources, as well as how descendant populations may have expanded, contracted, and interacted with one another.

Based on my review of recent archaeological and human genetic and skeletal morphological studies, I argue that the earliest South Americans initially arrived ~13,000 BC using a generalized, expedient tool kit of simple yet recognizable flakes that were part of a broader bifacial lithic tradition. Within ~1000 years, the earliest colonizers rapidly populated the continent via the western and eastern coastlines and interior riverways. Maritime resources were important, but early colonists were unimpeded from exploiting the extreme high-altitude environments of the Andes, the harsh tundra-like conditions of Patagonia, and the forested regions of the Amazon. Shortly thereafter, mobile foragers developed and employed diversified point technologies to exploit local resources.

The initial South American colonists had their origins in the first founding pulse of North American Paleoindians, yet some of them may have had a small, discernable amount of genetic diversity from a more obscure ancient Asian "population Y" that resided in northeastern Asia during the Terminal Pleistocene and shared affinities with the ancestors of living Australians, Andaman Islanders, and Papuans. Genetically and morphologically discernable differences in east-west population structures among early South Americans were established through initial fissioning along the aforementioned migration routes. Subsequent prehistoric population expansions occurred over the next 12,500 years as a result of the demographic impacts related to the shift to food production and resettlement policies of

pre-Columbian Andean states. Specifically, the distinct cranial morphology of prehistoric South Americans changed due to both biomechanical changes that resulted from dietary shifts, as well as population expansions that occurred throughout the Holocene. Likewise, the documented prehistoric changes in genetically influenced tooth trait frequencies, especially in the northern and central Andes between ~6000 BC and 2000 BC, were caused by the marked, climatically influenced increase in maize productivity and a dramatic economic shift to agricultural regimes, thereby causing a north-to-south demographically driven population expansion of agriculturalists that is also apparent in Y-chromosome and ancient nuclear DNA data. Additional population dispersals are apparent from other forms of molecular data.

I structure this review by first providing background on the current consensus regarding the source and timing of the initial colonization of the Western Hemisphere. I then briefly discuss Late Pleistocene South American physiography and climate to contextualize the consensus understandings (or, sometimes, lack thereof) regarding the timing, migration routes, and adaptations of the early colonizers of South America by marshaling evidence from the archaeological record, molecular studies, demographic modeling, and skeletal morphological research. In large part, because discrepancies in the datasets—sometimes based on living versus prehistoric South Americans—provide dramatically different snapshots through time, I also provide a scenario regarding how later mid-Holocene environmental changes and cultural responses impacted subsequent population dispersals. Given both the unwieldy task of trying to summarize prehistoric population dynamics for an entire continent, as well as the unbalanced nature of where research has historically been focused, our understanding is patchy, and therefore, by necessity, my treatment of the topics primarily focuses on those regions with the most research.

Background—Broader Considerations from Beringia and North America

The archaeological evidence indicates that people began to colonize northeastern Asia ~30,000 BC in the Yana River region (Graf and Buvit 2017; Hoffecker et al. 2016; Pitulko et al. 2014), prior to the Last Glacial Maximum (LGM) ~24,000–17,000 cal BC *sensu stricto* (Bromley et al. 2016; Clark et al. 2009). During the LGM the oceans were as much as ~130 m below current levels (Lambeck et al. 2014), thereby exposing a landmass—the Bering Land Bridge—that extended between northeastern Asia and Alaska. People migrated east into Beringia along this landmass (Goebel et al. 2008). Based on a recent review of securely dated sites in eastern Beringia (Graf and Buvit 2017), humans did not continuously occupy the region until ~15,000–13,600 BC. Canada and lower North America are thought to have been inaccessible to the occupants of Beringia during the LGM due to the coalescence of both the Laurentide glacier, which extended between the Atlantic and the Rocky Mountains, and the Cordilleran ice sheet, which extended from the Pacific Coast to the Rocky Mountains (Meltzer 2009). As I discuss in greater detail below, the ancestral population(s) that gave rise to modern North and South Americans underwent genetic differentiation

while in western Beringia during the LGM—a model referred to as the “Beringian standstill hypothesis” (Kitchen et al. 2008; Mulligan et al. 2008; Tamm et al. 2007).

A Pacific coastal route of migration from Beringia into lower North America was possible as early as ~15,000 cal BC as the Cordilleran ice sheet began to retreat (Lesnek et al. 2018; Taylor et al. 2014), while an internal “ice-free corridor” along the eastern Rocky Mountains does not seem to have been habitable by humans until ~10,600 cal BC (Pedersen et al. 2016; cf. Potter et al. 2017). Some scholars argue that a second migratory pulse from the North American arctic through the ice-free corridor also contributed to the population structure of North American populations (Llamas et al. 2016; Perego et al. 2009). However, Scheib et al. (2018) argue that apparent North American Paleoindian population structure resulted from an early bifurcation that resulted from an initial coastal migration.

The aforementioned climatological and physiographic issues are important for establishing the parameters on current models regarding both the timing and route(s) taken during the initial migratory event(s) into the Western Hemisphere, as well as for teasing out inconsistencies for both the pre-Clovis and Clovis first/blitzkrieg models as they relate to the initial colonization of South America. The consensus among archaeologists working on early sites in South America long ago moved beyond the Clovis first/blitzkrieg model, and most now accept that the peopling of the continent began prior to the emergence of Clovis technologies (Borrero 2016; Dillehay 2014a; Dillehay et al. 2015; Flegenheimer et al. 2014; Graf et al. 2014; Perez et al. 2016; Politis et al. 2016; Sandweiss 2015; Schmidt Dias and Bueno 2014b; Suárez 2014).

Following the discovery of Clovis artifacts (Figgins 1927), and in accordance with the Clovis first/blitzkrieg model (Haynes 1964), it is argued that the initial colonizers of North America were big game hunters, who came across the Bering Land Bridge from Asia following the end of the LGM, and then migrated south through the ice-free corridor (Hamilton and Buchanan 2007). Subsequently, they colonized Central and South America within a thousand years (Dillehay 2009; Goebel et al. 2008; Haynes 2002). The widespread distribution of distinctive, fluted Clovis points in direct association with late Ice Age megafauna in the United States, along with similar (albeit with different forms and technical execution) fishtail points in Central and South America appeared to confirm this model (Bird 1938; Lynch 1978; Mayer-Oakes and Bell 1960).

Recent reevaluations of radiocarbon data from North American Clovis sites, however, indicate that the technology was relatively short-lived, existing only for about 400 years (~11,200–10,800 cal BC) (Goebel et al. 2008; Waters and Stafford 2007; see Haynes et al. 2007 for an alternative perspective). South American sites with fluted fishtail projectile points are roughly contemporaneous with late Clovis sites: those from stratigraphic contexts with secure radiocarbon dates include El Inga, Ecuador (Mayer-Oakes and Bell 1960); Tagua Tagua (Montané 1968; Núñez et al. 1994a), Quebrada Santa Julia (Jackson et al. 2007), and Fell’s Cave, Chile (Bird 1946); and Cueva Casa del Minero, Cerro Tres Tetras, Los Toldos, Paso Otero, and Piedra Museo, Argentina (Cardich 1977; Fidalgo et al. 1986; Politis 1991; Prates et al. 2013).

In recent years, a number of widely accepted (though not universally, see Fiedel 2013), stratified pre-Clovis sites indicate a rapid post-LGM colonization of North America between ~13,500 and 11,500 cal BC. These sites include the Debra L. Friedkin site, Texas (Waters et al. 2018); Meadowcraft Rockshelter, Pennsylvania (Adavasio and Pedler 1997); Page-Ladson, Florida, (Halligan et al. 2016); Schaefer and Hebior, Wisconsin (Joyce 2006); and Paisley Cave, Oregon, (Gilbert et al. 2008). Additional possible pre-Clovis sites in South America include Huaca Prieta, ~13,000–11,300 cal BC (Dillehay et al. 2017) and Pikimachay Cave, ~13,800–12,900 cal BC (Yataco 2011), both in Peru; Taima-Taima, Venezuela, ~12,400–9800 cal BC (Bryan and Gruhn 1979); and Monte Verde II, ~12,500 cal BC (Dillehay et al. 2008) and Monte Verde I, ~16,500–12,500 cal BC (Dillehay et al. 2015), in Chile. The antiquity of these South American sites is not universally accepted due to persistent issues of associations and dating, or because the sites have not been fully reported and vetted (Borrero 2015; 2016; Sandweiss 2015; Suárez et al. 2014).

In the following section, I review the archaeological evidence related to the initial peopling of South America in greater detail. Although great archaeological research has occurred elsewhere on the continent (e.g., Bueno and Schmidt Dias 2015; Bush et al. 2016; Iriarte et al. 2017; Lourdeau 2012), our most coherent understanding of postcolonization population dynamics comes from the central Andes and Southern Cone regions.

The Terminal Pleistocene/Early Holocene Archaeological Record of South America

As a bioarchaeologist, I have no vested interest in when South America was first colonized. I concur with Bryan and Gruhn (2003) that we should not limit our understanding of the colonization of the Western Hemisphere and South America by applying arbitrary temporal boundaries. I am open to claims for early (i.e., peri-LGM) South American sites, but, at this point, I do not think the reported evidence is convincing. Recent calls for reevaluations of evidentiary expectations for early sites may result in the reconsideration of previously rejected early sites (Boëda 2015, Boëda et al. 2016; Dillehay 2014a, b; Politis 2015; Sandweiss 2015). However, a minimum of archaeological evidentiary expectations must be met if purported early sites are to be accepted, such as well-documented stratigraphic consistency of secure radiocarbon dates from the site; well-documented associations of artifacts with radiocarbon dates and strata; in the case of lithics, unambiguous evidence for anthropic flaking, or a modicum of evidence for the presence of irrefutably anthropogenic objects made from exotic materials; and the elimination of other taphonomic and/or nonhuman causes for the finds. I believe that the burden of proof lies with those archaeologists making claims for early South American sites (i.e., pre-13,000 cal BC), because—as is commonly stated—extraordinary claims require extraordinary evidence. Failure to meet minimal criteria of authenticity and reporting invites skepticism and allows for more parsimonious, better, nonanthropogenic arguments to be favored over the anthropic explanations.

Many researchers investigating the timing of the initial colonization of South America rely on comparative analyses of available radiocarbon data that are winnowed using rigorous sample criteria (papers in Bueno et al. 2013a; also Berón 2015; Delgado et al. 2015a; Dickau et al. 2015; Perez et al. 2016; Politis and Steele 2014; Schmidt Dias and Bueno 2014a; Suárez 2014). In my discussion I use published calibrated radiocarbon dates, when available, and the OxCal ShCal 13 algorithm to make published uncalibrated dates comparable to others. The following review is not an exhaustive treatment of all early South American sites but considers key Late Pleistocene and Early Holocene sites, recent developments, and emerging consensus among archaeologists working in South America (Fig. 1). Other publications provide more comprehensive treatments of early South American sites (Dillehay 2000; Flegenheimer et al. 2006; Lavallée 2000; Miotti et al. 2012). I begin with the current understanding of the environmental and physiographic conditions that the earliest South Americans encountered.

Late Pleistocene South American Physiography

The routes taken during the initial colonization of South America were influenced by major physiographic features, including the Late Pleistocene coastlines, the Andean mountains, the northern Guyana highlands, the Amazon River, and the extensive pampas and tundra-like deserts of the Southern Cone region (Dillehay 2009; Magnin et al. 2012; Miotti et al. 2012; Rothhammer and Dillehay 2009). Recent work in the extreme altitudes of the Andes indicates that none of these aforementioned features would have presented obstacles for early migrants (Capriles and Albarracín-Jordan 2013; Rademaker et al. 2016; Yacobaccio 2017).

The earliest inhabitants of the continent encountered environmental conditions and landscapes very different from those of today. In paleoenvironmental reconstructions, the northern and southern Andes were cooler, more humid, and more heavily forested than today (Clapperton 1993a, b; Dillehay 1989; Van der Hammen and Correal 2001). Glaciers in the central Andes were primarily at elevations >5000 masl; they were patchier and not nearly as extensive as glaciers in North America at the time (Bromley et al. 2009, 2011a, b, 2016; Clapperton 1993a, b). For tropical latitudes of the Andes, the LGM is locally dated to ~26,000–17,000 BC, followed by rapid deglaciation ~17,000–13,000 BC, with a brief hiatus at ~14,100 BC (Bromley et al. 2016), which dramatically ameliorated the long asserted glacial and environmental “barriers” to exploration and habitation of the high altitudes (Aldenderfer 2008). Glacial melting persisted thereafter (Bromley et al. 2009, 2011a, b, 2016).

During the Terminal Pleistocene, open savannas predominated in the northern regions of South America, whereas the plains of Brazil, eastern Bolivia, and southern Colombia and Venezuela were cooler, drier, and characterized by a mosaic of open forests and savannas, with some parts heavily forested, albeit less so than during the subsequent Holocene (Behling 1988; Colinvaux et al. 2000; De Oliveira et al. 1999; Ledru et al. 2006). The grassy pampas regions of southern Brazil, Uruguay, and Argentina were much cooler and more humid than today and were covered by steppe-like low herbs and shrubs (Moore 1978; Salgado-Laboriau 1997;



Fig. 1 Map of Late Pleistocene and Early Holocene sites discussed in the text

Villa-Martínez and Moreno 2007), while the far Southern Cone Patagonian regions of Chile and Argentina were characterized by frigid, humid steppe and desert-like tundra, respectively. The north coast of Peru was typified by coastal mangroves and dry seasonal forests (Dillehay 2011; Sandweiss 2003), parts of the hyper-arid Atacama Desert region were intermittently even more arid during the Terminal Pleistocene than today (Gayó et al. 2012; Sandweiss 2003), and wetter conditions, pastures, and forests prevailed in parts of the central Chilean coastline (Carabias et al. 2014; Valero-Garcés et al. 2005).

Subsequently, atmospheric temperatures and gases, such as CO² and methane, increased during the Early Holocene, while Pacific Ocean surface temperatures decreased in the southern hemisphere during the Middle Holocene (~5000–3000 cal BC) (Anderson et al. 2007; Sandweiss et al. 2007), due to glacial melt during the maximal temperature increases that occurred between ~4500 and 3200 BC (Thompson et al. 1995). Consequently, the intensity and variability of El Niño Southern Oscillation (ENSO) events declined from ~6000 to 2000 BC, followed by a return to current levels of frequency and variability of ENSO events (Carré et al. 2014).

