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Oral health and diet of a young Late Pleistocene woman from Quintana Roo, Mexico

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Abstract

Objectives: To increase understanding of the subsistence practices of the first Americans through analysis of the near-complete dentition of a young woman dating to the terminal Pleistocene of the Yucatan Peninsula, Mexico.

Materials and Methods: The skeleton is that of "Naia" a 15 to 17-year-old female from the submerged natural trap of Hoyo Negro found in association with remains of numerous extinct species of megafauna. Superbly preserved remains included the skull with 28 teeth, which are analyzed for evidence of caries, periodontal disease, wear patterns, and malocclusion.

Results: Naia exhibits a high frequency of dental caries, along with aggressive periodontal disease that threatened all her teeth, particularly her incisors. Dental attrition was extremely light for a hunter-gatherer, reaching to four on the Molnar scale on only one tooth. Lack of wear is associated with severe mandibular retrognathia, and low masticatory forces.

Discussion: Naia's dental condition is compared with that of other northern Paleoamericans, mostly females, dating before 11,000 cal BP. These exhibit a high degree of variability in both caries and tooth wear. All, however, exhibit rapid anterior wear owing to technological use of the front teeth. Naia exhibits the highest rate of caries, similar to that of the earliest South Americans, and one of the lowest rates of attrition. This demonstrates that she had a nonabrasive diet that was at least seasonally rich in carbohydrates. This does not mean her diet was low in meat, however, because similarly light dental attrition is seen in the Arch Lake female, a Paleoamerican from a big-game hunting society.

KEYWORDS
dental anthropology, Late Pleistocene, Mexico, oral health, Paleoindian diet

1 | INTRODUCTION

Subsistence practices of the earliest Americans remain one of the most contentious topics in Americanist archaeology. One camp points to proboscidian, bison and horse kills, and the high frequency of large mammals in zooarchaeological collections to assert that the earliest people were terrestrial big-game hunters (Haynes, 2013a; Surovell & Waguespack, 2009) who contributed to the widespread extinction of American megafauna (Cione, Tonni, & Siobelzon, 2009; Feidel, 2009; Haynes, 2013b). The other highlights the presence of smaller animals and berry seeds, or uses optimal foraging models based on the structure of modern ecosystems, to argue that the Paleoindians were more

Cucina and Chatters must be considered joint senior authors and corresponding authors; Cucina for issues related to dental anthropology and Chatters for issues related to Paleoamericans – Herrera Atoche contributed with the occlusion analysis, writing and revising.

likely to have been generalized foragers who often emphasized small animals (Cannon & Meltzer, 2004). This group believes the first Americans did not extinguish the megafauna (Borrero, 2009; Grayson & Meltzer, 2002). Archaeological evidence is, however, indirect and highly subject to selective reading. For example, the decision whether or not to include the smallest animals in an archaeofauna, or preserved berry seeds as human introduced, rather than background, strongly affects the inferences derived from that record.

Ancient human dentition, in particular the evidence for dental health, may be more informative about diet because it offers direct evidence of human feeding behavior. However, this information can be difficult to obtain, particularly for Late Pleistocene specimens. Data on Paleoamericans' dental health has been assembled for parts of North and South America (Da-Gloria & Larsen, 2014, 2017; Powell & Steele, 1994), but most of the skeletons in these analyses represent the early Holocene, after people had been adapting to local conditions for up to four millennia. Human skeletal remains dating to the Pleistocene, by which we mean > 12,000 years old, are very rare in the New World. Only three skeletons with intact dentition have been recovered so far that are confidently dated before 12,000 cal BP: the Buhl skeleton from Idaho (Green et al., 1998), Peñon II from the Valley of Mexico (Jiménez-López, Hernández Flores, Martínez Sosa, & Saucedo Arteaga, 2006), and a skeleton from the Hoyo Negro Site in Quintana Roo (Chatters et al., 2014).

Here we present detailed observations on the dentition of the individual from Hoyo Negro, a young woman whom the discovery team has dubbed "Naia." We address the extent and magnitude of dental caries, periodontal disease, periapical dental infection, wear, and occlusion. After describing the conditions in this one individual, we compare her with observations on other early Americans. In order to have a larger pool for discussion of diet and overall dental health of this early American, we broaden the comparative population to all available North American individuals who predate approximately 11,000 cal BP. To extend the comparison to South America, we also include two individuals from Brazil: Toca dos Coqueiros (Lessa & Guidon, 2002) and Antonião Cave (Peyre, Granat, & Guidon, 2009). These are reported as predating 11,000 cal BP, although the relationship between the skeletons and radiocarbon dates is equivocal.

2 | MATERIALS AND METHODS

The subject of this article is a human skeleton discovered in 2007 in Hoyo Negro, a natural trap deep within the underwater Sac Aktun cave system in Quintana Roo, Mexico (Attolini, 2010) (Figure 1). Two teeth and a rib were first collected in 2011 and reported in 2014 (Chatters et al., 2014). The rest of the skeleton, including the complete skull and mandible, was recovered between March 2014 and November 2018. The chronological age of this individual was established as terminal Pleistocene by radiocarbon (^{14}C) and uranium-thorium (T-Th) methods. Two nearly identical ^{14}C dates on enamel bioapatite placed her death between 12,900 and 12,700 cal BP; U-Th of overprinted calcite provided a terminus *ante quem* of 12,000 years ago (Chatters et al., 2014). Sex was determined to be female based on the morphology of the cranium, pelvic girdle and pubic symphysis (Buikstra & Ubelaker, 1994) while age at death was estimated based on epiphyseal fusions, and dental formation and eruption following the standards presented in Buikstra and Ubelaker (1994) and Hillson (2008). To assess age from dental formation, a Port X II Dental digital radiograph (Genoray Co. Ltd.®, Korea) at 60 kV and 2 mA was used to observe root development. In each tooth, mesial radiographs were obtained from a standard distance of 15 cm. Image processing was performed using Owandy Krystal® radiography system digital X-Easy (Owandy SA, Champs sur Marne, France).