Initial Migratory Route(s)

The earliest South American colonists came into the continent through the Isthmus of Panama— along coastlines and rivers (Dillehay et al. 2015; Miotti et al. 2012; Nami et al. 2018; Perez et al. 2016; Sandweiss 2008; Steele and Politis 2009; Suárez 2017), along inland routes into the Amazon and other interior river valleys (Anderson and Gillam 2000), or along the Andes (Lanata et al. 2008; Reich et al. 2012), sometime following the local LGM ~14,100 BC (Bromley et al. 2016). Although some scholars (deFrance et al. 2009; Dillehay et al. 2017; Sandweiss 2008) hypothesize an initial western Pacific coastal corridor route, with the adjacent central Andean highlands colonized ~1000 years later (Rademaker et al. 2013), others argue that early sites along the north coast of the Caribbean and eastern Southern Cone point to a rapid, simultaneous bicoastal migration (Miotti 2003; Nami 2016; Perez et al. 2016; Suárez 2017).

The modeling of securely dated early South American archaeological sites and genetic data indicate that only a few thousand individuals entered and rapidly dispersed throughout South America during initial colonization (Goldberg et al. 2016; Lanata et al. 2008; Perez et al. 2016; Steele and Politis 2009). However, attempts to simulate the initial timing and migration route(s) remain incomplete because much of the pre-LGM South American coastal shelf (and likely early coastal sites) are now submerged under ~100–120 m of water following glacial melt (Angulo et al. 2006; Carabias et al. 2014; Fairbanks 1989; Lambeck et al. 2002; Ponce et al. 2011; Violante and Parker 2004). Many of the earliest reported South American sites are currently located along a narrow coastal strip that was as much as 5–10 km from the Late Pleistocene/Early Holocene western coast and 150 km from the southeastern coast of the continent (Mackie et al. 2014; Miotti 2003; Ponce et al. 2011; Richardson 1973; Sandweiss 2003; Suárez 2017; Violante and Parker 2004). Further, early archaeological sites in the Amazonian region remain under explored (Dillehay 2000;

Lanata et al. 2008; Miotti et al. 2012). These factors create biases in attempts to model population dynamics toward sites located primarily in deserts, high altitudes, regions typified by heartier scrub vegetation, and modern coasts located several kilometers inland from ancient coastlines. With these factors in mind, I next consider the evidence for pre-LGM sites before discussing anthropic and widely accepted Late Pleistocene sites.

Pre-Last Glacial Maximum South America Sites?

Despite the ongoing debates regarding the initial timing of the arrival of the first colonists, most South American archaeologists moved beyond the Clovis first debate before North American archaeologists did, especially since the acceptance of the pre-Clovis status for Monte Verde II (Graf et al. 2014; Meltzer et al. 1997; cf. Fiedel 1999; Haynes et al. 2007). Some South American sites purported to date to ~50,000–30,000 BC, such as Pedra Furada, Brazil (Guidon and Delibrias 1986), and Pikimachay Cave, Peru (MacNeish et al. 1981), were the source of debate during the 1980s and 1990s (Dillehay and Collins 1988, 1991; Dillehay et al. 1999; Fiedel 2000; Lynch 1991; Meltzer et al. 1994; Parenti et al. 1996). A consensus developed during the 1990s that the earliest artifacts from Pedra Furada and Pikimachay Cave were questionable because they consisted of local materials from overhangs and cave ceilings and exhibited ambiguous evidence for anthropic flaking (Dillehay 2000; Meltzer 2009; Meltzer et al. 1994).

However, the timing of the initial colonization of South America continues to be a primary topic of research and debate (Boëda 2015; Boëda et al. 2014a; Borrero 2016; Dillehay 2012, 2014a; Lahaye et al. 2013; Politis 2015; Sandweiss 2015; Schmidt Dias and Bueno 2014b). Recent standardized surveys of calibrated radiocarbon data for South America indicate that evidence for pre-11,000 cal BC sites exists but is limited (Berón 2015; Bueno et al. 2013a; Delgado et al. 2015a; Dickau et al. 2015; Politis and Steele 2014; Schmidt Dias and Bueno 2014a; Suárez 2014), with the earliest accepted sites dating to ~13,000–12,000 cal BC (Fig. 1). Some South American sites alleged to predate ~13,000 cal BC—namely, Pubenza (Colombia), Pikimachay Cave (Peru), Monte Verde I (Chile), and Santa Elina, Toca da Tira Peia, and Pedra Furada (Brazil)—have not yet receive broad scholarly acceptance, and I focus on them below.

Plausible Early Sites that Are Underreported or Incompletely Vetted

Pubenza is an open-air site located in the Middle Magdalena River valley at ~450 masl. Mastodon (*Haplomastodon waringi*) and other faunal remains were found in direct association with eight stone flakes, including an exotic obsidian flake, in a layer dating as early as ~16,500–14,900 cal BC (Correal 1993; Van der Hammen and Correal 2001). Although the earliest radiocarbon date has a wide range of error, those from the overlying strata (~16,400–15,600 cal BC; ~12,300–11,700 cal BC) support the earliest date from the site (Aceituno and Rojas-Mora 2015). The Terminal Pleistocene status of the overlying strata is not in question; however, the sample

composition and stratigraphic relationships of the dated material, flakes, and faunal remains from the earlier strata have not been fully reported and require further investigation (Borrero 2015, 2016). The site's status as pre-LGM remains uncertain.

Preliminary reanalysis of worked faunal remains and recalibration of previously reported dates from Pikimachay Cave indicate anthropogenic flaking and butchering that tentatively dates to ~15,800–12,900 cal BC (Yataco 2011). Given Yataco's provisional results, the Pikimachay Cave materials require additional research before the anthropogenic nature of the artifacts, cut marks, and the earliest dates from the site can be established.

At Monte Verde I and southeast along Chinchihuapi Creek, Dillehay et al. (2015) report recent findings of 12 discrete features containing cobbles and trimmed unifacial tools made from exotic lithic materials in direct association with ash smudges and both burned and unburned faunal remains. The features are radiocarbon and OSL dated to between ~16,500 and 12,500 cal BC. Dillehay et al. (2015) argue that the area was not impacted by glacial activity and that the ephemeral deposits at Monte Verde I represent a location where early inhabitants intermittently foraged. Although there is no consensus on the antiquity of the recent findings from Monte Verde I, Dillehay et al. (2015) contend that the artifacts, directly associated faunal remains, and ash lens features are anthropic in nature. If the earliest pre-LGM dates from Monte Verde I receive scholarly acceptance, then, once again, the site will force archaeologists to reevaluate models regarding the peopling of the Americas.

Controversial and Problematic Purported Early Sites

More problematic are pre-LGM findings from Santa Elina (Vialou 2005), Toca da Tira Peia (Lahaye et al. 2013), and Pedra Furada (Boëda et al. 2014a, b). I am open to pre-LGM anthropogenic levels at Brazilian rockshelters with clear, convincing, and thorough documentation beyond what has already been reported. However, the anthropogenic status of the pre-LGM levels at these three sites remains debatable, at best (Borrero 2015, 2016; Sandweiss 2015). The earlier dates from these and other early Brazilian sites are problematic because of the difficulties in discerning geofacts from anthropically flaked quartz and quartzite (Dillehay 2000, 2014b; Feathers 2014; Knutson 2014; Tallavaara et al. 2010). As with many of the purported pre-LGM Brazilian sites, there are more recent Terminal Pleistocene/Early Holocene sites associated with the well-established Itaparica tradition (i.e., Baixão da Esperança, Caverna da Pedra Pintada, Lapa do Boquete, Baixão do Perna I, Santana do Riacho)—including more recent, overlying levels at Pedra Furada, Santa Elina, and Toca da Tira Peia—where unifacial flakes were produced and used, butchered faunal remains are present, and cave art is reported, thereby complicating matters (Aimola et al. 2014; Bachelet and Scheel-Ybert 2016; Kipnis et al. 2005; Schmidt Dias and Bueno 2014b; Vialou and Vialou 1989).

For Santa Elina—a rockshelter in the Matto Grosso region of southwest Brazil—Vialou (2003, 2005) reports local (i.e., from the roof of the rockshelter), unretouched unifacial flakes in association with Pleistocene fauna, namely giant ground sloth (*Glossotherium*), dating to ~21,200–20,500 cal BC. More recent levels dating to the Early Holocene include rock art, undisputed retouched unifacial tools, braided

fibers, and butchered animal remains (Bachelet and Scheel-Ybert 2016; Vialou 2005). Although Feathers (2014) acknowledges the difficulty in distinguishing the Terminal Pleistocene Santa Elina unifacial tools from geofacts, he suggests that the presence of two possibly perforated osteoderms in association with the purported tools bolsters the site's authenticity. Others, however, question the veracity of the tools and anthropic nature of the charcoal from the Late Pleistocene levels (Schmidt Dias and Bueno 2014b). A thorough documentation and dissemination of the data from Santa Elina will permit independent verification of the site's antiquity, its purported artifacts, and associated faunal remains.

At Pedra Furada, where claims for ~30,000–50,000 BC lithics made of materials from the roof of the rockshelter (Guidon 1986) and OLS dates of ~100,000 BC (Valladas et al. 2003) were rejected (Boëda et al. 2014a), Boëda et al. (2014b) report unretouched unifacial tools fashioned from high-quality quartz and quartzite dating to ~20,000 BC. They suggest that the unifacial tools are similar to Early Holocene trimmed unifacial quartz and quartzite tools of the Itaparica tradition known from other Serra da Capivara sites in the Piauí region of northeastern Brazil (Aimola et al. 2014; Feathers 2014; Lourdeau 2012). Boëda et al. (2014a, b) suggest that, although local in nature, the tools are of the highest-quality quartz and quartzite, and, therefore, indicate human selectivity of the locally available lithic materials. They also present microwear data to suggest that some of the quartz and quartzite tools exhibit evidence of use. They (Boëda et al. 2014a, b) report that the radiocarbon and OLS dates from burned features are consistent with the stratigraphic sequence.

However, at Pedra Furada there are no tools of exotic materials predating 12,000 BC, there are no floral or faunal remains reported from the controversial earlier levels, and the horizontal associations of purported hearths with the quartz and quartzite materials are not fully reported (Dillehay 2014b; Feathers 2014; Schmidt Dias and Bueno 2014a, b). No evidence is presented for burned soil underlying the hearths and charcoal. Further, the microwear analysis is underreported, incomplete, and unconvincing (Dillehay 2014b, Knutson 2014; Schmidt Dias and Bueno 2014a). Although Boëda et al. (2014a, b) imply that any critiques and failures to accept Pedra Furada and other early Brazilian sites are based on preconceived expectations, healthy skepticism resulting from inadequate reporting is not the same as dismissal and rejection. Scrutiny and scholarly interrogation are a normal part of scientific discourse.

A persisting issue with Pedra Furada, Santa Elina, Toca da Tira Peia, and the other purported pre-LGM Brazilian sites is that, aside from questionable lithics of local materials, there are no other indisputably documentable pre-LGM anthropic features or materials, such as processed floral or butchered faunal remains (Dillehay 2000, 2014b; Schmidt Dias and Bueno 2014b). Complicating matters, these same sites undeniably have post-LGM Terminal Pleistocene and Early Holocene retouched trimmed unifacial (and sometimes bifacial) tools in levels associated with butchered faunal remains, hearths, structures, and cave paintings. Dillehay (2014b) suggests that some of the lithics at Pedra Furada may represent intentionally flaked tools, but their status is unclear. While the researchers acknowledge difficulties of discerning naturally versus human-flaked quartz and quartzite pebble tools from these sites, they rely on taphonomic inference to support their assertions (Aimola

et al. 2014; Boëda et al. 2014a, b; Lahaye et al. 2013). Further, for Pedra Furada, the claims for anthropogenic layers dating to ~100,000–50,000 BC (Valladas et al. 2003) contribute to the skepticism.

Although I concur with both Bryan and Gruhn's (2003) and Dillehay's (2014a, b) call for the development of additional criteria for evaluating ephemeral sites that might have only a few informal, expedient tools, further reflection on our expectations for early sites will do nothing to resolve persistent issues of underreporting or the uncertainties in identifying anthropic flaking of quartz and quartzite tools. It is imperative to consider other possible nonanthropogenic origins for the pre-LGM tools from early Brazilian sites. Specifically, as discussed by Fiedel (2017b), bearded capuchin monkeys of the Serra da Capivara National Park use round and oval quartz and quartzite hammer stones and flat sandstone slab anvils as tools for cracking nuts (Fragaszy et al. 2004; Haslam et al. 2016; Visalberghi et al. 2009a, b, 2013). It is important to elaborate on Fiedel's (2017b) assessment to make clear *why* valid doubts exist regarding the veracity of the pre-LGM Brazilian sites: primate archaeological work by Haslam et al. (2016) documents pre-Columbian capuchin nut cracking in the region 700 years ago. Their observational studies indicate that bearded capuchins are highly selective in quartz and quartzite cobble weight (0.5–3.0 kg), size, shape, and quality (Haslam et al. 2016; Visalberghi et al. 2009a, 2013), preferentially preferring hard round and oval quartz and quartzite cobbles of high quality over those likely to fragment when used to crack open nuts (Visalberghi et al. 2009b, 2013). Additionally, bearded capuchins from Piauí transport hammer stones and nuts to sandstone blocks located in the talus zones adjacent to the escarpments and cliffs (Fragaszy et al. 2004; Visalberghi et al. 2013). The monkeys move hammer stones as far as 21 m and are known to transport labeled hammer stones between sandstone anvil sites of greater distances (Fragaszy et al. 2004; Visalberghi et al. 2013). Their hammer stones have pitting and dark nut residue from use and sometimes exhibit planar fracturing and flaking (Haslam et al. 2016; Visalberghi et al. 2013). Further, Visalberghi et al. (2009b) explain that quartz and quartzite hammer stones and sandstone anvils used by capuchins are found in the associated talus zones near ephemeral watercourses that form along the base of the escarpments during torrential downpours. The purported pre-LGM Brazilian sites are associated with similar locales from the same region and consist of the same local, high-quality quartz and quartzite cobbles as do the bearded capuchin palm-nut-processing locales.

The bearded capuchin archaeological sites are a sobering and parsimonious alternative explanation for the pre-LGM Brazilian sites, given their overlapping site locations and the similarities in tool quality, size, shape and form, wear, fracture patterns, and use locations. Archaeologically, I question how known bearded capuchin nut-cracking sites and tools might be differentiated from the purported pre-LGM Brazilian sites, especially since the sites overlap with capuchins nut-cracking locales associated with the same tools? I suspect that bearded capuchin tools are mistaken for anthropogenic tools from the early Brazilian sites. Ultimately, it is the responsibility of the archaeologists making extraordinary claims to convincingly document the differences between human tools and those made by bearded capuchins.

Further, the question remains: even if the purported pre-LGM Brazilian sites are anthropogenic, what is the significance of early sites containing unretouched

unifacial tools with no other evidence of human agency? How do dubious, under-reported early sites shed light on subsistence strategies and economic adaptations of the colonizers of the Western Hemisphere? Given that other Late Pleistocene South American, pre-Clovis sites having simple flake and trimmed unifacial tools are already established, what, then, is the relevance of the pre-LGM levels at Brazilian sites, and how do they contribute to our understanding of the colonization of South America, other than simply being earlier (Waters and Stafford 2014)?

Widely Accepted Early Lithic Technologies and Economic Adaptations of South America

Historically, scholarship on the earliest Americans has been defined by the search for identifiable bifacial points, such as Clovis, and their association with Pleistocene fauna. However, archaeologists working at Terminal Pleistocene sites in South America have long asserted that there is no *a priori* reason to assume that early sites should fit such expectations. Following the acceptance of a pre-Clovis date for Monte Verde II (Borrero 2008; Goebel et al. 2008; Meltzer et al. 1997; Politis et al. 2016), most archaeologists working at early South American sites focus their attention on understanding the earliest colonists' economic and dietary adaptations, exploration and exploitation of the landscape, rapid diversification of their subsistence strategies and technologies, and their social dynamics (Aceituno and Rojas-Mora 2015; deFrance et al. 2001; Dillehay 2011; Jackson et al. 2012; Kipnis 2003; Rademaker 2014; Ranere and López 2007; Sandweiss et al. 1998; Santos Vecino et al. 2015). The consensus is that the earliest South Americans arrived with generalized tool kits necessary to exploit both terrestrial prey and maritime resources, and, shortly thereafter, became familiar with local prey and lithic sources, but that early sites were not initially associated with bifacial points. In the following sections, I discuss widely accepted South American lithic technologies. These include edge-trimmed, El Jobo bifacial bipoints, fluted fishtail points, Paján, and Central Andean lithic points.

Edge-Trimmed Lithic Technologies

Dillehay (2000) suggests that Late Pleistocene edge-trimmed unifacial technologies likely emerged from a previous, as-of-yet-to-be-established lithic tradition of the Western Hemisphere. Most early sites with edge-trimmed unifacial tools date to ~12,200–12,000 cal BC, including El Abra II, Tibitó, and Tequendama I, in Colombia; numerous Late Pleistocene Itaparica, Umbu, and Lagoa Santa lithic sites located throughout southeastern Brazil; Las Vegas, Ecuador; Amotape, Quebrada Jaguay, and Quebrada Tacahuay along coastal Peru; and Arroyo Seco 2, Piedra Museo, Casa del Minero 1, Cerro Tres Tetas I, and possibly the earliest levels at Los Toldos 3 in Argentina.

A consensus exists among many archaeologists working at early South American sites that edge-trimmed unifacial tool technologies are contemporaneous with

and possibly a part of early industries that include bifacial flake tools (Aimola et al. 2014; Bryan and Gruhn 2003; Dillehay 2000; Lavallée 2000; Lourdeau 2012; Maggard and Dillehay 2011; Pino et al. 2013; Politis et al. 2016; Suárez 2015). As I discuss below, many early South American sites contain simple flakes, in addition to unifacial and bifacial lithics.

Edge-trimmed unifacial sites reported throughout the Magdalena Valley are among the earliest in Colombia (Aceituno and Rojas-Mora 2015; Delgado et al. 2015a). Although the lower range of antiquity for Pubenza (Delgado et al. 2015b) has yet to be resolved, the Terminal Pleistocene levels yielded simple flake tools, including an exotic obsidian flake, in association with mastodon (*Haplomastodon* sp.) and other fauna (Correal 1993; Van der Hammen and Correal 2001), similar to other better-known sites with unifacial tools in Colombia. El Jordán is another potential, underreported, open-air site in Colombia's central cordillera at an elevation of 2300 masl (Salgado López 1998) that produced a number of flakes from the lowest layer dating to ~14,000–13,000 cal BC (Aceituno and Rojas-Mora 2015).

Remains from classic edge-trimmed sites located within the Sabana de Bogotá region of the upper Magdalena Valley, Colombia, demonstrate that early South Americans exploited mastodon (*Haplomastodon* sp.), horse (*Equus* sp.), and deer (*Odocoileus virginianus*); they are found in higher (>2600 masl) altitude cool evergreen forests, at open-air sites such as Tibitó, and rockshelters like Tequendama and El Abra, ~11,800–8200 cal BC. The retouched unifacial lithics from these sites are referred to regionally as the “Abriense industry” and consist of both local and exotic materials (Aceituno and Rojas-Mora 2015; Correal 1982; Correal and Van der Hammen 1977; Delgado et al. 2015a; Hurt et al. 1977). Evidence from these sites suggests that early colonists of the Magdalena Valley made occasional (possibly seasonal?) forays into the cool wet *páramo* of the Sabana de Bogotá high altitudes.

The Late Pleistocene and Early Holocene Itaparica, Umbu, and Lagoa Santa traditions incorporate edge-trimmed unifacial technologies of the interior savannahs of northeastern and central Brazil that were utilized by the initial colonizers who arrived via interior Amazonian waterways (Bueno et al. 2013b; Moreno de Sousa 2017; Schmidt Dias and Bueno 2014a). Sites in the Amazonian biome of eastern and central Brazil that are typified by these technological adaptations include Santa Elina, Pedra Furada, Toca da Tira Peia, Lapa do Boquete, Santana do Riacho, Baixão do Perna I, Toca do Pica-Pau, and Sitio de Meio. These sites exhibit fairly uniform unifacial technologies beginning ~12,000 cal BC and persisting until ~6500 cal BC (Bueno and Schmidt Dias 2015; Lourdeau 2012). The inference is that by ~11,000 BC nearly all regions of Brazil were inhabited by peoples who subsisted on tropical forest nuts, fruits, river fish and shell fish, and other small Holocene prey (Aimola et al. 2014; Bueno and Schmidt Dias 2015; Lourdeau 2012; Roosevelt et al. 1996; Schmidt Dias 2004).

Many early sites located along the western coast of Ecuador, Peru, and Chile are also characterized by edge-trimmed lithics and exhibit a well-developed marine resource focus. Stothert et al. (2003; Stothert and Sánchez Mosquera 2011) report that inhabitants of pre-Las Vegas levels at Site 80 of the Santa Elena Peninsula, Ecuador, dating to ~11,800–8900 cal BC, exploited and processed rich marine,

estuarine, and terrestrial resources during the Late Pleistocene and Early Holocene using simple flakes and trimmed unifacial tools.

Likewise, early campsites sites with edge-trimmed unifacial lithics of the Amotape complex, dating to ~11,300–7000 cal BC, are known from the Sechura Desert region of northern Peru (Richardson 1973, 1978); faunal remains suggest that early foragers processed nearby estuarine and mangrove resources using flakes and cores made of local chalcedony and quartzite. Dillehay (2011), Maggard and Dillehay (2011) and Maggard (2015) report similar unifacial lithics associated with El Palto phase (~12,200–7600 cal BC) sites of the north coast of Peru. El Palto phase edge-trimmed unifacial lithics are commonly associated with the exploitation of coastal resources, whereas bifacial points are typically recovered from seasonal dry forest sites.

In Terminal Pleistocene deposits from the coastal terrace below the preceramic Huaca Prieta mound site, located at the mouth of the Chicama Valley, Peru, Dillehay et al. (2012, 2017) recovered numerous edge-trimmed unifacial flakes and tools used to process both marine and terrestrial resources. Associated lenses of ash and charcoal date to ~13,000–11,300 cal BC, possibly making Huaca Prieta one of the earliest securely dated sites on the continent. Given that no contemporaneous sites are known for the adjacent highlands of Ecuador and northern Peru, Dillehay (2014a) and Maggard (2015) hypothesize that the coastal Ecuadorian pre-Las Vegas and Peruvian El Palto phase sites provide evidence that foragers initially colonized the region via the Pacific Coast. Importantly, El Palto phase edge-trimmed unifacial lithics are part of a broader economic complex that includes bifacial fishtail and Paiján points.

Farther south, unifacial lithics and simple flake tools made of local materials are associated with the processing of marine resources, including fish and avifauna, at Terminal Pleistocene coastal sites of southern Peru. Well-known examples include Quebrada Jaguay, Quebrada Tacahuay, and the Ring site (deFrance et al. 2001; Reitz et al. 2016; Sandweiss et al. 1998). Charcoal taken from the earliest levels at Quebrada Jaguay dates to ~11,400–9500 cal BC (Sandweiss et al. 1998), whereas Quebrada Tacahuay and the Ring site date to ~10,900–9400 cal BC and ~10,000–9400 cal BC, respectively (deFrance et al. 2009; Reitz et al. 2016). Notably, obsidian recovered from Quebrada Jaguay was sourced to the Alca-I obsidian outcrop at the Pucuncho quarry and workshop located at an altitude of 4355 masl in adjacent highlands ~150 km north of Quebrada Jaguay, thereby indicating that by ~11,400 cal BC coastal inhabitants of southern Peru were either acquiring exotic lithic materials from the Andean highlands themselves or exchanged for them (Rademaker et al. 2014). Shellfish and other marine resources from Quebrada Jaguay point to seasonal occupation between the highlands and coast (Rademaker et al. 2016; Sandweiss et al. 1998). deFrance et al. (2009), on the other hand, interpret Quebrada Tacahuay as a specialized, year-round marine resource extraction and processing site, whereas Sandweiss et al. (1989) suggest that the broader spectrum of both marine and local terrestrial resources recovered from the Ring site indicate a diversity of resources captured using a variety of methods (i.e., netting, fishing). Unlike Quebrada Jaguay, neither the Ring site nor Quebrada Tacahuay provide evidence for nonlocal lithics or other exotic resources, which indicates that

well-developed, highly specialized maritime economies were in place on the south coast of Peru by the Terminal Pleistocene (Reitz et al. 2016).

Similar associations between early unifacial tools and a maritime focus is also apparent for the Terminal Pleistocene sites from the arid and hyper-arid northern and central Chilean coast at Quebrada de Las Conchas (Llagostera 1992), Huentelauquén (Jackson et al. 2011), Punta Ñagué (Jackson and Méndez 2005), among others. At Punta Ñagué, interpreted as a residential coastal base camp, Jackson and Méndez (2005) report the processing of fish, shellfish, and marine mammals with simple flakes dating to ~11,100–10,700 cal BC (Méndez 2013). Although the earliest radiocarbon dates are from marine shell and should be considered provisional given a potential reservoir effect, the antiquity of the site is similar to other nearby, previously discussed early sites that exhibit similar maritime adaptations. Similarly, at Quebrada de Las Conchas (Llagostera 1992) and Huentelauquén (Jackson et al. 2011), edge-trimmed unifacial tools and cobbles are associated with fish, shellfish, and marine mammals as early as ~9000 cal BC (Méndez 2013).

Also along the north central coast of Chile, excavations by Núñez et al. (1994b) at Quereo I revealed intentionally broken bones of mastodons (*Cuvieronius* sp.), horse (*Equus* sp.), paleolama (*Paleolama* sp.), giant sloth, and deer (*Antifer* sp.) in direct association with pointed sticks, flaked scrapers, and burned wood dating to ~9800–9100 cal BC, while the adjacent site located in the overlying stratigraphic layer (Quereo II) dates to ~10,800–9300 cal BC and exhibited abundant evidence for lithics and the butchering of the same fauna as the earlier layer. The multidisciplinary study revealed that Quereo was located in a mixed beach environment associated with a narrow *quebrada* where terrestrial fauna would have been funneled and killed.

Monte Verde, an ephemeral logistic camp located along the banks of the Maullín River 90 km inland from the Pleistocene coastline of southern Chile, also provides evidence for the use of expedient flake and cobble tools (Dillehay 1997; Dillehay et al. 2015). At Monte Verde II, Dillehay (1989, 1997) reports rectilinear and wish-bone-shaped structures, tent posts wrapped with knotted reed fiber, hides, wood, cutmarks on the remains of at least six mastodons (*Gomphotheriidae*), paleolama (*Paleolama* sp.), quids of seaweed, exotic cobbles, and organic materials from the adjacent coast to the west, in addition to three fragmented “El Jobo-like” lanceolate points. The seaweed and other organics recovered from Monte Verde II date to ~12,600 cal BC (Dillehay et al. 2008). Dillehay et al. (2015) also report an additional 12 discrete features containing cobbles and trimmed unifacial tools made from exotic lithics in direct association with ash smudges and both burned and unburned faunal remains at Monte Verde II that date between ~16,500–12,500 cal BC. Based on the exotic materials, expedient tools, and ephemeral features, Dillehay et al. (2015) argue that early inhabitants of the region intermittently foraged at Monte Verde II.

A number of securely dated cave and open-air sites from Patagonia in Argentina and the pampas of Argentina and southern Uruguay are associated with the processing of Pleistocene fauna using unifacial flakes and tools and point to an initial occupation of the region ~12,100 cal BC (Suárez 2014, 2017). The Arroyo Seco 2 site of the Argentinian pampa is the earliest site in the region, with two radiocarbon samples

from faunal material dating to ~12,100–11,800 cal BC and 11,600–11,400 cal BC (Politis and Steele, 2014; Politis et al. 2016; Suárez 2014, 2017). Pleistocene fauna, including giant sloth (*Megatherium* sp., *Glossotherium* sp.), horse (*Equus* sp., *Hippidion* sp.), and an extinct hooved mammal (*Toxodon* sp.) were butchered at Arroyo Seco 2 using expedient, unifacial flakes that exhibit minimal retouching made from exotic chert, basalt, quartzite, and other lithic materials were procured from sources located between 50–150 km from the site (Leipus and Landini 2014; Politis 2014; Politis et al. 2016; Salemme 2014).

Similarly, Miotti and Salemme (2003) and others (Prates et al. 2013) report edge-trimmed lithics in association with ground sloth (*Mylodon* sp.), gracile llama (*Lama gracilis*), and horse (*Hippidion saldiasi*) from the lowest anthropogenic layer (Unit 6) from Piedra Museo AEP-1. The overlying strata contain bifacial fishtail projectile points. The earliest date on charcoal taken from Unit 6 is ~11,700–11,100 cal BC; however, it is suspect given that other samples from the same layer ranged between ~10,800 and 9000 cal BC (Miotti and Salemme 2003; Steele and Politis 2009). These more acceptable dates from the site closely align with anthropogenic layers at Casa del Minero 1 and Cerro Tres Tetras 1, which date to ~10,800 cal BC (Suárez 2017). The earliest levels at those sites are associated with unifacial retouched flakes, side scrapers, hammer stones, and choppers. At Casa del Minero 1, Paunero (2003) reports unifacial lithics in association with processed gracile llama (*Lama gracilis*) remains but no extinct Pleistocene fauna.

Of similar antiquity, Urupez-2 located in the southern pampas region of Uruguay dates to ~12,000–11,600 cal BC and 11,700–11,300 cal BC (Suárez 2014), while K87 (Arroyo del Tigre) on the northern Uruguay River dates to ~11,200–11,100 cal BC (Suárez 2017). Once again, these sites are associated with expedient flakes, animal remains, and hearths in ephemeral butchering locations.