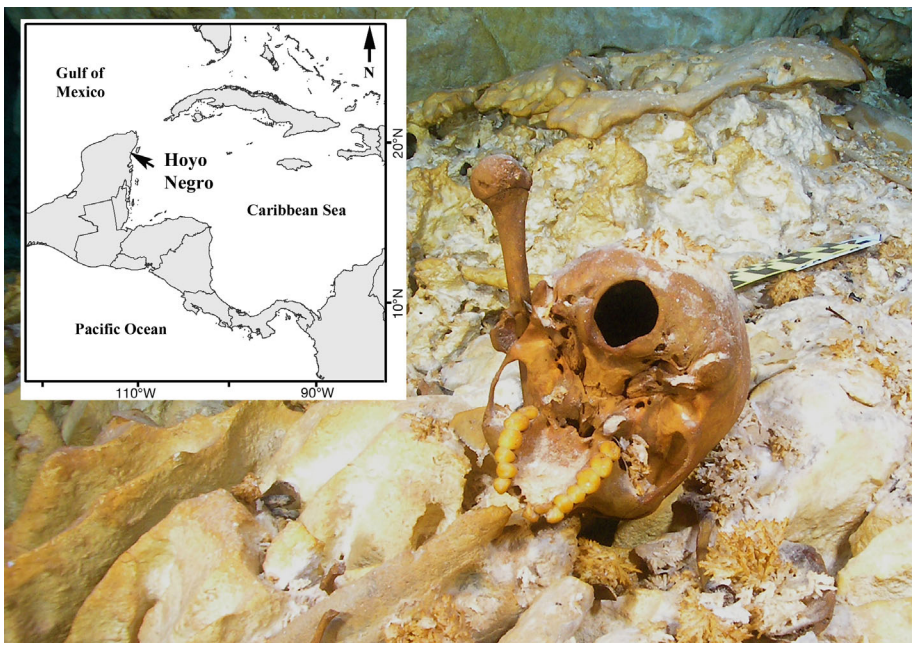

FIGURE 1 Map of the region showing the location of Hoyo Negro (a) and the skull of Naia as found on the bottom of the pit (photo by Daniel Rendon, Hoyo Negro Project)

Although first reported to have died between 16 and 19 years of age on the basis of underwater photographs (Chatters et al., 2014), first-hand study of the recovered skeleton indicates an age of 15–17 years (Chatters, Tiesler, Cucina, Arano Recio, & Erreguerena, 2017). This individual, officially called Hoyo Negro 5/48, has been named Naia by the recovery team; it is that name we use in this article.

The skull and mandible are very well preserved and complete except for small fractures of the nasal bones and a portion of the zygomatic process of one temporal. The mandible includes both condyles, which allows for a correct reconstruction of the anatomical occlusion of the maxilla and mandible. Of the original 32 teeth, 28 were in the skull at the time of discovery; 24 of them are still in their sockets (Figure 2). Four others (right maxillary central incisor, left maxillary third molar, left mandibular second premolar and left mandibular central incisor) were collected in 2011 and 2014 for special analyses—stable isotopes, radiocarbon, and aDNA (Chatters et al., 2014). The remaining four teeth were either lost shortly antemortem or fell out of the sockets as the skeleton decomposed; they are unlikely ever to be recovered.

Analysis of the dentition included observation and scoring of carious lesions, abscesses, alveolar resorption, linear enamel hypoplasia and dental wear. Occlusal problems of orthodontic origin were also assessed in order to infer whether normocclusion or any form of malocclusion affected occlusal wear and its interpretation.

Caries were scored when demineralization of the enamel or dentine surface affected a dental element. Enamel and cervical portions of the teeth were visually analyzed for carious lesions using a 4× magnifier. For the enamel, caries were scored on a 0–4 scale as follows: (0) no carious lesions observed, (1) demineralization is present but only affected the enamel, (2) the demineralization process penetrated into the dentine, (3) demineralization penetrated into the pulp chamber, and (4) at least half of the crown had been destroyed by the lesion (Cucina, Perera Cantillo, Sierra Sosa, & Tiesler, 2011; Cucina & Tiesler, 2003). The extent and deepness of a carious lesion is indicative of its chronicity, that is, the time it was actively forming within the oral cavity (Lanfranco & Eggers, 2010). In anthropology, carious lesions are considered to start from Grade 2, instead of Grade 1; it is a conservative approach that, although slightly underestimating the real rate of caries, prevents overestimation that might result from scoring pits that are not etiologically related to caries (for more detailed discussion, see Vega-Lizama & Cucina, 2014). For this reason, although lesions are scored here beginning with Grade 1, only lesions of Grade 2 or greater are used in comparisons with other skeletons.

Alveolar resorption due to periodontal inflammation was considered present either when a tooth root was exposed at least 1 mL between the rim of a socket and the cemento-enamel junction (CEJ), or when a dehiscence or fenestration was present in the adjacent alveolar bone (Hillson, 2008). These manifestations are separately noted in the table summarizing this feature.

The surface of dental enamel was analyzed on every available tooth to detect the presence of linear enamel hypoplastic defects as indicators of systemic stress during infancy and childhood (Goodman & Rose, 1990). Enamel surfaces were macroscopically analyzed using a 4× magnifier under tangential light (Cucina, 2011). These observations were augmented with observations in a 3-D model developed from microCT scans of the mandible.

The potential for periapical abscesses that did not reach the bone's external surface was assessed using the same Port X II Dental digital radiograph equipment that was employed for age estimation. Periapical abscesses were considered to be present when the X-rayed image indicated that the bone surrounding the apical portion of the root presented a clear osteolytic resorption.

Last, occlusal wear was recorded based on Molnar's (1971) scale, which ranges from Grade 1 (no wear facets) to Grade 8 (complete loss of the crown with the root serving as the occlusal surface). Where wear facets were just slightly beyond the lower limit for a grade, they were scored as a combination, as 1/2 or 2/3.

To assess potential orthodontic problems of occlusion, temporomandibular joints between maxilla and mandible were reconstructed anatomically to reproduce proper occlusion. This was accomplished by placing the mandibular condyles into the glenoid fossae of the temporal bones with a 3 mm-thick spacer to simulate the temporomandibular cartilage (Hansson, Torsten, Gunnar, & Sigvard, 1977) and

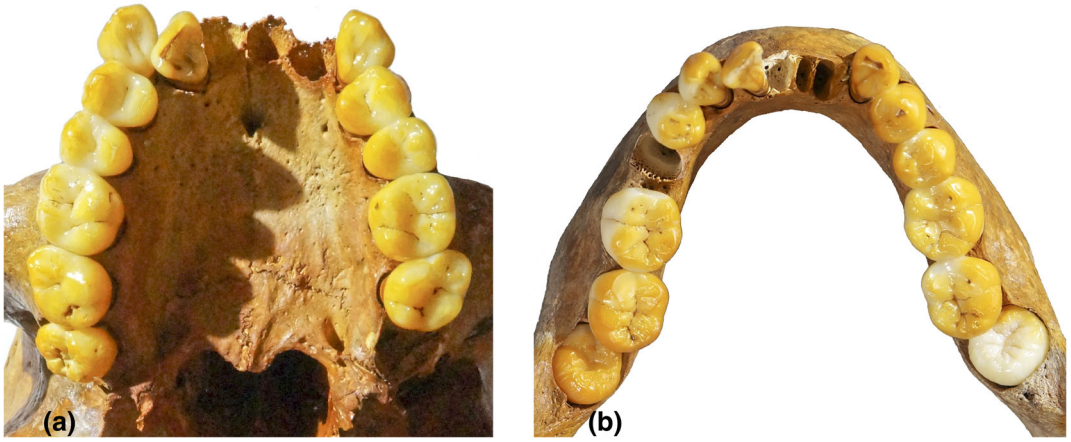

FIGURE 2 Naia's maxillary (a) and mandibular (b) dental arcades

positioning both jaws to fit the observed wear facets (Evensen & Ogaard, 2007).

3 | RESULTS

3.1 | Caries

Caries were scored directly on Naia's dental remains by the senior author in all cases but the maxillary right central incisor, maxillary left third molar and mandibular left second premolar. These were scored from photographs and 3-D models from microtomography and confirmed through direct observation by Chatters. The left maxillary third molar and most of the central incisor crown were destroyed during the dating and DNA extraction processes. The third molar was assessed from photographs. For the left mandibular central incisor, which was severely damaged during shipment to the DNA laboratory before being exposed to the air for photography, only the lingual surface of the enamel remained available for direct and photographic observation.

Fifteen out of 27 teeth available for analyses (55.6%) manifested at least one carious lesion when all degrees (1 through 4) are taken into consideration (Table 1). When only lesions of Grades 2 through 4 are considered (leaving aside minor superficial lesions affecting only the enamel), the percentage of affected teeth drops to 44.4%. Only one carious lesion, in the left maxillary central incisor, penetrated into the pulp chamber; no Grade 4 caries affected any of the available teeth (Figure 3a–d). The maxillary right incisors exhibited the most severe lesions, all of them more than 2 mm in diameter; two of those in I^1 have maximum dimensions of 5 mm (Figure 3c). The central incisor had fractured through the largest of these (Figure 3c), which was on the mesial edge, and the fractured surface had been subsequently worn smooth. No abscesses were detected in Naia's orthognatic bony structure.

3.2 | Alveolar resorption

This feature was recorded in every tooth socket; it was possible to record its presence also in the cases of missing teeth when the rim of the socket was clearly remodeled or depressed. In the case of the mandibular left central and lateral incisors, the alveolar bone was partly broken postmortem, exposing the root of the lateral incisor. However, this tooth shows evidence of fenestration as taphonomic change in the color of a circular area in the middle of the exposed root. This discoloration was never found in bone that was not

TABLE 1 Per tooth distribution of Naia's carious lesions and alveolar resorption

	Maxillary			Mandibular		
Side	Tooth	Degree of caries[a]	A. Resorp[b]	Tooth	Degree of caries	A. Resorp
Left	I1	–	X	I1	–	–
	I2	–	X	I2	0	–
	C	0	0	C	0	X*
	P3	0	X	P3	2	X
	P4	2	X	P4	2	X*
	M1	2	X	M1	0	X*
	M2	2	X	M2	0	0
	M3	0	–	M3	0	0
Right	I1	2, 2, 3	X	I1	–	X*
	I2	2, 2	X*	I2	–	X*
	C	0	X*	C	0	X*
	P3	2	X	P3	1	X
	P4	2	X	P4	1	X
	M1	0	X	M1	1	X
	M2	2	X	M2	2	0
	M3	2	0	M3	0	0
	Total teeth	Caries		Grade 1	Grade 2–4	
	27	15		3	12	
		55.6%			44.4%	
	Total sockets	A. Resorp				
	29	23				
		79.3%				

[a]The maxillary right central and lateral incisors present three and two carious lesions, respectively.
[b]A. Resop – Alveolar resorption. Asterisk indicates fenestration or resorption well beyond 1 mm.

FIGURE 3 Carious lesions in some of Naia's teeth: (a) maxillary right M2 and M3, (b) maxillary right I2, (c) buccal view of maxillary right I1, (d) maxillary left M1 and M2 showing very early stage of caries in the grooves of the M1 and Grade 2 caries in the M2

exposed directly to surrounding waters. Resorption could not be assessed in any way only in the maxillary left third molar. This was because the tooth had been removed before recovery of the skull, used for various analyses, and was no longer available. In the cases where fenestration or dehiscence occurred, this feature could be scored on most sockets even when teeth were absent, unless post-mortem damage had eliminated the alveolar rim.

Twenty-three out of 29 sockets (79.3%) presented depressed rims (Table 1). Fenestrae were present in three sockets and extreme alveolar recession in four others, as indicated in the table by asterisks. The most extreme examples of fenestration were observed in the medial and lateral right and the left lateral mandibular incisors (Figure 4a). Resorption was so extreme on the left lateral alveolus that only a narrow, incomplete band of bone remained at the alveolar rim above an opening over 3 mm in diameter. The alveolar bone was entirely missing from the right central incisor down to the inferior rim of the fenestra in the lateral socket. The alveolar wall was almost entirely resorbed between these two teeth, which may have been lost shortly antemortem. The wall between the central incisors is also fenestrated. Dark staining on the left lateral incisor indicates an opening of similar size was present there as well. Additional evidence of periodontal disease can be seen as spongy conditions in the interproximal alveolar rim between the left mandibular second premolar and first molar (Figure 4b), as well as in other teeth (Figure 4c,d). Figure 4d also shows one of the two fragments of dental calculus recorded in Naia's dentition; its presence might be related to some extent to alveolar resorption, as is discussed later on this article.

3.3 | Occlusal wear

Occlusal wear was scored on all available teeth (Table 2). Overall, loss of enamel through occlusal wear is minimal; only in a few cases are dentine patches present. The most-extensive exposure of dentine can be seen in the maxillary lateral incisor, in correspondence with the occlusal surface of the mandibular right canine; here dentine patches are larger, although the Grade 4 wear in this incisor is likely due to