It is notable that trimmed unifacial tools, unretouched flakes, cores, choppers, and hammer stones of exotic lithic materials are reported for these Patagonian sites but that bifacial points have yet to be recovered from the earliest levels (Prates et al. 2013; Suárez 2017). Although few potential sites with projectile points have been reported that predate ~11,100 cal BC from the Argentinian and southern Uruguayan grasslands (although see fishtail projectile point technologies discussion below), Prates et al. (2013) note that some of the debitage from the region has been identified as the product of bifacial flaking. Miotti (2003) argues that unifacial tools from earlier levels at Los Toldos 3, Piedra Museo AEP-1, and other Patagonian sites are part of the fishtail projectile point technologies. Further research is required to resolve this question.

Given the scarcity of higher-quality lithic materials in the region, the absence of bifacial points at the earliest sites is not an indication that bifacial points were not being used but, instead, is an indication that the early inhabitants of Patagonia retouched, reused, and repurposed bifacial points whenever possible. As both Andrefsky (1998) and Clarkson et al. (2015) suggest, flakes represent an expedient and disposable technology, whereas points are manufactured elsewhere and used by foragers in areas where high-quality lithic materials are scarce, impractical to transport, or when foragers are unfamiliar territory and uncertain where they might locate high-quality lithic materials. Likewise, Dillehay et al. (2017) report

that, ethnographically, local fisherfolk of the north coast of Perú often employ simple flakes that date back millennia, and that no bifaces (or fishhooks, nets, and harpoons) have been recovered from the archaeological assemblages covering thousands of years of occupation at Huaca Prieta.

In the following sections, I elaborate on the notion that edge-trimmed lithics represent a subset of broader foraging activities, as evidenced by sites where these lithics sometimes co-occur with well-documented early bifacial point technologies.

Early Bifacial Point Technologies of South America

Early bifacial point technologies in South America include El Jobo bipoints, fluted fishtail projectile points, stemmed Paján points, and central Andean triangular, shouldered diamond-shaped and laurel leaf points (Bryan and Gruhn 2003; Dillehay 2000, 2014a). Bifacial points generally are recovered from caves, rockshelters, or relatively small, open-environment locations, such as coastal areas, open grasslands, and areas of hardy steppe scrub vegetation such as the Andean puna, dry puna, and Patagonia; they are rarely recovered from early sites located in forested environments.

El Jobo Bipoints

Bipointed El Jobo lithics are *possibly* the earliest and least understood bifaces, given the paucity of excavated stratified sites associated with these lanceolate points (Dillehay 1999, 2000). Thus far, El Jobo points are confined to the coastal regions of Venezuela and, probably, at Monte Verde II although some have suggested a possible relationship to the Early Holocene Ayampitín bipoints that are one of many point types associated with central Andean lithics (Cruxent and Rouse 1959; Dillehay 2000; Lynch 1990). Among the best-known sites are El Jobo, Taima-Taima, Muaco, Cucuruchú, El Vano, and La Hundición in Venezuela. Cruxent (1970) reports more than 45 additional mastodon kill sites and surface discoveries in Venezuela that are associated with El Jobo points. The date of ~13,200–11,000 cal BC for El Jobo points is based on relatively few acceptable radiocarbon dates from three far-removed sites—Taima-Taima, El Vano, and Monte Verde II. Despite persistent questions regarding Taima-Taima, thermoluminescence dates provide independent support for a pre-10,000 BC antiquity for the site (Oliver and Alexander 1990).

El Jobo points were used by foragers to hunt mastodons and other Late Pleistocene fauna when they encountered those animals as they watered (Ardila 1991; Cruxent 1970; Dillehay 2000). Prior to the discovery of El Jobo-like points at Monte Verde II, Bryan (1991) suggested a limited geographic and temporal distribution for El Jobo points. It is unclear what relationship, if any, the makers of El Jobo points in Venezuela had to the users of similar bipointed bifaces in southern Chile (or to similar Early Holocene Ayampitín bipoints of the central Andean lithic tradition). It is also unclear how El Jobo points are related to other (slightly more recent?) Late Pleistocene bifaces, such as fluted fishtail projectile points, given their reported co-occurrence from surface collections at other underreported Venezuelan sites, such as

Siraba (Jaimes Quero 2003). Further, assuming that the points recovered at Monte Verde are related to El Jobo points, then we must ask if the inconsistent distribution (namely Venezuela and 6000 km away at Monte Verde) is the result of sampling error. Although I believe that El Jobo points date to the Late Pleistocene, more sites with secure dates are needed to resolve the antiquity of these bifacial bipoins.

The Fishtail Projectile (FTP) Point Technologies

Fishtail points are the best understood early lithic technology in South America, dating to ~11,300–9,300 cal BC (Borrero 2006; Dillehay 2000; Nami and Stanford 2016; Waters et al. 2015) and thus contemporaneous with the end of the North American Clovis tradition (Nami 2016; Nami and Stanford 2016). Extinct megafauna associated with fluted FTP, including ancient sloth (*Mylodon* sp.) and horse (*Parahipparion* sp.), at Fell's Cave and Palli Aike, Chile (Bird 1938), and similar points at El Ilalo, Ecuador (Mayer-Oakes and Bell 1960), were interpreted to support the “Clovis first” model. However, most archaeologists working in South America view Clovis and FTP point technologies as independent and technologically distinct bifacial point traditions (Dillehay 2000; Nami 2014; Politis 1991), with a great deal of variation in form and technical preparation (Castineira et al. 2012; Nami 2014; Suárez 2017). While FTP points often lack a flute, especially in the Southern Cone region (Borrero 2006; Politis 1991), the apparent basal flute may be a result of reduction processes; there also is evidence that the points were recycled, retouched, and used as knives (Dillehay 2000; Nami 2010, 2014, 2015; Suárez 2017).

The majority of stratified FTP point sites are in the highlands of Ecuador (Mayer-Oakes and Bell 1960), the Andean foothills and coastal slopes of northwestern Peru (Dillehay 2000), the grasslands of southern Brazil and northern Uruguay, and the Patagonian region of the Southern Cone (Borrero 1996; Nami 2014; Politis 1991; Suárez 2017; Waters et al. 2015). Additional securely dated, stratified FTP point sites are also reported for the southern highlands of Peru (Rademaker et al. 2014), coastal Chile (Jackson et al. 2007; Núñez et al. 1994a), Brazil (Loponte et al. 2016; Suárez 2017), and Uruguay (Suárez 2017). Surface finds of FTP points are known from coastal and highland Colombia (Correal 1986), coastal Venezuela (Jaimes Quero 2003; Nami 2016), Guyana (Nami 2014), coastal Ecuador (Carluci 1963), the northern highlands (Leon Canales et al. 2004) and southern coast of Peru (Wise 1989), as well as Brazil (Beltrão et al. 1986). Some investigators (Borrero and Franco 1997; Bryan and Gruhn 2003; Dillehay 2000; Scheinsohn 2003) concur that, based on their distribution, fishtail points are primarily recovered from either caves or open-air grassland sites and were likely part of a generalized hunting subsistence strategy.

In northwestern Peru, FTP points are known from a few ephemeral campsites dating to ~11,100–10,400 cal BC within the coastal plains and intervening pampas along the Andean foothills of the Jequetepeque, Chicama, and Moche Valleys (Dillehay 2000; Maggard 2015; Maggard and Dillehay 2011). Maggard and Dillehay (2011; Maggard 2015) argue that fishtail and Paján point technologies co-occur with edge-trimmed lithics that are all part of the El Palto phase on the north coast of Peru. During the Late Pleistocene, the coastal plains were characterized by a mixed

environment of open grasslands and cool, dry forests at slightly higher elevations (Dillehay 2011; Maggard and Dillehay 2011). Maggard (2015) notes that the association of FTP point sites of northern Peru with both terrestrial and marine resources reflects semispecialized hunting activities as part of a broader foraging economy and seasonal transhumance between the coastal valleys and adjacent highlands.

Two FTP points of pink chalcedony were recovered near the open-air obsidian workshop Pucuncho in the southern highlands of Peru at 4355 masl above the Majes Valley (Rademaker 2014). Tools at Pucuncho also include central Andean lithic points. Similarly, Yataco and Nami (2016) report FTP fragments and central Andean lithics in association with deer, camelids, and extinct horse in the earliest layers at Jaywamachay Cave, 3400 m within the sierra of Ayacucho and dating to ~10,500–8500 cal BC (see below). Radiocarbon dates for Pucuncho range between ~10,800 and 9500 cal BC and chronologically overlap with Quebrada Jaguay where an obsidian point was recovered and sourced to the Alca outcrop at the Pucuncho workshop (Rademaker et al. 2016; Sandweiss et al. 1998). Rademaker (2014) notes that Quebrada Jaguay and Pucuncho are the only coastal and highland sites clearly linked during the early settlement of the continent: by ~10,800 BC inhabitants of southern Peru were seasonally accessing both coastal and highland resources during the austral summer (Gruber 2018) and winter (Rademaker et al. 2016), respectively.

Farther south, along the central Chilean coast at Quebrada Santa Julia, and only 3 km from Punta Ñagué, Jackson et al. (2007) report a fluted point, flakes, a scraper, pebble tool, and other informal lithics recovered in association with a butchered horse (*Equus* sp.). Charcoal from a hearth at the site dates to ~11,100–10,700 cal BC (Jackson et al. 2007; Méndez 2013). The site is interpreted as a short-term butchering campsite, but Quebrada Santa Julia's overlapping radiocarbon dates, proximity, and possible relationship to the nearby fishing community at Punta Ñagué are provocative but far from conclusive given the uncertainties of their contemporaneity.

Also on the central Chilean coastline, Montané (1968) first reported butchered fauna, including horse (*Equus* sp.) and deer (*Antifer* sp.), associated with flakes and unifacial tools at the ancient lake-margin campsite Tagua Tagua I. Subsequent excavations at Tagua Tagua I and II yielded two complete exotic quartz fishtail points and a basal point fragment associated with butchered mastodon remains (*Stegomastodon* sp.) Núñez et al. (1994a). A radiocarbon date of ~11,300–10,900 cal BC (Méndez 2013) is problematic because of the wide range of error; more recent, acceptable dates of ~9500–8200 cal BC and 9,200 – 8,600 cal BC (Núñez et al. 1994a) establish the site as a megafauna hunting and processing site. The investigators note cut marks and intentional breakage of many faunal long bones at Tagua Tagua. Other readily portable elements such as ribs are missing, which indicates they were transported to an unidentified nearby base camp. The investigators suggest that Pleistocene fauna were mired in a marsh and became easy prey. It is notable that Tagua Tagua is located relatively close to the modern coast and would be considered an “edge-trimmed tradition” site without the later excavations by Núñez et al. (1994a).

Bird (1938) recovered fishtail points at Fell's Cave in association with a hearth and extinct fauna, including horse (*Parahipparion* sp.), sloth (*Myiodon* sp.), and guanaco (*Lama guanicoe*) and contemporaneous flake and ground stone tools (Bird 1988). More recently, Waters et al. (2015) report that the earliest levels at Fell's

Cave date to ~10,800–10,200 cal BC. Similarly, at Cueva del Medio, investigators (Martin et al. 2015; Nami 2014) report multiple layers of occupation containing fishtail points, scrapers, knives, and other lithic debitage in association with butchered horse (*Hippidium* sp.), mylodon (*Mylodon* sp.), guanaco (*Lama gracilis*), deer, and possibly extinct feline remains (*Felis listai*). The earliest anthropic layer at the site was dated to ~13,100–11,900 cal BC based on a composite sample and so is problematic (Méndez 2013). However, dates from subsequent levels at the site are ~11,100–10,600 cal BC, 10,600–10,100 cal BC, and 9300–8800 cal BC (Martin et al. 2015; Méndez 2013), suggesting that the earlier date has stratigraphic integrity.

Sites with fishtail points are, perhaps, most concentrated in the Patagonian Argentinian and Uruguayan pampas of the Southern Cone (Dillehay 2000; Flegenheimer and Weitzel, 2017; Nami, 2014). More recent levels at Southern Cone sites previously mentioned for their earlier unifacial lithics—Piedra Museo, Arroyo Seco, Urupez, and Arroyo del Tigre—are associated with Pleistocene fauna and date to ~10,800–10,200 cal BC (Cardich et al. 1973; Fidalgo et al. 1986; Miotti and Salemme 2003; Suárez 2017). The context and use of Southern Cone fishtail points indicate use for the hunting, butchering, and processing of hides (Nami 2007; Politis 1991; Suárez 2015). Further, sequentially consistent radiocarbon dates at Fell's Cave, Cueva del Medio, and other fishtail point sites speak to repeated, short-term occupations by Patagonian hunter-gatherers (Bird 1988; Borrero 2008; Borrero and Franco 1997; Méndez 2013; Nami 2014). The presence of exotic lithic materials at these Late Pleistocene sites indicates high mobility and possible exchange networks among foragers occupying Patagonia and the pampas of Argentina and Uruguay (Borrero 2015; Scheinsohn 2003; Suárez 2017). Although Pleistocene fauna were hunted by early Southern Cone inhabitants, they do not appear to have been the primary focus of their subsistence strategies; instead, hunting activities throughout the region primarily targeted camelids (Borrero 2001; Mengoni Goñalons 1986; Miotti 2003; Nami 2007; Politis 1991).

Given the *potentially* earlier antiquity and concentration of FTP point technologies in the Southern Cone than elsewhere (Flegenheimer and Weitzel 2017; Nami 2014), some suggest that South American FTP points originated in Patagonia and, subsequently, were adopted elsewhere (Bryan 1991; Bryan and Gruhn 2003; Dillehay 2000). Suárez (2017) and Perez et al. (2016) argue that the early appearance and distribution of FTP sites in the pampas of Argentina and Uruguay suggest a rapid bicoastal migration of early South American colonists prior to their exploration of interior regions. As I discuss below, there is evidence for temporal overlap between FTP lithics and later regionally diversified lithics during the transition to the Early Holocene as South American hunters and gatherers developed specialized technologies to exploit local resources.

Regional Specializations During the Late Pleistocene to Early Holocene Transition in South America

Although the chronological and technical relationships among the aforementioned lithic technologies remain unresolved (Dillehay 2000, 2014a; Maggard

2015), there is temporal overlap between edge-trimmed and FTP point technologies with more recent regional technologies, such as central Andean lithics and Paiján. These diverse sets of lithic technologies reflect prey and resource availability during the Late Pleistocene to Early Holocene transition.

Central Andean Lithic Points and Colonization of the Central Andean Highlands

As conditions ameliorated in the Andean highlands and glaciers retreated during the Terminal Pleistocene and Early Holocene, humans began exploiting high-altitude (>2500 masl) resources as evidenced by the proliferation of central Andean lithic (CAL) sites reported from southern Colombia and Ecuador down to northern Chile and Argentina (Dillehay 2000, 2014a). Central Andean lithics are characterized by a variety of point types, including bifacial shouldered and unshouldered diamond-shaped, triangular, and bipointed, leaf-shaped (Ayampitín) points, although these diagnostic points are also recovered with flakes, retouched flakes, hammer stones, and other implements used to process faunal remains. CAL points are recovered from caves, especially, but also from open-air campsites and hunting blinds (Rick 1980; Santoro and Núñez 1987).

Invariably, the faunal remains from CAL point sites indicate increasing economic specialization and reduced mobility in the sierra and high grassland puna during the Late Pleistocene and Early Holocene; specifically, hunters focused on camelids (*Vicugna* sp. and *Lama* sp.) and cervids (*Hippocamelus* sp.) along with other fauna, including rodents and lizards (Lavallée 2000; Lynch 1990; Rademaker et al. 2014, 2016; Rick 1980). Megafauna were absent.

A debate regarding the initial occupation of high-altitude environments continues (Capriles et al. 2016; Rademaker et al. 2016). Some scholars argue that the west coast was settled prior to the central Andean highlands (Rademaker et al. 2013; Yacobaccio 2017), whereas others maintain that the harsh conditions and glaciers were a barrier to human colonization of the highlands prior to 9000 cal BC (Aldenderfer 2008; Dillehay 2014a). This assertion is incorrect, given that Rademaker et al. (2014, 2016) report dates for the Cuncaicha campsite and Pucuncho quarry in the Pucuncho Basin, Peru, ranging from ~10,400–9300 cal BC. These sites were coterminous with Late Pleistocene coastal sites, such as Quebrada Jaguay. Capriles et al. (2016) take issue with both the antiquity and characterization of Cuncaicha, suggesting that the site is too early and not a residential site; Rademaker et al. (2016) counter that the Pucuncho Basin was free of glaciers at the time and that there is evidence for the seasonal butchering and processing of camelids (*Vicugna* sp. and *Lama* sp.) and deer (*Hippocamelus* sp.).

Additional sites that exhibit CAL point technologies dating to the Late Pleistocene–Early Holocene transition are found in Ecuador, Peru, the altiplano of Bolivia, and the dry puna of northern Chile. Most high-altitude CAL sites date to ~10,100–6000 cal BC (Rademaker et al. 2013), which indicates that the adjacent western coastal region was settled prior to exploration of the central Andean highlands.

Paiján Points

Paiján stemmed, bifacial needle-point lithic sites date to ~11,000–7600 cal BC and are primarily reported from the north and central Peruvian coast and *quebradas* of the Andean foothills (Dillehay 2000; Maggard 2015; Maggard and Dillehay 2011). Similar, roughly contemporaneous points are reported from Ecuador (Mayer-Oakes 1986), Colombia (Ardila 1991; Illera and Gnecco 1986), northern Chile (Núñez et al. 2005), and southern Chile (Dillehay et al. 2015). Other lithic technologies, such as grinding stones, flakes, limaces, and scrapers, are recovered in association with Paiján open-air sites in the Zaña, Jequetepeque, Chicama, Moche, and Casma Valleys of northern Peru, during the transition to a settled life toward the end of the El Palto phase (Dillehay et al. 2003).

Paleoenvironmental reconstructions indicate that Paiján sites were located in mixed environments that included coastal, dry forests and, in the upper reaches of the *quebrada* systems, cool, wet, resource rich forests (Dillehay 2011; Maggard 2015). Given the evidence for sedentism at these sites during the transition to the Early Holocene, Dillehay and Maggard (Dillehay 2011; Dillehay et al. 2003; Maggard 2015; Maggard and Dillehay 2011) suggest a concomitant, emergence of social complexity in the region.

Summary of Terminal Pleistocene/Early Holocene South American Colonization, Adaptations, and Strategies

Sparse yet convincing evidence indicates that South America likely was colonized ~13,000–12,000 BC in northwestern, western, and Patagonian regions, with a more widespread occupation by ~11,500 BC. Although not yet resolved, initial colonization of the western coast by users of edge-trimmed unifacial tools likely preceded the occupation of the Andean highlands by ~1,000 years (Dillehay 2000, 2014a; Rademaker et al. 2013). The relationships between edge-trimmed unifacial and flake technologies with early bifacial points, such as El Jobo, fishtail, Paiján, and central Andean lithics, indicate there was temporal overlap and regional specialization in South American lithic technologies by ~11,500–11,000 BC that reflects differing resource availability (Dillehay 2000, 2014a; Maggard 2015).

I suggest that edge-trimmed and flake tool kits, such as Amotape, Abriense, and Tequendamense, represent either expedient tools fashioned from local materials and used to process resources such as fish and shell fish, and during occasional (seasonal?) forays for smaller game and flora in less familiar areas, or that such tool kits were employed in regions where the availability of quality lithic materials, such as obsidian and chert, were scarce or less certain. Accordingly, early South American colonists chose to conserve, recover, reuse, and recycle bifacial tools for larger prey, especially in expansive biomes with relatively low faunal density. According to Clarkson et al. (2015), unretouched flakes are preferred and more efficient for simple tasks, requiring only 2 min to prepare; bifacial and retouched tools are often used when the locations of quality lithic

sources are uncertain, unpredictable, or scarce. This accords with instances when foragers are on exploratory hunts in unfamiliar territory or when carrying sufficient raw materials is not feasible.

Indeed, Dillehay et al. (2017) report that, ethnographically, fisherfolk of the north coast of Peru employ simple, yet recognizable, expedient flake technologies that date back millennia, and that no bifaces (or fishhooks, nets, or harpoons) were recovered from the lithic assemblage covering thousands of years at the preceramic Huaca Prieta site. If this is true for other early South Americans, then simple flake and unifacial tools may represent a subset of broader subsistence technologies related to widely recognized bifacial point technologies. Although there is empirical evidence to support this hypothesis, it is an assertion that is not yet well established (see below). This issue is important for informing the development of models regarding how early South American lithic technologies reflect subsistence-based scheduling of resource exploitation, mobility, patterned use of landscapes, and potential population growth (or relative lack thereof) (Mendez et al. 2018).

Data from Terminal Pleistocene and Early Holocene sites of the Andes indicate that early inhabitants practiced seasonal transhumance either between the puna and coast, or between the sierra and lower intermontane valleys by ~10,800 BC (Lavallée 2000; Lynch et al. 1985; Rademaker et al. 2014; Sandweiss et al. 1998) or along the coast (deFrance et al. 2009). Foragers already familiar with their resource landscapes may develop flexible scheduling choices regarding their mobility so as to optimally exploit plants and prey based upon their patchiness, predictability, and seasonal availability (Aldenderfer 2008). The age profiles of fauna from sites such as Guitarrero Cave (Lynch et al. 1985), Telarmachay (Lavallée 2000), and Cuncaicha, (Rademaker et al. 2014, 2016), Peru, indicate seasonal hunting and butchering of camelids by mobile foragers that corresponds with the animals' seasonal births and migrations. Further, sites with CAL points, such as Pucuncho and Toquepala provide evidence, albeit limited, for either seasonal movement or exchange between the coast and highlands by ~11,200 cal BC; Lynch (1980) reports a mollusk shell at Guitarrero Cave. Similarly, at the high-altitude Pucuncho obsidian quarry, Rademaker (2014) reports pink chalcedony from the adjacent west coast, while obsidian from the Alca source at Pucuncho was recovered from Quebrada Jaguay, which is located near the pink chalcedony source (Sandweiss et al. 1998). Faunal remains dating to 10,800 cal BC indicate that Cuncaicha, near the Pucuncho quarry, was a seasonal butchering and processing site (Rademaker et al. 2016), while isotopic analysis of mollusks from Quebrada Jaguay indicates that coastal resources were exploited during the austral summer months (Gruver 2018). Ravines (1972) reports a mollusk shell and a shark tooth at Toquepala Cave, while other sites located farther south, such as Monte Verde II, provide evidence that coastal cobbles and plants such as seaweed were procured from the coast and used at inland campsites, possibly as early as ~16,500–12,500 cal BC (Dillehay et al. 2015). This archaeological evidence for increased diversity in Late Pleistocene–Early Holocene lithic technologies is related to economic specialization, seasonally scheduled resource exploitation, sedentism, and food production during the Early and Middle Holocene, as described in the following section.

Early and Middle Holocene Transitions and Economic Adaptations

Other sites point to early South American inhabitants' economic specializations, reduced mobility, and manipulation of their landscapes and plants. Maggard's (2015) work on the El Palto phase (~12,200–7600 cal BC) of the Jequetepeque Valley, Peru, indicates that by the Early Holocene, the presence of domestic structures, locally sourced lithics, and faunal reflect increased economic specialization and restricted mobility. In the high altitudes of the central Andes, isotopic analyses of human skeletal remains dating to ~7,000 cal BC from the Cuncaicha rockshelter (4355 masl) (Chala-Aldana et al. 2017), indicate that Early Holocene inhabitants of the Pucuncho Basin resided there year-round and consumed local resources, thereby suggesting that restricted mobility and emergent economic specialization were established by the Early Holocene.

Some data suggest that, rather than passively adapting to constraints and limitations imposed by locally available environments, South Americans began modifying their landscapes to create habitats for their favored resources. For example, evidence for Late Pleistocene fires in Colombia (Clapperton 1993a) may represent early South Americans' attempts create habitats better suited for their preferred trees and plant species (Gnecco and Aceituno 2006; Santos Vecino et al. 2015). Grinding implements and plant microfossils indicate that northwestern Colombians were processing and cultivating plants such as palm nuts and arrowroot during the Late Pleistocene–Early Holocene transition. Similarly, by ~8000–7,000 cal BC, evidence exists for the cultivation of domesticates, such as cucurbits, peanuts, and cotton at the Las Vegas site, Ecuador (Stohtert et al. 2003), and the Zaña Valley in northern Peru (Dillehay et al. 2007), while botanical remains from Guitarrero Cave and Tres Ventanas, Peru, indicate that in the sierra of the central Andes people were using domesticated chili peppers, tubers, common beans, jack beans, and lucuma fruit (Pearsall 2008).

Conditions during the mid-Holocene climatic optimum (~5000–3000 cal BC) favored a shift from simple river-plain horticultural cultivation of tropical domesticates to a dedicated agricultural economy. Those conditions increased the productivity of C3 cultigens such as *Zea mays*, sedges, and other Western Hemisphere cultivars (Pearsall 2008). Evidence for *Zea mays* is present in South America by ~6000 cal BC in Colombia, by ~5000 cal BC in northwestern Ecuador (Pearsall 2008), ~4800–4600 cal BC on the north coast of Peru, (Grobman et al. 2012), by ~4500 cal BC in the southern Ayacucho highlands (Yataco 2014) of Peru, and in domestic contexts in the far southern highlands of Peru by 2000 cal BC (Perry et al. 2006). Although maize was not a staple crop prior to ~2500–2000 cal BC in Peru (Grobman et al. 2012), it was ubiquitous throughout the central Andes by ~2100 BC (Bonavia and Grobman 1999). Terracing and irrigation canals were in use by ~4000–3000 cal BC in the northern coastal valleys of Peru (Dillehay et al. 2005), by ~3000–2400 cal BC in the northern highlands or Peru (Grieder and Bueno Mendoza 1985), and by ~2500 cal BC in the southern highlands of Peru (Pearsall 2008). At the risk of over generalizing, the use of such labor-intensive technologies is interpreted as indicating a shift to agricultural economic regimes.

Our archaeological understanding of the initial colonization and economic adaptations of early South Americans is important for establishing the parameters necessary to discern subsequent biologically based estimates for intra-continental prehistoric migrations and population dynamics. The shift from foraging to food production had dramatic demographic impacts on population growth as well as genetically and morphologically discernable population expansions, as discussed below.

Molecular Studies on the Initial Colonization and Prehistoric Population Dynamics of South America

Our current understanding of the biological affinities, shared ancestry, migratory routes, and subsequent population dynamics for the first Americans (i.e., Paleoindians or Paleoamericans) is informed by molecular studies of extant populations, although ancient DNA (aDNA) is playing an increasingly important role in informing current debates. Deoxyribonucleic Acid (DNA) can be passed on from generation to generation either uniparentally (inherited from only one parent), or biparentally (inherited from both parents). Nuclear DNA (nDNA) is inherited from both parents, whereas nonrecombinant uniparental DNA can be inherited from either the matriline, in the case of mitochondrial DNA (mtDNA), or through the patriline, in the case of Y-chromosome DNA (NRY). These data, each with their own limitations, provide complementary information regarding population dynamics (Templeton 2006). Space does not permit a full discussion of these methods (for accessible reviews see Bisso-Machado et al. 2011; Cappellini et al. 2018; Llamas et al. 2017).

Regardless of the molecular data analyses used, mtDNA and NRY haplogroup data indicate that all Native Americans are related to an ancestral population that resided in Beringia during the Terminal Pleistocene prior to the end of LGM. Coalescence dates using molecular data indicate a shared common ancestry ~18,000–13,000 BC (Battaglia et al. 2013; Bisso-Machado et al. 2011); however, a study by Llamas et al. (2016) that used completely sequenced mitogenomes for 96 pre-Columbian South Americans adds precision to these estimates: following a period of ~9000–2400 years of isolation in Beringia, a small number of eastern Beringians rapidly migrated along the west coast of North, Central, and South America beginning ~14,000 BC. The researchers' aDNA data help refine the Beringian standstill model and accords well with the end of the LGM.

Single Migration?

Although the ultimate shared common ancestry with northeast Asians is undisputed, there is little consensus regarding the timing and number of migrations that occurred during the peopling of the Western Hemisphere. A plurality of researchers who examine autosomal microsatellites (Kitchen et al. 2008; Lewis and Long 2008; Wang et al. 2007), Y-chromosome variation, and modern mtDNA (Zegura et al.

2004) suggest that all New World populations are derived from a single ancestral migration.

Specifically, investigators arguing for a single migratory source for all Native American genetic variability point out that the five major founding mtDNA haplogroups (as well as their minor haplogroup variants) are similar to those reported for living Siberians (Perego et al. 2010; Schurr and Sherry 2004). Given that these variants are found throughout the New World, it is likely that all mtDNA variability is due to a single migratory event. Similar arguments are made regarding the ubiquitous distribution of two Y-chromosome haplogroups C and Q throughout the Western Hemisphere (Bisso-Machado et al. 2011) and the presence of the private allele D9S1120 (Wang et al. 2007). Population structure analysis by Wang et al. (2007) of 24 Native American groups using mtDNA sequencing indicates that although variation is lower than for other world populations, variation in the Americas mtDNA is greatest among northern North Americans and decreases with distance from Beringia among Central and South Americans. In South America, relatively little population structure exists between western South Americans and central Andeans; however, eastern South Americans exhibit more variation (Wang et al. 2007); others (Lewis and Long 2008) maintain that variation among native South Americans is low and that the insignificant haplogroup frequency differences between western and eastern South Americans are explained by a single migratory event.

Two Migratory Events?