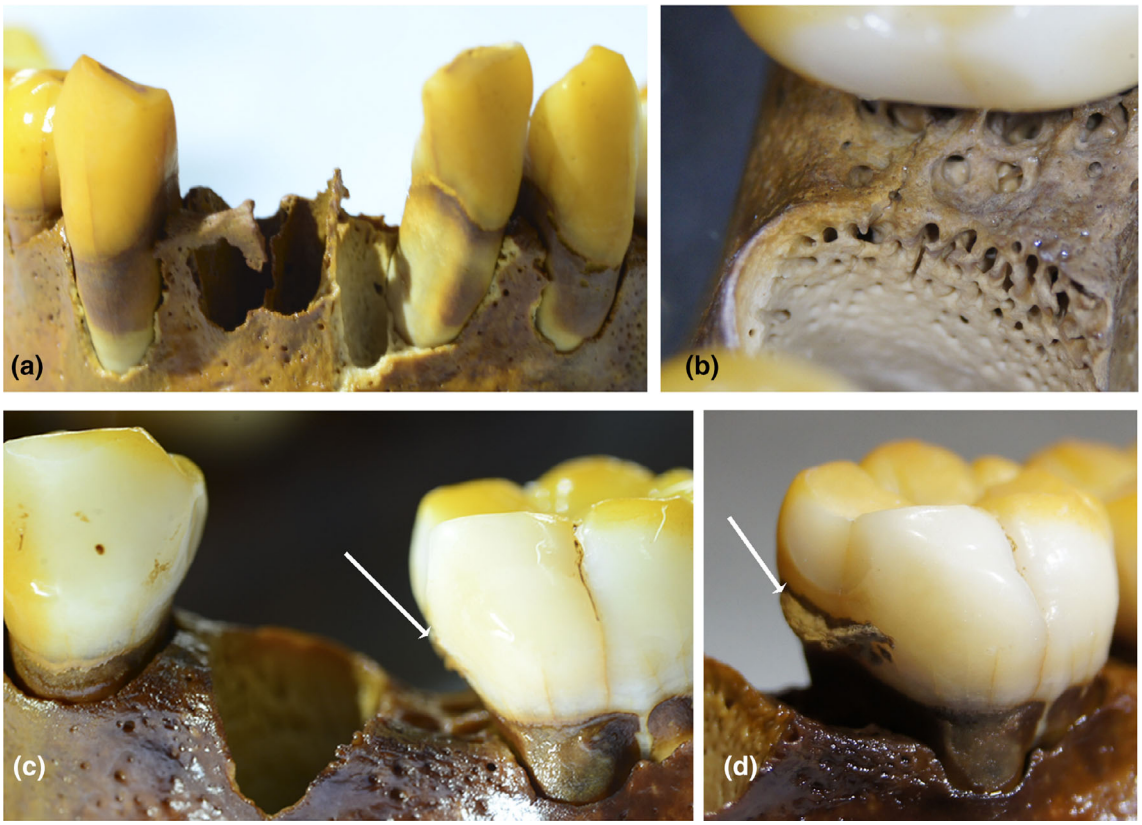

FIGURE 4 Fenestration, alveolar resorption, and calculus: (a) mandibular anterior teeth, (b) close up of interproximal bone reaction between mandibular left P2 and M1, (c) alveolar resorption of mandibular left P1, P2, and M1, (d) detail of calculus in the mandibular left M1 (arrow in (c) and (d) points to the position of calculus in the M1)

malocclusion (the upper right canine is pushed outside of the occlusal plane because of dental crowding, while the lateral incisor is moved inside the anatomically normal occlusal plane), forming a reclined mesiodistal plane that increased the depth of dentine exposure. The maxillary central incisor shows Grade 3 occlusal wear in the mesial portion of the incisal edge. Unfortunately, a carious lesion had removed part of the crown, which makes it impossible to assess the extent of wear on this portion of the edge. As for the first permanent molars, two of them have been scored as Grade 2/3 because each shows just one pinpoint exposure of dentine; based on Molnar's scale description and drawings, such a pattern fits neither Grade 2, nor Grade 3.

3.4 | Mechanical damage

The higher degree of occlusal wear affects Naia's incisors. Interestingly, three of the incisors also show clear evidence of use-related breakage. The occlusal plane of the mandibular left central incisor shows two or three notches produced by minor fractures in the enamel, and the incisal edge appears finely crushed (Figure 5a,b). Fine conchoidal fractures can also be seen on the lingual edges of the occlusal surface of the lateral left mandibular incisor (Figure 5c). Finally, the mesial edge of the maxillary central incisor (Figure 3c) has broken away along the thinned rim of a large carious lesion and has subsequently become polished by occlusal wear. Such damage is likely due to mechanical forces exerted on the incisal surface, which probably resulted from the use of the incisors as third hand or to break hard objects.

3.5 | Hypoplasia

No linear hypoplastic defects were macroscopically detected on the enamel surface of any tooth during visual analysis. However, images obtained from a micro CT scan taken at 40 μm slice interval show a light horizontal groove in the cervical third of the crowns of both mandibular canines.

A deep horizontal groove was observed on the upper central right incisor (Figure 3c). However, in order to be considered the result of systemic metabolic disruption, similar grooves must be visible in all teeth forming at the same time as the central incisor, such as the maxillary lateral incisor, both mandibular incisors, mandibular canines, and first molars (Goodman & Armelagos, 1985), but none of them manifested any matching anomaly. It is likely, therefore, that such a groove, which eventually harbored a carious lesion, might have been the result of a congenital defect, a localized trauma during crown's formation or a postmortem dissolution effect.

3.6 | Occlusion

From the perspective of occlusion, Naia manifested crowding in her anterior dentition, as well as impacted teeth. Also, she presents an

TABLE 2 Degree of occlusal wear using Molnar' scale (1971)

	Maxillary		Mandibular	
		Wear		Wear
Left	I1	–	I1	3
	I2	–	I2	3
	C	1	C	2
	P3	2	P3	3
	P4	2	P4	–
	M1	2	M1	2/3[a]
	M2	2	M2	2
	M3	1	M3	1
Right	I1	3[b]	I1	–
	I2	4	I2	–
	C	1	C	3
	P3	2	P3	3
	P4	2	P4	2
	M1	2	M1	2/3
	M2	2	M2	2
	M3	1	M3	1

[a]Molnar' scale reports that Grade 3 is characterized by small patches of dentine, while Grade 2 shows no dentine. Some of Naia's teeth show only one pinpoint exposure of the underlying dentine, which does not match completely with Molnar's standard drawing.
[b]Occlusal wear in the maxillary central incisor only affected the mesial half of the incisal surface, while the distal half is seemingly not affected by wear.

Angle class II malocclusion, in the form of mandibular retrognathia, affecting canines, premolars and molars (Figure 6). Specifically, in a normocclusion, the distal cusps of the mandibular first permanent molar should articulate with the mesial cusps of the maxillary first permanent molar (i.e., the mandibular first molar should be in front of its maxillary counterpart). As Figure 6 shows, instead, the opposite occurs. Naia also presents a sharp curve of Spee, which is a measure of concavity of the occlusal plane of the mandible in an antero-posterior direction (Hayes, 2014). Its presence is indicative of limited masticatory force exerted on the occlusal surface (Hayes, 2014). Such curvature is common among modern human populations.

Anterior crowding had affected both dental arcades, and the upper right lateral incisor was in a crossbite relationship with the mandible. On the other hand, only the mandible presented posterior crowding in the third molars; both third molars, though still unerupted, were clearly impacting the second molars, as the X-ray shows (Figure 7).