Other molecular studies argue for at least two migratory pulses from Beringia during the colonization of the Western Hemisphere following the LGM. Echoing results of previous mtDNA studies, Perego et al. (2009) argue that two rare variants of mtDNA, D4h3 and X2a, appear to be unique to the Western Hemisphere. The distribution and estimated time depth of these two haplogroups suggest that an earlier and rapid colonization of the west coast of the Americas occurred by populations who had higher frequencies of the D4h3 haplotypes, while a simultaneous or slightly later colonization occurred through the McKenzie ice-free corridor by another population typified by higher frequencies of the X2a haplotypes. Similarly, Kashani et al. (2011) report that haplotypes X2a and C4c exhibit a distribution among Native Americans who they posit colonized North America through the ice-free corridor. Other studies suggest there were two independent migratory pulses into the Western Hemisphere from Beringia (Llamas et al. 2016) and into South America (Fehren-Schmitz et al. 2010; Raghavan et al. 2015; Skoglund et al. 2015). Generally, these investigators suggest a rapid dispersal via the west coast of North America, followed by a bottleneck as people entered South America (Bodner et al. 2012; Fagundes et al. 2008; O'Fallon and Fehren-Schmitz 2011). Similar arguments have been made for NRY data (Battaglia et al. 2013; Jota et al. 2016; Scliar et al. 2014).

Some investigators argue that the molecular data point to two colonizing migrations during the peopling of South America (Battaglia et al. 2013; Bodner et al. 2012; de Saint Pierre et al. 2012a, b; Fehren-Schmitz et al. 2010; Perego et al. 2009, 2010). Those positing two events, largely based on mtDNA variation, argue for an

early initial colonization along the west coast of South America, followed by a subsequent migratory event. Accordingly, the first wave would correspond to populations with higher frequencies of mtDNA haplogroups C1 and D1, whereas the second wave corresponds to populations exhibiting higher frequencies of haplogroups A2 and B2. Southern Andeans and northeastern South Americans, corresponding to the descendants of the early colonization event, exhibit relatively low frequencies of haplogroups A2 and B2 and higher frequencies of haplogroups C1 and D1, while northern Andeans and northwestern South Americans, representing descendants of the subsequent migratory event, exhibit higher frequencies of haplogroups A2 and B2 and low frequencies of C1 and D1. Arguing for an early coastal entry into South America, Bodner et al. (2012) report that the rare D1g and D1j mtDNA haplotypes are restricted to the Southern Cone region, whereas de Saint Pierre et al. (2012a, b) report an exclusively Southern Cone distribution for subgroups B2i2 and C1b13. Accordingly, the initial South American colonization event occurred along the west coast of the continent soon after the colonization of the west coast of North and Central America. The subsequent migratory event occurred shortly after and occurred either along the north coast of South America and/or through the Amazonian interior and had its origins among the preexisting North Americans who migrated through the ice-free corridor, thereby contributing to North American substructure (Raghavan et al. 2014, 2015; Rasmussen et al. 2014, 2015; Reich et al. 2012).

Also suggestive of two migratory events, recent nDNA studies suggest that some living Amazonians have a slightly higher proportion of Australo-Melanesian ancestry (i.e., populations indigenous to Andaman Islands, Australia, and Papua New Guinea) than other northeastern Asians and Native Americans (Raghavan et al. 2015; Skoglund et al. 2015). Specifically, based on their genome-wide analyses, Skoglund et al. (2015) found that the Australasian signature among Amazonians is completely absent among indigenous North and Central Americans. Rather than suggesting an independent Australasian migration into the Western Hemisphere, they posit that a previously unidentified ancient northeastern Asian population—*population Y*—contributed to the initial colonization of *both* the Americas and Australasia. Although a more recent high-resolution aDNA study supports the presence of population Y loci among a limited number of prehistoric South American remains (Moreno-Mayar et al. 2018), another study that includes more ancient genomes suggests that apparent population Y genetic contributions are a part of variation that already existed among aDNA Paleoindian sequences (Posth et al. 2018).

A similar dual colonization scenario for South America is proposed for NRY haplogroups. Among indigenous living South Americans, NRY haplogroup Q1a3a* is the most common, with variants of the haplogroup—Q1a3a1, Q1a3a2, and Q1a3a3—thus far being exclusive to South America (Karafet et al. 2008). Q1a3a2, a less common variant, is found among northern Amazonians, but is thought to be a recent derivation, while haplogroup C-P39 is present among relatively few northern coastal South Americans (Bortolini et al. 2014). Further, Battaglia et al. (2013) report South American sublineages for NRY haplogroup Q1a3a1a-M3. Based on the haplogroup's distribution and more recent sublineages in Central and South America, some investigators posit that the antiquity of the Q1a3a1a4-SA01 sublineage,

found exclusively in South America, resulted from a demographic expansion from Mesoamerica dating to ~5300 BC that corresponds with the spread of maize agriculture into the Andes. Others (Jota et al. 2016; Scliar et al. 2014) arrive at similar conclusions and suggest that subclades of Q1a3a1a-M3 (specifically, Q1a3a1a4-SA05 and Q1a3a1a-Z19319) are unique to the Peruvian Andes and Amazon and resulted from demographic expansions associated with preceramic cultivation of cassava, pumpkin, and sweet potato.

Some of the aforementioned discrepancies among molecular datasets are due to the nature of the data examined and partly to methodological issues: namely, it is difficult to estimate the degree to which modern DNA data was affected by resettlement policies of both ethnohistorically known Andean—e.g., the Inka, Aymara—and pre-Inka polities such as the Tiwanaku. This problem is compounded by prehistoric epidemics that devastated South American populations (Livi-Accì 2006; Llamas et al. 2016; O’Fallon and Fehren-Schmitz 2011), with estimates of ~90% post-European contact population decline on the west coast of Peru (Cook 1981). These factors confound attempts to extrapolate the molecular variation for the living to infer >13,000 years of prehistoric population dynamics in ancient South America.

Ancient DNA (aDNA)

To date, with rare exceptions (Malaspinas et al. 2014; Malhi et al. 2007), the aDNA from pre-Columbian skeletal and mummified remains shares common ancestry with northeastern Asian populations (Casas-Vargas et al. 2011; de la Fuente et al. 2015; Fehren-Schmitz et al. 2014, 2015; Llamas et al. 2016; Posth et al. 2018; Rasmussen et al. 2014, 2015; Shinoda et al. 2010). However, in an ancient mtDNA study by Malhi et al. (2007), two individuals from China Lake, British Columbia, ~5,000 cal BC, are characterized by haplogroup M, an mtDNA haplogroup variant found among Asian populations but no other known Native Americans. Further, Llamas et al. (2016) indicate that none of the 96 mtDNA haplotypes they report for pre-Columbian South Americans are known among modern Native Americans, while Moreno-Mayar et al. (2018) report a previously unknown basic ancient Native American genetic sequence for a Late Pleistocene Alaskan child, thereby confirming that haplogroup extinction and discontinuities have occurred for mtDNA haplogroups and haplotypes.

Fehren-Schmitz et al. (2010, 2011, 2014) document significant diachronic differences in ancient mtDNA haplogroup frequencies for prehistoric central Andeans of southern Peru; while they posit that these discordant ancient mtDNA frequencies indicate an early, rapid peopling of South America via the western coast, they also suggest that subsequent mtDNA changes were due to a demographic expansion and population dispersals caused by the collapse of the Middle Horizon highland Wari empire.

Ancient mtDNA haplogroups for Early and Mid-Holocene remains from the central Peruvian highland Lauricocha Cave are also discordant (Fehren-Schmitz et al. 2015); while most living central Andean highlanders are typified by haplogroup B2, four of the five sequenced Lauricocha remains are characterized by

haplogroup A2, and the fifth is characterized by a novel form of the B2 haplogroup. While it is unclear if these are anomalous results, Fehren-Schmitz et al.'s (2010, 2011, 2014) conclusions are similar to those reached by Moraga et al. (2005), who report on ancient mtDNA frequencies for southern central Andeans from the highlands of Bolivia and north coast of Chile. Specifically, the investigators document relatively high frequencies of haplogroup A among preceramic Chinchorro remains from the Azapa Valley, Chile, while subsequent Middle Horizon and Late Intermediate period populations became increasingly characterized by haplogroups B as a result of population displacement during the collapse of the Middle Horizon Tiwanaku empire.

Ancient NRY haplotypes for all 19 individuals sequenced by Fehren-Schmitz et al. (2011) from the Nazca drainage belong to haplogroup Q1a3a*(xM3), which is the most common among living South Americans. Similarly, Fehren-Schmitz et al. (2015) report that NRY haplotypes for three early and middle Holocene individuals from Lauricocha Cave are characterized by Q1a3a* (xM3) and Q1a3a1* (Q-M3). Both are founding lineages for the Western Hemisphere and are present among living central Andeans. Thus far, no other ancient NRY data are reported and, therefore, are of limited value in helping distinguish subsequent population dynamics during the colonization of South America.

While it is difficult to reconcile the aforementioned nuclear and mtDNA studies, they are not necessarily mutually exclusive with respect to the timing and route of the initial colonization of South America. Given the consensus that South Americans experienced a bottleneck as they passed down through the Isthmus of Panama, then ancient nDNA variation among them was derived from a restricted amount of variation that already existed among the initial colonizers of the Western Hemisphere.

However, independent aDNA studies by Moreno-Mayar et al. (2018) and Posth et al. (2018) paint a more complex scenario for prehistoric population dynamics in South America and provide compelling evidence for multiple precontact dispersals into the continent. Minimally, following an initial genetic subdivision of North American Paleoindians into eastern and western populations, there was an early colonization of South America by Paleoindians similar to those represented by the western Clovis-era Anzick-1 individual. The initial colonization was followed by another dispersal into South America around ~7000 BC that replaced the earlier population, followed by yet another expansion into the Andes by ~2200 BC (Posth et al. 2018). The study by Posth et al. (2018) calls into question previous interpretations of mtDNA and NRY haplogroup distributions, given that the apparently “rare” variants of each were already present among the earliest South Americans.

Although aDNA studies continue to refine our understanding of the origins and number of migrations of ancient South Americans, the study of the skeletal and dental morphology of prehistoric South Americans has also, historically, played a role in developing models that are tested using molecular and archaeological data. Due to their low cost and well-established, nondestructive methods, morphological studies provide an important complementary role for understanding of the prehistoric population dynamics in South America. In the following section, I review current

perspectives on the number of migrations and origins of ancient South Americans as inferred from morphological studies.

Skeletal Morphological Studies on the Initial Colonization of South America and Subsequent Prehistoric Population Dispersals

Genetically influenced morphological characteristics, or phenetic traits, also contribute to our understanding of the initial peopling of South America. Most biodistance studies for South America suggest that the continent was peopled by two independent migratory events related to the peopling of the Western Hemisphere. Following the initial colonization of South America, however, the nature of the subsequent migratory event(s)—whether due to the complete replacement of the Paleoindians by a subsequent prehistoric migration, or by demographically driven expansion—remains unresolved. Although the general consensus from morphological studies lends support to the molecular two-stage peopling model for South America, I reiterate that both the molecular and morphological studies rely on different data sets from different, incomplete samples.

Basis of Morphological Traits

Morphological skeletal characteristics of the skeleton—craniofacial shape and size, tooth size, nonmetric cranial and dental characteristics (such as additional sutures, sutural bones, variation in the presence and number of cranial foramina, the number and size of tooth crown cusps and roots)—are also referred to as phenetic traits because of the uncertain degree of underlying genetic and environmental influence. Most characteristics are polygenic and exhibit intermediate to high levels of heritability (for accessible reviews, see Pilloud and Hefner 2016). The biodistance and population structure estimates derived from phenetic data largely reflect those derived from genetic data (Adachi et al. 2003; Herrera et al. 2014; Hubbard et al. 2015; Ricaut et al. 2010).

Despite issues of missing data due to broken and missing skeletal and dental elements, cranial modifications, and tooth wear, phenetic studies can employ larger and (presumably) more representative ancient samples than genetic studies. Further, advances and increased accessibility to biodistance, population structure, and genetic modeling statistics (especially for nonmetric traits) have increased the usefulness of phenetic traits. However, phenetic traits are subject to all of the same sampling issues, representativeness, etc., that affect ancient DNA studies.

Craniometric and Odontometric Studies

Although Native Americans have long been recognized to resemble Asians (Hrdlicka 1923), some 20th century scholars contended that the variation exhibited by New World populations must have arisen from more than one migratory event. Some suggested there were “proto-Mongoloids” who preceded subsequent

migrations by “Mongoloids” (MacCurdy 1923). Currently, a plurality of bioarchaeologists believe that two migratory events occurred during the peopling of the Americas (González-José et al. 2005; Jantz and Owsley 2001; Powell 2000; Steele and Powell 1999). Echoing MacCurdy (1923), they posit that spatio-temporal trends indicate a generalized Asian, or proto-Mongoloid, dental and cranial morphology typified preceramic populations of Baja California (González-José et al. 2003), Mesoamerica (Haydenblit 1996), and South America (González-José et al. 2008; Hubbe et al. 2015; Huffman 2014; Lahr 1996; Neves et al. 2014; Powell and Neves 1999; Sardi et al. 2005; Strauss et al. 2015; Sutter 2005, 2009).

Some skeletal morphologists argue that an initial proto-Mongoloid or Paleoamerican colonization in South America was followed by a Mongoloid or Amerindian migration (Lahr 1996; Neves et al. 2014; Powell and Neves 1999). Others suggest that the second migratory event resulted in the replacement of the preexisting South American proto-Mongoloid/Paleoamericans by subsequent Amerindians (González-José et al. 2008; Hubbe et al. 2015; Huffman 2014; Strauss et al. 2015). Powell and Neves (1999) caution, however, that the prehistoric morphological patterns observed may have resulted from the initial population structure and subsequent microevolutionary processes that acted on the earliest colonists. Likewise, others suggest that the observed cranial morphological differences between early and subsequent South American populations resulted from differentiation and microevolutionary processes following initial colonization (González-José et al. 2008; Sardi et al. 2005; Sutter 2007, 2009, n.d.).

In their population structure analyses, Hubbe et al. (2015) find that Paleoindians from Lagoa Santa, Brazil, and Sabana de Bogotá region, Colombia, exhibit similar levels of craniometric variation demonstrated elsewhere in the world, but their between group variation is extremely low. They argue that the higher levels of phenetic variability among more recent South American remains resulted from a subsequent migration into South America. Similarly, research on craniometric variation in Colombia indicates a similar shift in cranial morphology during the Middle to Late Holocene transition (~2000 BC) that Delgado (2012, 2016) attributes to the arrival of agriculturalists.

Although the aforementioned craniometric studies are intriguing, molecular studies indicate that “Paleoamerican” cranial morphology is not associated with atypical, non-Native American DNA (Posth et al. 2018; Raghavan et al. 2015). For example, despite having a proto-Mongoloid or Paleoamerican skull, the Kennewick Man’s X2a mtDNA haplogroup is consistent with the founding Native American lineages (Rasmussen et al. 2015), as are the Paleoamerican-appearing remains from Yucatan, Mexico (Chatters et al. 2014). Likewise, Perez et al.’s (2009) comparison of prehistoric Argentinian Paleoamerican-appearing skulls to their ancient mtDNA data failed to find any nonfounding Native American haplogroups, indicating, again, a lack of correspondence between interpretations made using cranial morphology and mtDNA data. Similar results and conclusions were reached in an aDNA study that included Paleoindian remains from Lapo do Santo, Brazil (Posth et al. 2018). Other Paleoindians, such as the Anzick-1 child from Montana (Rasmussen et al. 2014), are also characterized by founding mtDNA haplogroup lineages. These sobering aDNA studies indicate that the same genetic ancestry for both

early Paleoamerican/Paleoindian remains and all living Native Americans, despite apparent morphological differences in their crania. Indeed, some craniometric studies (González-José et al. 2005; Lieberman 2008; Paschetta et al. 2010; von Cramon-Taubadel 2014) cite the shift from a foraging diet to food production as responsible for apparent diachronic changes in cranial length and robusticity, with foraging associated with higher levels of dolichocephaly and cranial robusticity, while agricultural diets resulted in decreased cranial and masticatory robusticity and greater degrees of brachycephalization. Others posit that colder climatic conditions resulted in greater thyroid hormone production and basal metabolic rates that led to a more robust Paleoamerican-like skeletal appearance (Leonard et al. 2002), as has been reported for Late Holocene and early historic Fuegians (Perez et al. 2007).

Dental Morphological Studies

In seminal studies that analyzed genetically influenced tooth crown and root trait frequencies for both Asian and Western Hemisphere populations, Turner (1985) argued that all Native Americans are descended from three discrete migrations from northeastern Asia, with the Paleoindians being ancestral to all Amerind-speaking North, Central, and South Americans (also sometimes referred to as “Macro-Indians”). Turner’s surveys of tooth trait variability reveal that northeastern Asians and all Native Americans exhibit more complex patterns of tooth cusps and roots—a pattern he refers to as “sinodonty”—relative to Southeast Asians, who he suggests are typified by “sundadonty.” Subsequently, genetic, linguistic, and archaeological data were presented in support of Turner’s “three-wave” model (Greenberg et al. 1986). Yet investigators who reanalyzed some of Turner’s samples question his conclusions and point out that his Paleoindian sample is distinct from more recent Western Hemisphere samples (Powell 2000). Further, many dental morphologists (Delgado 2012; Powell and Neves 1999; Stojanowski and Johnson 2015; Stojanowski et al. 2013a, b; Sutter 2005, 2009) have questioned the value of the dichotomous, typological sinodonty/sundadonty labels for Asians and Native Americans.

I have argued (Sutter 2005, 2009) that Turner’s (1985) South American sample combines all dentitions, irrespective of their chronological or geographic affiliation, into a single sample, thereby making it impossible to evaluate the validity of his conclusions for prehistoric South Americans. Based on my own studies of prehistoric Andean dental trait variation (Sutter 2005, 2007, 2009, n.d.), the spatio-temporal trends among prehistoric Andeans indicate there were at least two migrations into South America: an early migration represented by the Paleoindians and their preceramic descendants, followed by a more recent (i.e., ~3800 BC) demographically driven expansion of food-producing populations from Central America, who subsequently expanded south into South America and interbred with the neighboring foragers (Fig. 2).

Others have also documented a similar shift from sundadont-like tooth trait frequencies for North American Paleoindian and Early Holocene remains toward sinodonty among recent populations (Powell 2000; Stojanowski et al. 2013a, b; Stojanowski and Johnson 2015), similar to a shift between preceramic and subsequent

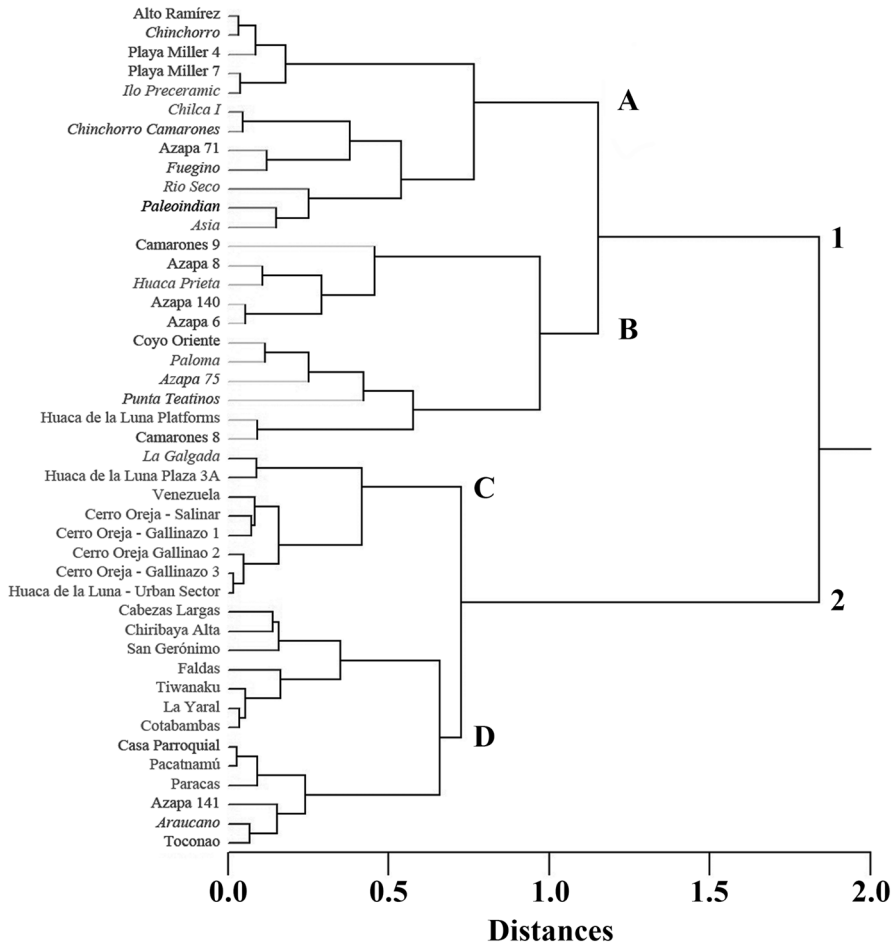


Fig. 2 Hierarchical cluster analysis of Mahalanobis' squared distance results for comparisons between 44 prehistoric Andean skeletal samples (after Sutter 2007, n.d., fig. 2). The samples in Cluster 1 have lower frequencies of complex tooth cusp and root traits, while those in Cluster 2 are characterized by relatively higher frequencies of complex traits. Nearly all samples within Cluster 1 are either preceramic (1A) or food-producing populations from the Southern Cone (1B), while nearly all of those within Cluster 2 represent food-producing populations of the northern (2C) and central Andes (2D)

populations in Mesoamerica (Haydenblit 1996). The comparison by Stojanowski et al. (2013a) of dental traits for Early Holocene remains indicates that both Early Holocene and coastal populations exhibit distinct trait frequencies from inland North Americans, thereby indicating a separate coastal migration that echoes interpretations put forth by some geneticists (see above).

For South America, others report similar spatio-temporal patterns for a shift from sundadont-like to sinodont-like tooth trait frequencies associated with the transition to agriculture. Specifically, Rodríguez and Colatoni (2015) suggest that Early Holocene (i.e., pre-5000 BC) skeletal samples from Colombia

are typified by sundadont-like trait frequencies, while those dating to the Mid-Holocene (~5000–1000 BC) exhibit a gradual shift toward sinodont-like frequencies. Likewise, Ortiz (2013) reports on tooth trait comparisons for six prehispanic South American populations from Bolivia, Chile, Venezuela, the north coast of Peru, southern highlands of Peru, and Amazonian Peru that indicate Late Holocene populations of Chile, Venezuela, and the northern coast of Peru exhibit sinodont-like trait frequencies, whereas samples from the southern Peruvian highlands, Bolivia, and Amazonian Peru exhibit sundadont-like frequencies. Similarly, Huffman's (2014) examination of nonmetric dental traits for both the Early and Late Holocene Amazonian and western South America indicates differing population dynamics for eastern versus western and southern South America. She reports similar sundadont-like trait frequencies for the Brazilian Sambaquí, Early Holocene Lagoa Santa, and Late Holocene Botocudo Indian samples from Brazil, while her Late Holocene samples from Peru and Chile are more sinodont-like and distinctive from her Brazilian samples. Finally, both I (Sutter 2009, n.d.) and Lahr and Haydenblit (1995) report that aceramic remains from Patagonia exhibit sundadont-like trait frequencies.

Turner and Scott (Scott et al. 2016; Scott and Turner 1997; Turner 2006; Turner and Scott 2007) argue that claims of sundadonty in the Western Hemisphere result from other investigators' inability to correctly score the nonmetric dental traits due to excessive occlusal wear of the teeth. Yet, as I (Sutter 2005, 2009) and others (Powell 2000; Stojanowski and Johnson 2015; Stojanowski et al. 2013a, b) have pointed out, Turner and Scott's dismissal is unfounded, given that many of the traits exhibiting sundadont-like frequencies are based on torsion of teeth in their sockets (central incisor winging), congenital absence of key teeth, and root numbers of key teeth, all characteristics that are unaffected by occlusal wear.

In addition to all preceramic Andeans, I have reported sundadont-like tooth trait frequencies for many later pre- and perihistoric Southern Cone agriculturalists that exhibited relatively little occlusal wear (Sutter 2005, 2007, 2009, n.d.), while others, too, have reported similar spatio-temporal patterns in trait frequencies (Delgado 2012; Huffman 2014; Lahr and Haydenblit 1995; Ortiz 2013; Rodriguez and Colatonia 2015). Further, Powell (2000) and, independently, Stojanowski and Johnson (2015) examined the impact of dental wear on tooth trait scoring differences between Turner's and Powell's scores for remains from the Early Holocene Windover site, Florida. Although Stojanowski and Johnson (2015) note significant interobserver differences for certain traits, they report that there is no evidence that occlusal wear resulted in Powell's (2000) conclusion that the Windover sample was characterized by sundadonty.

Turner's (1985) results for South America are likely an artifact of sample composition that lumps together a multitude of samples from different times and locations, some with poor and mixed provenience (see Turner and Scott 2007, p. 1915). A more recent study that reexamined Turner's original data (Scott et al. 2016) reports on "early South American" and "late South American" samples, but the composition of those samples still glosses critical regional and temporal trends in Turner's South American dental trait data. At a minimum, Turner's South American sample provides no basis for inferring prehistoric population dynamics and simply classifies

them all as “sinodonts,” a typological label that fails to shed light on prehistoric population dynamics.

In sum, the consensus among skeletal and dental morphologist is that at least two prehistoric migratory events occurred in South America. There is disagreement regarding the ultimate origins of the earliest South Americans with some craniometric studies suggesting that there was, perhaps, an earlier, more generalized population from Asia that first colonized the continent that was subsequently replaced, while dental morphological studies generally posit that a subsequent migration resulted from a demographical expansion of preexisting Native Americans. Both models provide demographic inferences and have archaeological implications that I explore in the next section.

Demographic Modeling, Population Growth, and Ancient South American Population Dispersals

Demographic modeling studies suggest that both the environment and subsistence strategies placed limitations on prehistoric South Americans' effective population size and growth rate through the Mid-Holocene (Goldberg et al. 2016; Perez et al. 2016, 2017). Prior to the shift to food production, Late Pleistocene and Early Holocene South American foragers and horticulturalists were typified by small, regionally interconnected, sedentary and semisedentary communities that were limited in their population growth. Demographic modeling indicates that Early and Middle Holocene South Americans' regional population sizes remained relatively low and sparse until the shift to agricultural ~3700 BC–2100 cal BC (Goldberg et al. (2016). Subsequently, favorable environmental conditions and an economic shift to intensive food production regimes during the Middle Holocene led to a three-fold increase in intensive agriculturalists, especially those of the northern and central Andes. Importantly, the simple cultivation of domesticates that typifies horticulture, which occurred much earlier, did not result in the dramatic demographic growth. Rather, it was the adaptation of intensive agricultural regimes that facilitated the demographic shift.

With the exception of Patagonia, similar demographic expansions occurred in other parts of eastern South America between ~3500 and 1500 BC (Goldberg et al. 2016). Similarly, Gayó et al. (2015) place the demographic shift in the southern central Andes at ~2000 BC, while Perez et al. (2017) estimate, based on mtDNA and radiocarbon data, that population increases occurred around ~7000–4000 BC for the Southern Cone region. For this period, Perez et al. (2017) report that southern central Andean population growth accelerated 15 times faster than in northwestern Patagonia, where a mixed economy and low population growth persisted throughout the Late Holocene, despite the introduction of agriculture.

Although the precise timing of these demographic expansions requires additional data and refinement, independent support for current interpretations comes from recent genetic studies, which indicate that east-west differences in South American population structure resulted from the initial colonizations (Raghavan et al., 2015; Reich et al., 2012; Wang et al. 2007). Subsequent regional differences persisted

between eastern South Americans and Patagonians, whereas populations from the northern and central Andes received significant external admixture from Central America after ~4200 BC (Posth et al. 2018). Similarly, Lindo et al. (2018) report genetic continuity in the central Andes since ~1800 cal BC.

Although molecular and morphological studies posit two or more ancient extra-continental population dispersals into South America, only rarely do they provide definitive mechanisms or causes (although see Battaglia et al. 2013; Jota et al. 2016; and Scliar et al. 2014). Using prehistoric diachronic and regional trends in tooth trait frequencies among 44 well-dated Andean skeletal samples, which represent more than 2400 individuals, I have tested competing hypotheses proposed to explain this variation (Sutter 2007, n.d.). These models include a single Paleoindian migration into South America, a second that posits the complete replacement of preexisting Paleoindian populations by a subsequent extra-continental migration, and a third model that hypothesizes a north-to-south demographically driven expansion with the spread of agriculture. Statistical comparisons of the biodistances to the competing models best support a demic expansion (Sutter 2007, n.d.). Rather than a single migration or a large-scale migration resulting in complete population replacement of the preexisting South Americans without admixture, the biodistance data indicate that a second dispersal into the central Andes resulted from gene flow by early Mesoamerican food-producing populations beginning ~6500 BC. This demographically driven gene flow occurred because of their higher rates of fertility relative to neighboring foraging and horticultural populations. Accordingly, by chance, Mesoamerican food producers were characterized by higher frequencies of complex tooth traits relative to South American preceramic populations who were direct descendants of Paleoindians.

The concept of demic expansion is used to explain genetic and morphological transitions associated with agriculture and population expansions elsewhere in the world (Barbujani et al. 1994; Cavalli-Sforza et al. 1993; Pinhasi and Pluciennik 2004; Regueiro et al. 2013; Sokal et al. 1991) and requires differential reproductive rates between adjacent populations. The higher fertility of agriculturalists relative to that of foragers and horticulturalists is well documented (Bentley et al. 1993a, b; Campbell and Wood 1988). The swamping of smaller preexisting populations' genetic signals by larger ones is sometimes referred to as *extinction by hybridization* (Levin 2002), or *leaky replacement* (Gibbons 2011). For ancient South Americans, this scenario accords well with both demographic modeling (Goldberg et al. 2016; Perez et al. 2017) and aDNA studies that posit a population dispersal from prehistoric Mesoamerica into the central Andes ~4200 BC (Moreno-Mayar et al. 2018; Posth et al. 2018).