4 | DISCUSSION

Naia had lightly worn teeth that exhibited numerous, mostly small, carious lesions. She had active periodontal disease serious enough that her lower incisors had lost the majority of the anterior walls of their alveoli but did not yet suffer any dental abscesses. In order to better understand what these features, particularly the lack of attrition and high level of caries, mean with respect to diet, Naia is compared with other Paleoamerican individuals from and North and South America (Table 3). For North America, consideration is limited to adults or late subadults predating approximately 11,000 cal BP for which sufficient detail on dental health was available from texts or photographs. These individuals come closest to the earliest occupants of the northern hemisphere and are the nearest in antiquity to Naia. All but one is female. Investigator reports were relied upon for counts of dental caries. Wear patterns, periodontal disease indicators and abscesses were scored by us based on published photographs, as well as photographs and casts in Chatters' research collection. Where an author did not mention caries, it was assumed that the investigator made no observation of caries presence or absence. The information was listed as not available (N.A.) unless one of us had first-hand knowledge of the skeleton in question. Comparative individuals from the North American continent were selected based on sex, age at death, and chronological period. In Table 3, approximate chronological ages are provided in calibrated years BP, with the median of the calibrated age range listed except where age is based solely on bracketing radiocarbon dates. In that case, the calibrated age range is given. Although two other human skeletons from Quintana Roo may date as early as 11,000 cal BP (González-González et al., 2008; Stinnesbeck et al., 2017), one lacks a complete enough dental assemblage and the other has been insufficiently reported for inclusion. Two South American individuals that are reported as from the Late Pleistocene, but probably date to the earliest Holocene, are included for contrast. The level of detail provided for those individuals is lower, reflecting the quality of data available from published sources.

4.1 | Periodontal disease and abscess

Exposure of tooth roots, which we used as an indicator of periodontal disease, often results from severe occlusal wear as the teeth continuously erupt in order to maintain the occlusal contact (Hillson, 2008). This seems to have been the case with the Horn Shelter male and the lady of Antonião reported by Peyre et al. (2009). In Naia's case, however, the exposure of the roots is completely unrelated to occlusal wear. It is due to periodontal disease. Given Naia's young age, the extended degree of resorption, fenestration and dehiscence is to be considered the result of a generalized aggressive inflammation that affected, to different degrees, almost all of her tooth sockets (Armitage, 1999). Aggressive periodontal disease differs from the chronic form by the fact that it affects individuals at young ages (Armitage & Cullinan, 2010). It is characterized by rapid bone destruction (as we can see in Naia's dental sockets) and is the result of multifactorial systemic causes, which include genetic immunological predisposition, environmental factors (e.g., microbial factors and personal hygiene), and local factors (Armitage, 1999). Most of the factors triggering aggressive periodontitis are easily detected in living patients, but the etiology of this disease cannot be diagnosed in a defleshed skeleton. What we can say is that the coincidence of resorption, fenestration and dehiscence clearly attest to intense

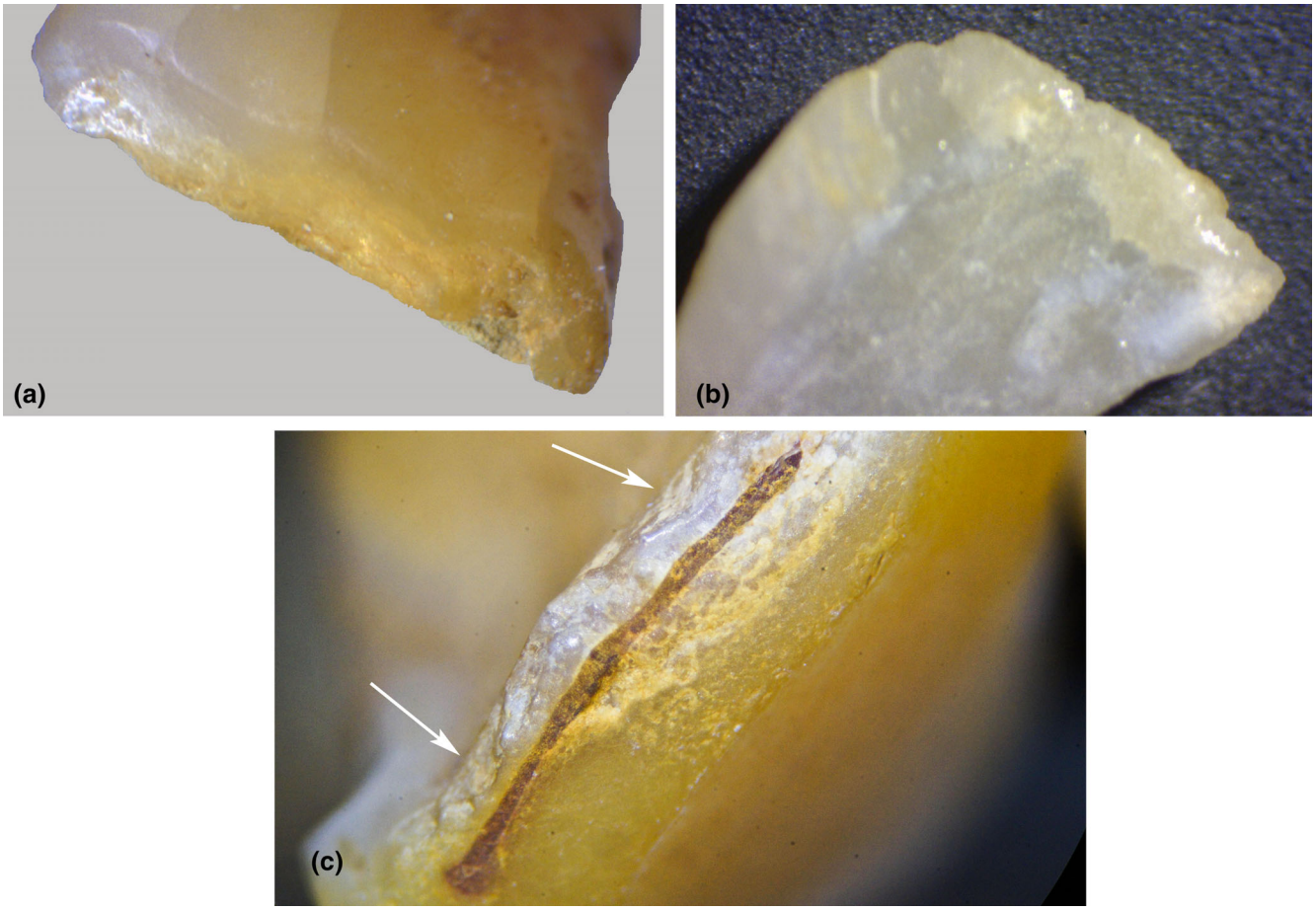

FIGURE 5 (a) Dental chipping of the occlusal surface of mandibular left I1, (b) acid-cleaned enamel of mandibular left I1 showing internal fracturing of the incisal edge of the enamel parallel with the lingual surface (whiter arc), (c) incisal view of mandibular left I2; arrows point to the chipped enamel

inflammatory processes actively affecting Naia's periodontal tissue at the time she died (Hillson, 2008).