Considering these results in light of broader paleoecological, botanical, and archaeological evidence, I hypothesize (Sutter 2005, 2007, 2009, n.d.) that the demic expansion proceeded south through the northern and central Andes into the desert regions of northern Chile and northwestern Argentina where its demographic impact was reduced due to less-irrigable land and agricultural productivity that characterizes the Southern Cone region (Falabella et al. 2008; Gil et al. 2009; ONERN 1984; Pearsall 2008; Rodriguez 1989) (Fig. 3). Agricultural productivity decreases from north to south in the southern central Andean region, and therefore

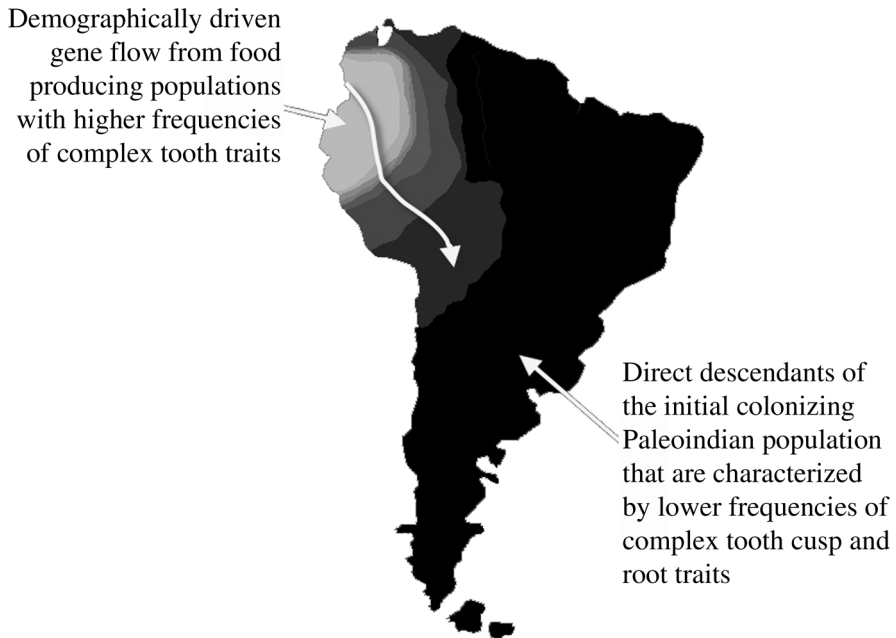


Fig. 3 The hypothesized demic expansion of food producers into South America via the Isthmus of Panama. This demographically driven expansion resulted from an increased fertility of preexisting Central American sinodont populations. The demic expansion began during the mid-Holocene climatic optimum but its impact was dramatically reduced south of the Peruvian-Chilean border due decreased agricultural productivity in the Atacama Desert (after Sutter 2009, fig. 2.3)

the demographic differential that drove the gene flow would have been substantially decreased. In support of this model, high-resolution aDNA studies find genetic continuity among ancient Amazonians and Patagonians with Paleoindians (Moreno-Mayar et al. 2018; Posth et al. 2018).

Although speculative and difficult to substantiate with the currently available data, I suspect that the impact of the Mid-Holocene demic expansion into the central Andes and Amazonia was blunted due to relatively higher population densities in those regions that resulted from independent demographic momentum that began shortly after the initial fissioning and subdivision of early South Americans. These are hypotheses that require testing and refinement using additional data.

Final Considerations, Future Directions, and Conclusions

The current consensus is that Native Americans are derived from northeastern Asians who resided in Beringia or Siberia prior to the end of the LGM, and that, subsequently, there were two migratory events from that source: one earlier migration along the western coast of the Americas that began shortly after ~15,000 cal BC that experienced a bottleneck as it rapidly expanded through the Isthmus of Panama and down the west coast of South America; and a subsequent expansion from

Beringia that occurred down through the ice-free corridor ~10,600 cal BC (Pedersen et al. 2016). Although far from conclusive, a plurality of archaeologists, geneticists, and demographic modelers believe that the initial colonization of South America was rapid and occurred along both the Pacific and Atlantic Coasts, with people making their way into the interior via rivers, natural causeways, and along dry *quebradas* and valleys (Aceituno and Rojas-Mora 2015; Anderson and Gillam 2000; Moreno-Mayar et al. 2018; Rothhammer and Dillehay 2009; Suarez 2017).

A number of sites—El Abra, Taima-Taima, Huaca Prieta, Monte Verde II—point to an initial colonization of South America by ~13,000–11,500 BC, while other sites, such as Monte Verde I, Pubenza, and Urupez, indicate that South America may have been colonized as early as ~16,500–12,500 BC. Although the anthropogenic nature and Late Pleistocene status of Monte Verde I (Dillehay et al. 2015), Pubenza (Van der Hammen and Correal 2001), and Urupez (Suárez 2017) are not in dispute, further scrutiny and consideration will help determine their precise antiquity and how those sites fit into the broader peopling of the Western Hemisphere.

The small number of initial colonizers were broad-spectrum hunter-gatherers who fashioned both unifacial and bipoined bifacial points, such as El Jobo and fish-tail points, depending on the resources, tasks, and opportunities available to them; megafauna, smaller fauna, and plants were all part of the colonizers' diets (Dillehay 2000, 2014a). By ~12,000–11,000 BC, as early South Americans became familiar with the locations of critical resources, they began scheduling their economic activities according to the seasonal availability of those resources; by ~10,800 BC specialized lithic technologies and sites, such as seasonal coastal fishing communities and highland hunting camps, were already in place to exploit marine resources and terrestrial fauna, with people making winter forays into the Andean highlands to hunt and to secure lithic resources (Gruver 2018; Rademaker et al. 2016; Sandweiss et al. 1998).

Fully dedicated fishing communities were present along the west coast of Peru by ~11,500 BC. People began inhabiting the highlands shortly before ~10,800 BC and developed diverse, semispecialized hunting technologies, such as central Andean lithics, adapted for the exploitation of camelids, cervids, and rodents. Simultaneously, along the western coast and slopes of the Andes, complementary coastal foragers and semispecialized hunting strategies emerged (Dillehay et al. 2012, 2017; deFrance et al. 2009; Reitz et al. 2016; Stothert et al. 2003; Stothert and Sánchez Mosquera 2011; Sandweiss et al. 1998). A semisedentary lifestyle, community specialization, and social complexity emerged along the coasts of Ecuador and northern Peru (Maggard 2015; Maggard and Dillehay 2011). These early inhabitants continued to use edge-trimmed lithics along with fishtail and Paján points. The relationships and contacts between highland and west coast peoples, whether direct or indirect, are apparent, but additional data are needed to clarify the matter.

In the grasslands of the Southern Cone, megafauna and camelids were hunted by highly mobile, specialized hunters using fishtail points at a time when an exchange network developed, likely by ~12,000 BC (Suárez 2017). Amazonian foragers using Itaparica, Umbu, and related unifacial technologies began exploiting fruits, oil-rich nuts, freshwater fish and shellfish, and small terrestrial prey by ~12,000 cal BC (Bueno and Schmidt Dias 2015; Lourdeau 2012). This lifeway remained largely

unchanged in the Amazon through the Late Holocene. By ~8000 BC, peoples of northwestern South America and the northern and central Andes were manipulating their environment and cultivating early domesticated plants, such as cucurbits and tubers (Gnecco and Aceituno 2006; Pearsall 2008; Piperno and Stothert 2003; Santos Vecino et al. 2015).

The earliest South Americans were a subset of the same founding northeastern Asian population from Beringia that initially colonized North America. Both past and present indigenous South Americans are characterized by relatively little genetic variation, and much of the variation that existed in prehistory was lost due to prehistoric population dynamics and recent demographic collapses caused by contact with European colonizers. Molecular studies indicate that a small number of individuals may have harbored previously unidentified genetic variation that was present among initial colonizers from northeastern Asia (i.e., from a hypothesized population Y) that contributed to some Amazonian and Australasian populations. Other complimentary aDNA, mtDNA, and NRY studies reveal that some haplogroup variation was subsequently lost due to intrahemispheric prehistoric population dynamics. NRY data indicate that a subsequent expansion associated with the spread of maize agriculture was the driving force behind the dispersal of subclades of haplogroup Q from Mesoamerica into the Andes. High-resolution aDNA data also point to a dispersal into the central Andes around ~4200 BC. Following population differentiation, other more recent population expansions associated with the population management policies and collapse of central Andean empires are apparent in ancient mtDNA data.

The plurality of dental morphological studies indicate that greater variation existed among ancient North (Powell 2000; Stojanowski et al. 2013b), Central (Haydenblit 1996), and South Americans (Lahr and Haydenblit 1995; Ortiz 2013; Sutter 2005, 2009, n.d.) than that initially described by Turner (1985; Greenberg et al. 1986; Turner and Scott 2007; Scott et al. 2016), and that some Western Hemisphere populations are characterized by sundadont-like tooth trait frequencies. Echoing the consensus from the molecular data, this phenetic variability resulted from an initial population structure that stemmed from bottlenecks and fissioning that occurred as the Paleoindians colonized the uninhabited landscapes of North and South America. The early dental morphological variability that once existed was lost through subsequent, intrahemispheric population dynamics (i.e., population declines, expansions, migrations). However, because most dental morphologists focus on confirming or rejecting Turner's typological sinodonty—sundadonty dichotomy for indigenous Americans, important questions regarding population dynamics and evolutionary processes have received less attention. Given the recent development of appropriate methods and statistical software, future dental studies should include explicit hypothetical model testing and borrow available procedures from genetics to examine temporal changes in population structure. By doing so, important relationships between changes in dental morphological frequencies and paleoenvironmental and prehistoric societal changes (i.e., expansions, colonizations, population dispersals following societal collapse) can be explored.

Given the current “state of the art” knowledge regarding the initial colonization and subsequent pre-Columbian South American population dynamics, there are

many uncertainties and unanswered questions. Despite nearly 20 years since the pre-Clovis status of Monte Verde was established (Meltzer et al. 1997), some archaeologists working in South America still feel the need to fight already-won battles by reporting ever-earlier sites. For some reason, some archaeologists repeatedly fail to adequately report their findings or establish anthropogenic causes for the purported archaeological record for their sites. The initial colonization of South America represents a multidimensional, multifaceted topic that is more than the question of “how early?” Those arguing for pre-LGM South American sites must concern themselves with complete, thorough reporting of their data; the elimination of more parsimonious, alternative, natural explanations; and a full engagement with the broader scholarship on the peopling of the Western Hemisphere before crying foul and evoking an intellectual straw man for the shortcomings in their own inadequate reporting. I see limited value in knowing if there is a site in South America that dates to ~50,000 BC unless it can be placed within a broader scholarly framework.

There are a number of important archaeological questions that remain unresolved. Perhaps foremost is the great “known unknown” of how many early archaeological sites were destroyed or remain submerged under ~100 m of water due to the subsequent rise in the sea level. I suspect that as underwater remote-operated vehicles improve and become more affordable, they will assist in identifying potential underwater sites. Further, as many researchers point out, our understanding of early Amazonian sites is nearly nonexistent. Other important questions include what was the effective population size of the colonizing population of South America? What relationship(s) existed among users of the early South American lithic technologies? To what degree did early South Americans’ economic strategies involve transhumance and/or exchange with other contemporaneous people?

In what ways can phenotypic data complement our understanding of prehistoric population dynamics based on molecular data, or, perhaps, which molecular data sets are best suited for teasing out prehistoric population dynamics? Ancient uniparental molecular data sets, such as mtDNA and NRY? High-resolution whole genome sequencing of ancient remains? Although granting agencies like to fund the newest/latest methodological developments, it may be that uniparental molecular data sets and phenotypic data are best suited for addressing prehistoric population dynamics in cases where all prehistoric peoples were derived from the same narrow range of genetic variation. A better understanding of the correspondence with underlying genetic systems of phenotypic characteristics may also help address prehistoric population dynamics.

It goes without saying (given that nearly everyone says the same thing) that our understanding of the origins, demographic processes, subsistence and technological strategies, and interpopulational dynamics would benefit from additional data and more multidisciplinary research programs. While molecular estimates for the initial effective population size of early South Americans is forthcoming (personal communication, Fehren-Schmidt 2019), any clarity on this question will be based on the genetic sequences of relatively few ancient South Americans. Both geneticists and skeletal morphologists would benefit from developing additional population genetics statistics to model hypothesized subsequent migratory events, gene flow, and population expansions and contractions (both at the

continental and regional level). Similarly, modelers and demographers should consider expanding their repertoire of statistics and sites to accommodate Terminal Pleistocene sites that lack precise radiocarbon dates, but for which relative chronologies are well established; at present, most studies examining the questions of migratory routes and continent-wide demography rely on sites with secure radiocarbon dates. By excluding those sites that lack radiocarbon dates yet have well-established relative chronologies might dramatically bias our understandings of the parameters regarding the initial colonization. Similarly, modelers might benefit by providing demographic estimates using now-submerged South American coastlines and estimates of habitable areas during the Terminal Pleistocene (Gautney 2018).

More work on developing terrestrial hunting subsistence models, such as that by Aldenderfer (1998), Borrero (2008), Dillehay (2000), and Rademaker et al. (2014), is welcome. In addition to the physiological and logistic difficulties in conducting research at altitudes >2500 masl, there was a hiatus on work in the Peruvian highlands during the 1980s–1990s due to terrorist activities. Additional geological and archaeological research in the Andean highlands will help clarify questions regarding early colonists' initial occupation, transhumance and seasonality, and subsistence activities. Further, research in the Andean highlands may broaden our understanding of the relationships among different, apparently contemporaneous lithic technologies. Namely, were lithic choices primarily economic in nature, or did social factors come into play (and to what degree?) in the decision making of early colonizers? By expanding the kinds of questions that we ask of the archaeological record, we can develop a better understanding regarding prey selection, hunting methods, economic decision making, and social relations among the initial colonizers of South America. Likewise, the same can be said of Amazonia; difficult working conditions and underfunding have impeded the work in the central and western Amazon, although this has been changing in recent decades.

Since I began to write this paper, our understanding of events surrounding the initial colonization of South America has changed dramatically. All of the traditional fields of anthropology have made substantial contributions, and, I expect, future collaborative multidisciplinary efforts will prove fruitful. I am sure that many of the unresolved issues that I have raised will be better understood, and that new questions will arise. I am also certain, as I was when I began investigating early South Americans, that those unforeseen findings will force me and other researchers to reconsider our current understandings.

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