The presence of calculus buildup, as a local factor, might in part explain the presence of such aggressive systemic inflammation. Naia presented shelves of calculus on two of her teeth, although her prolonged exposure to wetting and slow drying before being submerged, and long period immersion after sea level rose appear to have caused any other calculus she may have had to slough off. Although much of the calculus has been lost, the remnants do allow us to suggest that it might have contributed to the gums' inflammation and resultant periodontal resorption. However, the limited record of calculus makes it impossible to firmly link the tartar to all instances of resorption and fenestration, in particular given the disease's multifactorial and complex origins.

Despite the wide range of ages-at-death among the group in Table 3, evidence of extensive periodontal disease is present for all North American individuals in our comparative set for which this feature has been described. Abscesses and tooth loss are, on the other hand, relatively uncommon. This second observation is in contrast with the conclusion drawn by Powell and Steele (1994), but almost half of the individuals in their data set represent much more recent societies and, potentially, subsistence regimes. We should note, however, that an individual's biological age might be a factor in both the extent of dental attrition and the exposure of pulp cavities to bacterial attack. The Horn Shelter male, the oldest individual in this group, had evidence of but a single distinguishable abscess, despite his advanced age and antemortem loss of several teeth. In looking at his occlusal surfaces, many of which were worn well into the roots, it is evident that secondary dentine had kept up with attrition, preventing abscess in most cases. This was also true of the more recent, ~40-year-old Kennewick Man (Chatters, 2000; Owsley, Williams, & Bruwelheide, 2014), but not of the similar-aged (both biologically and chronologically) Spirit Cave and Wizards Beach males. Both of the latter suffered from dental abscesses at the time of death (Edgar, 1997).

4.2 | Dental wear and occlusion

One of the most notable features of Naia's dentition is the very limited extent of occlusal wear, which is particularly evident in the posterior teeth. Paleoamericans are generally described to have had moderate to severe occlusal wear due to the heavy attrition caused by chewing hard and fibrous food. General agreement exists among

FIGURE 6 Right lateral view of Naia's occlusion showing mandibular retrognathia. The white arrow highlights the retrograded position of the mandibular M1 in relation to the maxillary M1

FIGURE 7 Radiographic image showing the impacted mandibular left M3

scholars that such severe wear is typical of a hunting and gathering mode of subsistence (Holt & Formicola, 2008; Owsley et al., 2014; Powell & Steele, 1994). Usually, heavy occlusal wear begins as soon as permanent teeth erupt. For example, an 8 to 9-year-old child from Garrincho Cave in Brazil estimated to be greater than 10,000 years old (Peyre et al., 2009) shows flattened occlusal surfaces and relatively large patches of dentine in its M1 s (Molnar's Grade 4). Given that the permanent first molar erupts at around 6 years of age, this is significant attrition in the span of just 2–4 years.

Some of the individuals listed in Table 3 seem to fit this pattern of high attrition, but degrees of wear are in fact highly variable. The older male from Horn Shelter, young woman from Buhl, Idaho, and middle aged (for her time) woman from Whitewater Draw had severely worn teeth. Teeth of the Wilson Leonard II and Gordon Creek women, both in their 20s were somewhat less severely worn for their age, particularly in comparison to the younger Buhl woman. Naia and the Arch Lake woman, who died around the same age as Buhl, both had light occlusal wear.

Occlusal attrition is multifactorial, and is strongly dependent on the kind of food ingested, the way food is prepared, and the force exerted during mastication (Sciulli, 1997; Smith, 1984). The use of stone grinding-tools, which introduce grit, among Archaic hunter-gatherers and agriculturalists is a factor in the rapidity of occlusal wear (Smith, 1984). Grinding tools are not known from Late Pleistocene archaeological deposits, so this artificial way of including particles can be ruled out for the individuals discussed in this study. In the absence of grinding technology, mastication of tough, fibrous food, or food impregnated with soil particles must be considered a causative factor for tooth wear. Conversely, meat, unless prepared by grinding or consumed in an environment that introduces a lot of abrasive grit, does not tend to be a wear-inducing food. As Teaford and El Zaatari (2014) have observed, meat is not a hard substance, and may produce scratches onto the enamel only if gritty particles contaminate it. Moreover, the masticatory forces exerted to chew meat for such a prolonged time in order for it to produce considerable occlusal wear should also produce interproximal wear (Hinton, 1982). In this perspective, Naia's dentition indicates that she had used her teeth to masticate soft foodstuff, with very little if no inclusion of tough, fibrous aliments.

This inference seems to be supported by the Angle's class II mandibular retrognathia detected in Naia's occlusal structure, as well as in her pronounced curve of Spee. Malocclusion is a very widespread problem in modern times (Evensen & Ogaard, 2007; Fiorin, Ibanéz-Gimeno, Cadafalch, & Malgosa, 2017; Rose & Roblee, 2009; Wang, Zeng, Zhang, & Yang, 2012). Rando, Hillson, and Antoine (2014) suggest that two crucial moments in history might have produced an increase of malocclusions; the first was the introduction of agriculture and the second the industrial revolution. In both cases, the ingestion of processed food reduced the mastication force, hence affecting the growth and development of the jaws as well as the amount of grinding of the teeth. This in turn influenced the position of the teeth. In fact, it is extensive mastication and progressive occlusal wear that provide teeth with adequate room for them to align properly within the dental arcades without problems of crowding and impaction (Rose & Roblee, 2009). This process, or lack of its progression, may be sufficient to explain the Angle's class II retrognathia in Naia. This degree of retrognathia sometimes also has a hereditary component (Cakan, Ulker, & Taner, 2012; Cassidy, Harris, Tolley, & Keim, 1998), often being associated with a variety of syndromes (Paladini, 2010). However, these syndromes are commonly associated with other

TABLE 3 Composition of the dental characteristics of Naia and other Late Pleistocene/Early Holocene individuals described in the literature

Individual	Sex	Age	Wear (range)	Caries	Abscess/ AMTL	Periodontal disease	Source(s)
North America							
Naia (12.8 Ka)	F	15–17	1–3	44.4%	0/0	Extensive	This study
Buhl (12.6 Ka)	F	17–21	2–7	0%	0/0	N.A.	Green et al., 1998
Penon III (12.7 Ka)	F	24–26	2–5	17%	0/0	Extensive >2 mm	Jiménez-López et al., 2006
Arch Lake (11.4 Ka)	F	17–21	1–3	N.A.	N.A.	N.A.	Owsley, Jodry, Stafford, Haynes, & Stanford, 2010
Wilson-Leonard II (11 Ka)	F	20–25	2–5	6.2% (9.3%)	1 / 1	Extensive	Steele, 1998
Whitewater Draw (11.7–8.5 Ka)	F	27–34	Marked	0%[2]	N.A.	N.A.	Waters, 1986
Gordon Cr. (11.2 Ka)	F	25–30	2–5	0%	N.A.	Extensive	Breternitz, Swedlund, & Anderson, 1971
Horn Shelter (10.9 Ka)	M	35–45	5–8	0%[4]	0/0	N.A.	Young, Patrick, & Steele, 1987; Young, 1988
South America							
Toca dos Coqueiros (Brazil) (11.1 Ka)	M	35–45	4–7	22.2%	?/0	Extensive >1.5 mm	Lessa & Guidon, 2002; Nelson, 2005
Antonião Cave (Brazil) (11 Ka)	F	20–22	Severe	31.6%	N.A.	Limited	Peyre, 1993; Peyre et al., 2009

malformations, like cleft palate, that are not present in Naia. This reinforces the idea that environmental factors are among the primary causes for the degree of malocclusion in this individual (Cakan et al., 2012; Cassidy et al., 1998). Interestingly, although we see no obvious indication for retrognathia in the upper dental arcade of the Arch Lake woman, the published photograph of her left mandibular ramus (Owsley et al., 2010, fig. 9) shows a particularly oblique gonial angle of 130°. Given that the ramus is the insertion of the masseter and pterygoid muscles, this slight bone indicates this woman, like Naia, fed herself without the need for strenuous mastication.

4.3 | Teeth as tools

Despite the broad range in the *degree* of wear among the earliest North Americans, the *pattern* of wear is broadly similar, as Figure 8 shows. Anterior teeth, regardless of their eruption order, tend to be much more heavily worn than the posterior-most teeth. This pattern, which is also known to occur in remains of the European Upper Paleolithic, has previously been noted in the North American skeletons dating to the earliest Holocene (Powell & Steele, 1994). Powell and Steele attributed this pattern to the use of anterior teeth as tools, noting that it was even more extreme than seen in Eskimos, who are known to have engaged in this behavior. The degree of use varies remarkably among the individuals, with Buhl (Green et al., 1998) and Horn Shelter (Young, 1988) showing incisors and even premolars worn to or nearly to the roots, with labiolingually convex surfaces. This feature has also been reported in the much more recent Kennewick Man (Chatters, 2000; Owsley et al., 2014). Wilson Leonard II (Steele, 1998), instead, shows remarkable lingual wear in the upper central incisors, while wear in the lower anterior teeth is flat. This may be due to a minor degree of the retrognathia we see in Naia. Naia

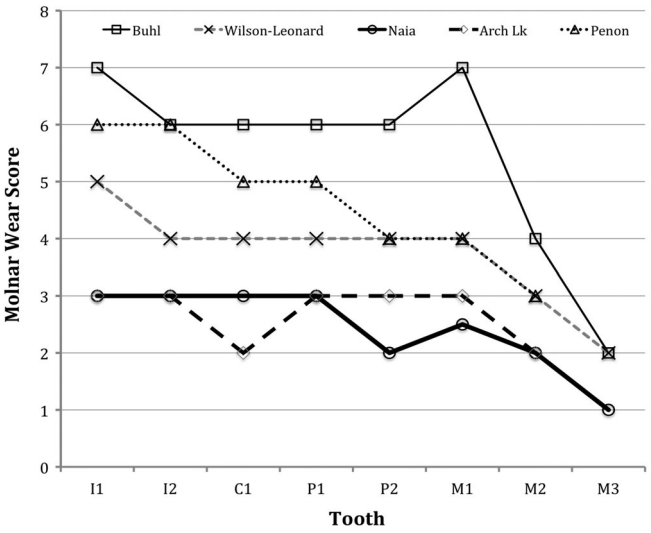

FIGURE 8 Comparative distribution of occlusal wear in five Late Pleistocene females from North America

presents relatively much lighter anterior tooth wear compared to most of her female contemporaries. She does, however exhibit chipping in the incisal surfaces of the mandibular incisors, clearly attesting to the fact that she, too, used her front teeth as tools to work hard objects.

4.4 | Caries and diet

The development of caries in human dentition is due to the activity of commensal bacteria in the oral cavity, which is triggered by the presence of carbohydrates in the diet (Hillson, 2008). It is enabled by sugars much more than starches. High rates of caries are (too) often associated with the introduction of agriculture (Turner, 1979). The

rate of caries in human populations has greatly increased worldwide since the Neolithic Revolution, yet a high frequency of infectious carious lesions is not bound to mean "agriculture"; carbohydrates are not ingested only through consuming cultivated crops. Watson (2008) discussed the intake of cactus fruits as the main cause for the insurgence of caries in prehistoric people in Northwestern Mexico before the introduction of agriculture. Similarly, fruits high in sugars (specifically from palm dates) are considered to be the factor triggering caries in an Iron Age population from the Arabian Peninsula (Nelson, Lukacs, & Yule, 1999).

Forty-four percent of Naia's teeth manifest at least one carious lesion that penetrates into the dentine; three others were in the initial stages. Only one had penetrated into the pulp cavity. The depth of an infectious lesion is indicative of its rate formation and chronicity (Lanfranco & Eggers, 2010). Carious lesions are the result of a fairly long-lasting decay process, which depends on a wide range of factors, including oral hygiene, an individual's resistance to oral bacteria, saliva pH, quality and quantity of sugary food ingested, rate of remineralization of the enamel tissue and more (Hillson, 2008). This multifactorial nature makes it difficult to quantify the amount of time it took for a cavity to become clearly visible in the tooth. It is not, however, a matter of days for a lesion to appear and reach the dentine; rather it is a matter of months or even years. The fact that Naia manifested many caries is strongly indicative of the intake of large amounts of cariogenic foodstuff, at least during some period of time. The relative superficiality of all but a few of the lesions suggests that most of them started forming within the same period of time, probably the last couple of years of her life. We have evidence from the condition of her pelvic bone that Naia had experienced a pregnancy within those last few years (Chatters et al., 2017), which would have altered her body chemistry and led to an increased propensity for caries. Females are known to be predisposed to the development of caries more than males, due in part to the nutritional stresses of pregnancy and general aspects of female endocrinology (Lukacs, 2011; Lukacs & Largaespada, 2006). The suggestion that Naia's caries may have primarily occurred late in her life and been related to her reproductive status is tentative, however, because of the complex nature of cariogenic infection and the large number of variables involved in caries formation.

The unusually large number of caries in Naia is a marked contrast with findings from other Late Pleistocene/early Holocene individuals in North America, who are typically described as having little or no caries (Holt & Formicola, 2008; Powell & Steele, 1994). The individuals in our comparative group are generally consistent with that expectation. Of the six North Americans for which we can consider this variable, only two, Peñon and Wilson-Leonard, had some caries, and these lesions were small. Dental wear may have influenced this finding. Except for the young woman from Arch Lake, who was only slightly older than Naia, all other individuals had moderate to heavy tooth wear, as noted above. The teeth of most of these individuals, particularly the Horn Shelter male and Buhl woman, may simply have worn away too rapidly for the bacteria producing caries to gain a foothold.

The early Brazilian individuals in Table 3 more closely resemble Naia in their degree of caries formation, although they exhibit heavier wear. This greater frequency of caries seems to have been typical of tropical Brazil in the earliest Holocene. In a study of the earliest skeletons from the Lagoa Santa region in Brazil, Da-Gloria and Larsen (2017) report an overall caries frequency of 7.85% in a population of males and females. Caries were more common in the females, for whom they reached a frequency as high as 21.6%. Dental wear in these women was also high. The authors concluded that this pattern resulted from a broad-spectrum diet that included fruits and tubers, with a lower intake of animal protein. This is consistent with observations of the early Holocene environment around Antonião Cave and Toca dos Coqueiros. Valli (2018) generally describes the regional paleoenviroment of the Cerra de Capivara National Park, where both sites are located, as characterized by a mosaic of open, wooded or scrubland areas, wetter than in modern times, but with karstic areas displaying different microenvironments from the flat alluvial plains of the region. In such an environment, people of the Early Holocene likely relied on mixed foraging strategies (Lessa & Guidon, 2002), which included intake of cariogenic foodstuff, as the high rate of caries in both the man of Toca dos Coqueiros and the lady of Antonião suggests. Lessa and Guidon (2002) propose that cacti were fairly common in the region, which would make these Brazilian cases similar to those described by Watson (2008) for prehistoric northwestern Mexico.

4.5 | Naia's diet

Naia's high frequency of caries and low level of occlusal wear indicates a diet low in grit and coarse fiber and high in simple carbohydrates. It would be easy to jump from this observation to the conclusion that this also means a diet low in meat and, thus, argues against the long-standing idea that the earliest Americans were big game hunters. Such a conclusion, however, would be simplistic. Two lines of evidence run counter to it. First, the Arch Lake woman (Owsley et al., 2010) had almost the same level of dental wear as Naia and, given that she was likely a few years older at death, had a lower attrition rate. Unfortunately, her teeth were not well enough preserved for us to be certain she lacked small caries like those seen in Naia, but no large lesions are visible in photos of the surviving teeth. This woman, found in the staked plains of eastern New Mexico, is inferred to have been a member of a bison hunting population (Owsley et al., 2010). This is strongly indicated by her stable isotope ratios, which include a Δ15N of 13.1 per mil, showing her to be a terrestrial carnivore and a Δ13C of -14.2 per mil, indicating C4 grasses were probably the base of the food chain. The archaeological culture of the region was Plainview, which is understood to have based its subsistence on bison. The staked plains during that period would not have offered much in the way of simple carbohydrates. Light wear is not inconsistent with a meat-heavy diet.

Second, the middle Holocene skeletal assemblages from the DeMoss and Braden sites in Idaho, reported by Pavesic, Yohe, Owsley, and Camp-Hill (2016) further argue against a simple equation

between caries, wear and diet. Braden is located on the Boise River in the relatively low-relief steppes of southern Idaho and DeMoss in an area of forests and mountain meadows in the central part of the state. They appear to have participated in the same culture, known as Western Idaho Burial complex and used comparable technologies. They were probably familiar with the same range of food resources. Individuals from Braden exhibited relatively high levels of dental wear and only 6.2% caries; stable carbon and nitrogen isotopes indicate a diet high in salmon. Those from DeMoss had high Δ15N levels characteristic of terrestrial carnivores and a high frequency of caries (17.5%; Chatters' notes on this collection indicate a much higher rate). Based on our first-hand experience with both collections, the DeMoss population exhibited much lower levels of dental attrition; permanent premolars and molars often exhibiting massive caries and virtually no wear. The archaeological record of Central Idaho demonstrates a strong emphasis on big-game hunting (Butler, 1986). Pavesic et al. (2016) concluded that the DeMoss diet was high in camas root, which reduces to a sugary mass after prolonged baking. Given the low level of wear, though, and abundance today of huckleberries (*Vaccinium* sp.) and other fruiting species in those mountains, consumption of berries rather than gritty roots may be a better explanation. Regardless, big-game hunting and high levels of caries are not mutually exclusive.

5 | CONCLUSION

The take-away lesson from information on caries, dental wear, and malocclusion is that Naia had a soft diet that required low masticatory forces and that, at least from time to time, included a significant amount of simple carbohydrates. That Naia exerted low masticatory forces is confirmed by the fact that the teeth showing higher degrees of dental wear are those that also show occlusal chipping. This suggests wear in anterior teeth was due to both malocclusion and to the use of anterior teeth for extramasticatory functions, the latter being very common in Late Pleistocene individuals. The aggressive state of periodontal disease does not permit inferences regarding Naia's diet, however, given the disease's multifactorial and genetic complexity.

Like all *Homo sapiens*, Naia was an omnivore but it is highly unlikely that her diet included consumption of roots, which would have introduced coarse fiber and grit, and thus caused rapid dental wear. Neither did she consume coarse-fibered but sugary plants like agave or maguay. The source of the carbohydrates in her diet was probably fruit and/or honey. Only one well-dated pollen record exists for the terminal Pleistocene in the vicinity of the Yucatan: Lake Peten Itza in northern Guatemala. It indicates that, during the terminal Pleistocene deglaciation, vegetation of the area was a thorn woodland (Hodell et al., 2008). Toward the end of the deglaciation, after around 14,000 years ago, plants now common to the lowland jungles had begun to appear in small numbers. Under those conditions, fruit could have been cactus fruit, soft young mesquite pods, or some of the other succulent tree fruits the region now offers. The Yucatan, particularly its drier northwest, has been known for its honey since early Spanish times. Consuming fruit and honey, among the most easily gathered and readily digestible foods any environment has to offer, Naia's people appear to have been opportunistic foragers. Unfortunately, for the ongoing debate about Paleoindian subsistence practices, Naia's dental health says nothing about their degree of reliance on and impacts to big game.

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DATA SHARING STATEMENT

The skeletal remains of Naia are currently stored in the Anthropology Museum in Mexico City. Access to the skeletal remains is no longer in the hands of the corresponding authors. The majority of data that support the findings of this study are presented in the article itself. The remainder addressing other Paleoamericans is available from the corresponding authors upon request.

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